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A TEXT BOOK OF PHYSIOLOGY.

PUBLISHED BY
JAMES MACLEHOSE AND SONS, GLASGOW,
Publishers to the University.

MACMILLAN AND CO., LONDON AND NEW YORK.
London, - - - *Hamilton, Adams and Co.*
Cambridge, - - *Macmillan and Bowes.*
Edinburgh, - - *Douglas and Foulis.*

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A TEXT BOOK

OF

PHYSIOLOGY

BY

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PROFESSOR OF THE INSTITUTES OF MEDICINE IN THE UNIVERSITY OF GLASGOW,
FELLOW OF THE ROYAL COLLEGE OF PHYSICIANS OF EDINBURGH.

INCLUDING

HISTOLOGY BY PHILIPP STÖHR, M.D.,

PROFESSOR OF ANATOMY IN THE UNIVERSITY OF ZÜRICH.

IN TWO VOLUMES.

VOL. II.—SPECIAL PHYSIOLOGY.

GLASGOW:
JAMES MACLEHOSE & SONS,
Publishers to the University.
1889.

SPECIAL PHYSIOLOGY:

INCLUDING

NUTRITION, INNERVATION, AND REPRODUCTION.

BY

JOHN GRAY M'KENDRICK, M.D., LL.D., F.R.S.,
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PRINTED AT THE UNIVERSITY PRESS, GLASGOW,
BY ROBERT MACLEHOSE.

PREFACE.

It has been my endeavour throughout this volume to lay before the reader the main facts of physiological science, and, as far as possible, to state these facts in terms of measurement. The time has gone past for vague generalities in the description of physiological phenomena, and physiology is, year by year, drawing nearer to her true position as a science, dealing as strictly with the phenomena and basis of organic life as physics deals with those of dead matter. At the same time, it is impossible altogether to resist the promptings of speculative inquiry, and I have accordingly yielded to these in several instances—in particular, in treating of the phenomena that lie behind a cardiac contraction, and in discussing the intimate nature of nervous action.

I have specially to thank Dr. William Snodgrass, M.A., the Muirhead Demonstrator of Physiology in the University of Glasgow, for much valuable assistance in the preparation of this volume, and for reading the proof sheets as it passed through the press. My friend, Mr. R. F. Muirhead, M.A., B.Sc., kindly aided me in the part relating to some of the optical phenomena of vision. The value of the volume has also been enhanced by the description of the method employed by my friend, Professor A. Crum Brown, in studying the relations of the semicircular canals.

I beg to express my obligations to certain articles in Hermann's great *Handbuch der Physiologie*, in six volumes, and also to Munk's *Physiologie des Menschen und der Säugethiere*. The latter work has supplied me with not a few facts bearing on the physiology of the domestic animals. By the kindness of Messrs. A. & C. Black, I was also able to make some use of various physiological articles written by me for the *Encyclopædia Britannica*, 9th ed. The histological woodcuts have been largely derived from Stöhr's *Lehrbuch der Histologie*, under the arrangement mentioned in the preface to *General Physiology*.

JOHN G. M'KENDRICK.

University of Glasgow,
1st October, 1889.

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TEXT BOOK OF PHYSIOLOGY.

SECTION I.

NUTRITION. FOOD. DIGESTION.

CHAP. I.—THE NATURE AND PURPOSES OF NUTRITION.

By *nutrition* is understood a series of functions by which matter is introduced into the body, becomes for a time incorporated with the tissues and fluids, and is afterwards separated from the body by various channels. The matter thus introduced in the form of food and drink, along with the oxygen obtained in respiration, undergoes chemical changes during its passage through the body by which energy becomes either kinetic or potential. As a result of this exchange of matter between the organism and the outer world, and of the transformations of energy involved in this exchange, the functions of the various organs are performed. The term nutrition may be limited strictly to the processes by which living tissues take from the blood certain matters, and convert such matters into their own substance, or store them up after undergoing various transformations. Each living tissue element, when it performs the function peculiar to it, is the seat of physical and chemical operations, chiefly of a molecular character, with the result that a part of its substance undergoes a certain amount of tear and wear; that is to say, the complex organic bodies forming the substance of the tissue are split up into simpler ones. The process of nutrition may be regarded as that by which the tissue substance is reconstructed, so that it can again perform its function.

NOTE.—The special functions of the human body will be discussed under the heads of Nutrition, Innervation, and Reproduction. These functions are closely connected. Thus innervation, or the functions of the nervous system, depends on nutrition, and each stage of the process of nutrition may be influenced by the nervous system. In like manner, reproduction at all stages, in the higher animals, depends, directly or indirectly, on nutrition and innervation.

It is convenient for practical purposes, however, to view nutrition as a complex train of processes, or as a process consisting of many stages, each of which has for its object the maintenance in healthy action of each tissue and organ, and the maintenance of the body as a whole. This mode of regarding nutrition will be found useful to the student of medicine when he is called upon to study the phenomena of disease. Thus in the great majority of diseases, the emaciated look and the feeble movements of the patient indicate that the process of nutrition is not duly performed, and it becomes the duty of the physician to ascertain what stage or stages of the process are at fault. In some cases it will be found that the error lies in the processes by which food is prepared for assimilation, in other cases there is failure in some of the operations by which blood is formed, in a third class the mechanism by which this blood is circulated through the body and brought into close contact with the living tissues is not working in a proper manner, while in many others nutrition is not duly performed in consequence of the fault of one or other of the excretory organs, so that waste matters which exercise a baneful effect on living tissue are not eliminated from the blood. The student should habituate himself to the observation of diseased conditions from the physiological point of view, and this habit will not only lead him to see how nutrition may be deranged in many ways, but to arrive at the scientific explanation of some of the complications of disease. It must also give him the conviction that impaired nutrition is to be treated by an endeavour to restore the deranged processes to their healthy state, and that for this purpose a sound knowledge of the process of nutrition itself is a preliminary step.

It will be instructive at this point to take a survey of the stages of the process of nutrition. Each living tissue element is bathed in a fluid from which it receives the materials required for its nourishment and by which it breathes. It requires nutritive matter and oxygen. The nutritive and respiratory fluid is derived from the blood. The formation of blood and the introduction into the blood of oxygen are accomplished by a series of processes. The principles that determine the proper kind of food and drink, as influenced by work, climate, age, etc., require discussion. These may be considered as the *laws of dietetics.* In the first place, the materials that constitute food are usually very unlike the constituents of blood, and the food is therefore subjected to various chemical and physical processes in the alimentary canal. The result of these processes is that the materials of the food are so altered as to be readily absorbed. These chemical and physical processes constitute *digestion*, and they include the various mechanical actions by which the food is broken down in the mouth, swallowed, and propelled along the alimentary canal, and also the physical and chemical actions of various fluids secreted by glands and mixed with the food, such as the saliva, the gastric juice, the intestinal juice, the pancreatic juice, and the bile. The food stuffs thus rendered soluble form *chyme*, and are then absorbed either by the blood-vessels in the mucous membrane of the alimentary canal or, as *chyle*, by the lacteals in the villi of the small intestine. The chyle is conveyed to the mesenteric glands, thence to the *receptaculum chyli*, and by the thoracic duct, to the vascular system, being poured into the blood at the junction of the left internal jugular with the left subclavian vein. This stage of the process is termed *absorption*, and by it the blood receives fresh supplies of nutritive material at frequent intervals. But the blood receives matter from other sources. Oxygen is added to it by the process of *respiration*, and it receives materials, either in the form of fluids holding matters in solution, or in the form of coloured and colourless blood corpuscles from the glands of the *lymphatic system*, sometimes termed *blood glands*, such as the spleen, and the lymphatic glands found in many parts of the body. The stages of the process connected with the making of blood may be termed *sanguification*. The *blood* thus formed is a fluid holding the corpuscles in suspension and many substances in solution, and in particular its coloured corpuscles contain the pigment *hæmoglobin* which, uniting in the capillaries of the pulmonary air cells with oxygen, carries this all-important element to the living tissues. By the hydraulic mechanism of the *circulation* the blood is then propelled through the body so as to bring it into close relation to every tissue element. From the blood in the capillaries, a fluid transudes, the *lymph*, which bathes the tissues and, as already mentioned, supplies these with nutritive matter and with oxygen. This constitutes *nutrition*, and on it the phenomena of growth and the performance of the specific function of the tissue depend. Closely connected with the nutrition of tissue is the nutrition of the cells of glands by which *secretion* is performed. Thus such cells receive matters from the blood and by metabolic changes elaborate these into the secretion of a particular gland.

In the performance of its function by a tissue, various waste products, such as water, carbonic acid, and complex nitrogenous matters are formed, and these, along with the excess of nutritive matter that transuded from the vessels, are absorbed partly by the capillary vessels, but chiefly by a special set of vessels, the *lymphatics*, which act in a sense as drainage tubes for the removal of such waste matters. The *lymph* thus formed passes to *lymphatic* glands, or to *blood glands*, and like the chyle absorbed from the alimentary canal, is also ultimately poured into the blood. The blood is thus, on the one hand, receiving new supplies of nutritive materials, some of which it gives up to the tissues, and, on the other, it is receiving various waste matters which are the result of the activity of tissues. These waste substances deteriorate the quality of the blood, interfere with healthy nutrition, and they also may act directly as poisons on living tissue elements. They are therefore eliminated by various organs, and the process of elimination is termed *excretion.* Thus carbonic acid and water are removed by the lungs in the process of *respiration;* water, saline matters, pigments, and nitrogenous matters are removed by the kidneys; matters of a similar kind — although in much smaller amount—are separated by the skin; various pigmentary matters, conjugated nitrogenous acids, cholesterin, salts, and water are separated by the liver in the form of bile; and, lastly, saline substances, nitrogenous matters, and water are removed by the bowels along with the refuse matters of undigested food as fæces.

It is important to observe that an organ may be engaged in more than one process. Thus oxygen is introduced into the blood, and carbonic acid and water are eliminated from it by the lungs in respiration. Again, the cells of the liver not only have to do with the removal of certain matters from the blood in the form of bile, but they are also the seat of metabolic changes, by which carbohydrates and probably other substances may be stored up as *glycogen,* and by which proteid substances may be decomposed with the formation of urea.

Each of the stages of the process of nutrition above mentioned may include many subsidiary processes. These should always be studied with reference to the end to be attained, either the making of blood, the circulation of blood, or the depuration of blood. The constitution of the blood is the central subject of consideration, and all other processes are to be viewed in their relation to it.

As one of the results of the nutritive processes, in addition to the specific function of the organ or tissue involved, we have the liberation of *heat.* A certain mean temperature is necessary for the performance of function, and the tissues of warm-blooded animals can perform their functions only within a limited range of but a few degrees. There are therefore arrangements in the body closely connected with nutrition, by which the requisite temperature is maintained, and these will be considered under the head of the *Regulation of animal heat.* The student should expressly note that there is no one organ concerned in the production of heat, and that the liberation of heat is only the result of the chemical and physical operations taking place in the body. The body, however, is unlike such a machine as a steam engine in this respect, that whereas in a steam engine the heat produced diminishes the amount of energy available as work, without aiding in any way the efficient working of the machine, on the other hand, the heat produced in the body is not only not useless but is absolutely essential to the life and efficient functional activity of its tissues.

CHAP. II.—FOOD AND THE LAWS OF DIETETICS.

Under the term *Food* we include those substances, either in the solid or the fluid form, which are required for the nutrition of the body. Living tissues are the seat of various metabolic processes, and on these their vital activities depend. Chemical transformations occur and chemical compounds of simpler constitution are thus formed which are to be regarded as waste products, fit only for removal from the body. There is thus a daily loss of matter, or rather matter is being almost continuously separated from the body, by the lungs in respiration, by the skin, by the kidneys, and in the fæces. Thus an adult doing a moderate amount of work eliminates by the lungs about 900 grms. of carbonic acid, representing 245 grms. of carbon, that is $\frac{12 \times 900}{44} = 245$. In addition, the small amount of carbonic acid separated by the skin represents about 2·5 grms. of carbon; the carbon in the urea, uric acid, and other nitrogenous matters separated by the kidneys may be estimated at from 6 to 10 grms.; and lastly, the carbon in the organic matters of the fæces may be taken at from 15 to 20 grms. The total carbon eliminated thus amounts to from 250 to 280 grms.

About 30 grms. of urea, CH_4N_2O, are eliminated by the kidneys daily. These contain 14 grms. of nitrogen, for $\frac{28 \times 30}{60} = 14$. Add to this say 2 grms. of nitrogen contained in other nitrogenous bodies found in the urine—uric acid, creatinin, pigment, etc.—and 3 grms. of nitrogen obtainable from the fæces, and the nitrogen reaches a total of about 19 grms. Further, about 6 grms. of hydrogen and 680 grms. of oxygen are separated, but it is not so important to note the amount of these, as it will be shown that the dietetic value of a food depends chiefly on the amount of carbon and of nitrogen it contains. In addition, about 32 grms. of various salts—chlorides, sulphates, phosphates, etc.—are separated, chiefly by the kidneys and the bowels. It is sufficient to observe in the meantime that over 1000 grms. of matter are separated daily along with a variable amount of water. Food is therefore necessary to make up for this loss of matter.

There is, however, another aspect of the question. The body is not merely losing matter, but energy is being expended in the form chiefly of heat and motion. Thus, during 24 hours, the kinetic energy of the pulsations of the heart in an adult man amounts approximately to 50,400 kilogrammetres,[1] the energy of the muscles of respiration to 11,700 kilog.m., the energy expended by the man in doing mechanical work for 8 hours to 125,000 kilog.m., while the heat produced during the whole 24 hours, expressed in the same terms, amounts to no less than 620,000 kilog.m. The total energy expended thus amounts, in round numbers, to 807,100 kilog.m., or about 5,800,000 foot-pounds. This energy must be supplied by the processes occurring between the food and the oxygen introduced in respiration.

We have now to consider the nature of the materials employed as foods with the view of ascertaining how far these satisfy the requirements of the body, so as to make up for the losses of matter and of energy above indicated. A study of the chemical constitution of the body has shown that it consists of proteid or albuminous matters, fats, carbohydrates, salts, and water. The same kind of proximate principles must exist in a suitable diet. This may be regarded as the first law of dietetics. However the dietaries of members of the human race may vary, from the coarse food of the savage to the elaborate cuisine of civilized life, it will be found that if they are sufficient to maintain health and vigour, they always contain, in greater or less amount, the proximate principles above enumerated. The same law applies to the food of carnivorous and herbivorous animals, as proximate principles of the same kind exist in flesh and in cereals and other products of the soil.

Experience has guided man in his choice of food, and if we take the dietary of a civilized race it is remarkable that chemical analysis shows that a sufficient diet always contains the requisite amounts of carbon and nitrogen. Thus Moleschott has fixed the following diet for a man performing a moderate amount of work, and it will be seen that it contains about 280 grms. of carbon, and 18·88 grms. of nitrogen, nearly the amounts lost by the body in 24 hours. Thus—

---

[1] 1 kilogrammetre = 7·23308 foot-pounds; 1 foot-pound = ·138254 kilogrammetre.

TABLE I.

	N. in grms.	C. in grms.
120 grms. of dry albuminate (4·232 oz. avoird.), - -	18·88	64·18
90 grms. of fat (3·174 oz. avoird.), - - - - -	...	70·20
330 grms. of carbohydrate and starch (11·640 oz. avoird.),	...	146·82
Total, - - - - - -	18·88	281·20

We can estimate the energy represented by this dietary by ascertaining, by calorimetric methods, the amount of heat produced by its complete oxidation, and it may be expressed either as calories,[1] or as kilogrammetres. It has thus been ascertained that the complete oxidation of 1 grm. of dry albumin will yield energy to the extent of 1805 kilog.m., while 1 grm. of fat will yield 3841 kilog.m., and 1 grm. of starch will yield 1657 kilog.m. From these data the energy of the above diet can be calculated. Thus—

TABLE II.

Dry albumin, -	120 × 1805	=	216,600	kilogrammetres.
Fat, - - -	90 × 3841	=	345,690	,,
Starch, - -	330 × 1657	=	546,810	,,
Total, - -			1,109,100	,,

This amount is considerably more than the estimated amount of energy expended—807,100 kilog.m., but the discrepancy will be accounted for when we remember that the food materials do not undergo complete oxidation in the body. It is enough for the argument that the amount of food which has been found, both on theoretical grounds and as a matter of experience, to be sufficient for an adult man during 24 hours, will yield more than enough energy to make up for the loss of energy by his body during that time.

We shall next consider the dietaries that experience has proved to be necessary for adult men engaged in various employments and living in different conditions, with the view of ascertaining the relative quantities of the different proximate principles. The following table, compiled from the investigations of Sir Lyon Playfair,[2] and giving the results in oz. avoird.,[3] is instructive :—

---

[1] Heat units,—a *calorie* being the amount of heat that will raise the temperature of 1 grm. of water 1° C.

[2] On the Food of Man in Relation to his Useful Work. Lecture at the Royal Institution, London, April, 1865.

[3] 1 oz. avoird. = 28·35 grms.

TABLE III.

	Proteids.	Fats.	Carbo-hydrates.	Salts.	Total.	Dynamic value in foot-tons.[1]
Subsistence diet,[2] -	2·230	0·84	11·690	...	14·760	2453
Soldiers during peace,[3]	4·215	1·397	18·690	0·714	25·016	4026
Soldiers in the field,[4] -	5·410	2·410	17·920	0·680	26·420	4458
Royal Engineers, -	5·080	2·910	22·220	0·930	31·140	5232
Navvy, - - -	5·640	2·340	20·410	...	28·390	4849
English Sailors, - -	5·000	2·370	14·390	...	21·760	3911
Prisoner under 7 days,	1·800	0·480	10·712	...	12·992	...
,, under 21 days,	2·448	0·608	14·792	...	17·848	...
,, with hard labour, -	4·075	1·557	18·806	1·963	26·401	4072
,, with light labour, -	3·508	0·315	16·727	1·715	22·265	3577
,, with industrial employment	3·710	1·562	17·310	1·616	24·198	3787
,, with long sentence of penal servitude, -	3·784	1·580	19·864	0·972	26·200	4193
,, undergoing punishment	1·296	0·256	8·160	0·368	10·080	1541

This table shows that those employed in active service, involving sustained muscular exertion, require more food than those following lighter avocations. Contrast, for example, the amount supplied to the infantry soldier in time of peace with the amount given when he is more active in the field. In the case of the engineer and the navvy doing a still larger amount of bodily work, the amount must be increased. Again, a study of prison dietaries brings out the same fact. When a prisoner is obliged to perform a certain amount of work, the amount of food supplied must also be increased, and if he is obliged to engage in hard labour, he must receive a diet as large as that of a soldier in the field. An adult may barely live on a mere subsistence diet, in which the amount of food supplied is only half that of a navvy engaged in hard work. Taking the diet of Moleschott,[5] usually accepted as fairly indicating the amount required by men doing a moderate amount of work, we arrive at the following dietary :—

---

[1] To convert foot-tons into kilogrammetres divide by ·003285.

[2] Needlewomen, convalescents, diet in Lancashire famine of 1865.

[3] English, French, Prussian, and Austrian soldiers.

[4] English soldiers in Crimean war. This represents diet of active labourers.

[5] Quoted from Pavy, *On Food and Dietetics*, 1875, p. 452.

TABLE IV.

	In grms.	In grains avoird.	In ounces avoird.
Proteids, - - -	120	1852	4·232
Fats, - - -	90	1388	3·174
Carbohydrates, -	330	5092	11·640
Salts, - - -	30	462	1·058
Total, - -	570	8794	20·104

These figures represent the amount of water-free solids. Ordinary food contains about half its weight of water, so that the total weight of the food that would yield 20 ounces of dry matter will be about 40 ounces. In addition to the water in the food, from 50 to 60 ounces will be used daily in the fluid form, and the total amount of water ingested will thus be from 70 to 80 ounces. Considering the evidence given in Table III., the dietaries of men in various occupations, it may be concluded that 20·104 oz. avoird. of water free solids is too small an amount for men engaged in ordinary work. Not less than 25 oz. may be taken as a fair amount, and the quantity of the various constituents should be in the proportions given in Table IV.

TABLE V.

	Water.	Proteids.	Starch.	Sugar.	Fat.	Salts.
Bread, - - -	37	8·1	47·4	3·6	1·6	2·3
Wheat flour, - -	15	10·8	66·3	4·2	2·0	1·7
Oatmeal, - - -	15	12·6	58·4	5·4	5·6	3·0
Rice, - - -	13	6·3	79·1	0·4	0·7	0·5
Peas, - - -	15	23·0	55·4	2·0	2·1	2·5
Arrowroot, - -	18	...	82·0	...	...	...
Potatoes, - - -	75	2·1	18·8	3·2	0·2	0·7
New milk, - -	86	4·1	...	5·2	3·9	0·8
Cheese, - - -	36·8	33·5	...	...	24·3	5·4
Lean beef, - -	72	19·3	...	...	3·6	5·1
Fat beef, - - -	51	14·8	...	...	29·8	4·4
Mutton, - - -	72	18·3	...	...	4·9	4·8
Veal, - - -	63	16·5	...	...	15·8	4·7
Fat pork, - - -	39	9·8	...	...	48·9	2·3
Tripe, - - -	68	13·2	...	...	16·4	2·4
Poultry, - - -	74	21·0	...	...	3·8	1·2
White fish, - -	78	18·1	...	...	2·9	1·0
Salmon, - - -	77	16·1	...	...	5·5	1·5
Egg, - - -	74	14·0	...	...	10·5	1·5
Butter, - - -	15	...	...	...	83·0	2·0
Oats, - - -	12·4	10·4	57·8	11·2 (cellulose)		3·0
Meadow hay, - -	13·0	9·5	40·9	26·7 (do.)		6·8
Rye straw, - -	13·8	3·9	34·7	40·1 (do.)		6·5
Red clover,[1] - -	78·0	3·5	8·0	8·0 (do.)		1·7

---

[1] The analysis of the last four substances from Munk's *Physiologie des Menschen und der Säugethiere* is introduced to show the composition of food used by domestic animals.

Food, however, is not supplied in the form of proximate principles, but as bread, meat, and other articles of diet with which we are familiar. It is therefore necessary, in the next place, to ascertain the amount of the proximate principles in such substances, and this may be most conveniently given as their percentage composition. Table V., on the preceding page, from the investigations of Letheby[1] and Parkes,[2] gives the percentage composition of various articles of diet.

The figures in Table V. show that some substances, such as bread, flour, oatmeal, peas, cheese, beef, mutton, and veal, fish, and eggs, are rich in proteids, while others are poor in proteids and rich in carbohydrates, such as rice, arrowroot, and potatoes. Fats, cheese, pork, and butter are rich in fatty substances, and it should be observed that substances on which alone life may be sustained, with, of course, the addition of water, are substances containing all the proximate constituents in something like the proportions we have ascertained to be necessary in an adequate diet. Such substances include bread, wheat flour, oatmeal, milk, beef, poultry, and fish. Again, a study of this table indicates the advantage gained by combining articles of food so that the deficiency of one in a particular proximate principle may be compensated by its abundance in the other. Thus by combining bread and cheese, bread and meat, potatoes and meat, we can form a suitable diet.

Suppose it were required to frame a dietary for healthy adults from certain specified articles of food that were available. One method is to ascertain the percentage composition of the articles of food from Table V. and calculate the weight required to yield the amount of proximate principles stated in Table IV. Another method is to select the articles of food on the basis that 18·88 grms. (291·3 grains) of nitrogen and 281·2 grms. (4339·5 grains) of carbon must be supplied. For this purpose it is necessary to know the ratio of the carbon to the nitrogen in various articles of diet. This is given in Table VI. (opposite page), by Payen,[3] which shows the amount of nitrogen and of carbon per cent., and the figures expressing the amount of carbon also include the amount of hydrogen in the substance. Further, by multiplying the figures representing the amount of nitrogen by 6·5, we obtain a close approximation to the percentage amount of proteid matter.

Referring to the dietary given by Moleschott in Table I. as sufficient for an adult man performing ordinary work, in which 120 grms. of dry albuminate, 90 grms. of fat, and 330 grms. of carbohydrate are stated, Table VII. (opposite page) shows the weight in grammes of certain articles of diet required to yield these amounts.[4]

---

[1] Letheby, *On Food*, Cantor Lectures, 1870.

[2] Parkes, *Practical Hygiene*, 1886.

[3] Payen, *Substances Alimentaires*, Paris, 1865.

[4] Beaunis, *Physiologie Humaine*, tome i. p. 627.

TABLE VI.

	Nitrogen.	Carbon.		Nitrogen.	Carbon.
Beef without bone,	3·000	11·00	Barley,	1·900	40·00
Roast beef,	3·528	17·76	Rice,	1·800	41·00
Salt cod fish,	5·020	16·00	Oatmeal,	1·950	44·00
Sardines in oil,	6·000	29·00	Potatoes,	0·330	11·00
Salt herrings,	3·110	23·00	Dried figs,	0·990	34·00
Eggs,	1·900	13·50	Infusion of 3½ oz. of coffee,	1·000	9·00
Cow's milk,	0·660	8·00	Infusion of 308½ grains of tea,	0·200	2·10
Oysters,	2·130	7·180	Chocolate, 3½ oz.,	1·520	58·00
Cheshire cheese,	4·126	41·04	Fresh butter,	0·640	83·00
Beans,	4·500	42·00			
Peas,	3·660	44·00			
Flour,	1·640	38·50			

TABLE VII.

	For 120 grms. of proteids.		For 90 grms. of fat and 330 grms. of carbohydrate.
Cheese,	350	Maize,	532
Lentils,	453	Wheat bread,	543
Peas,	537	Lentils,	693
Beef,	566	Peas,	704
Hen's eggs,	893	Eggs,	776
Wheat bread,	1332	Cheese,	1730
Maize,	1515	Potatoes,	1751
Potatoes,	6000	Beef,	1945

Experience has shown that the diet most suitable for man should contain about 1 part of proteid or nitrogenous food to from 3·5 to 4·5 parts of non-nitrogenous. Liebig showed the relative nutritive value of various articles of food from this point of view in the following table.[1]

TABLE VIII.

	Nitrogenous.	Non-nitrogenous.		Nitrogenous.	Non-nitrogenous.
Veal,	10	1	Woman's milk,	10	40
Beef,	10	17	Wheaten flour,	10	46
Peas,	10	23	Oatmeal,	10	50
Fat mutton,	10	27	Potatoes,	10	86
Fat pork,	10	30	Rice,	10	123
Cow's milk,	10	30			

We have next to consider the dynamic value of various kinds of foods. We can ascertain this by determining by means of the calorimeter, how much heat is evolved in the oxidation of a given weight of the substance. The energy thus set free as heat is then represented in units of force, or kilog.m. Table II., p. 7, shows the energy produced by the oxidation of the materials constituting Moleschott's model diet, and the

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[1] Pavy, *Food and Dietetics*, p. 443.

following table from Frankland[1] gives the energy produced by complete oxidation of 1 gramme (15·432 grains) of various articles of food. It also shows that certain substances are not completely oxidized in the body, so that they furnish less energy to the body than is theoretically possible.

TABLE IX.

NAME OF FOOD.	Percentage of Water.	Force producing value—		
		In Calories.	In Kilogrammetres.[2]	
			When burnt in Oxygen.	When oxidized in Body.
Cod liver oil,	...	9107	3857	3857
Beef fat,	...	9069	3841	3841
Butter,	...	7264	3077	3077
Cheshire cheese,	24·0	4647	1969	1846
Oatmeal,	...	4004	1696	1665
Flour,	...	3936	1669	1627
Pease-meal,	...	3936	1667	1598
Arrowroot,	...	3912	1657	1657
Ground rice,	...	3813	1615	1591
Yolk of egg,	47·0	3423	1449	1400
Lump sugar,	...	3348	1418	1418
Hard boiled egg,	62·3	2383	1009	966
Bread crumb,	44·0	2231	945	910
Mackerel,	70·5	1789	758	683
Lean beef,	70·5	1567	664	604
Guiness' stout,	88·4	1076	455	455
Potatoes,	73·0	1013	429	422
Whiting,	80·0	904	383	325
Bass' ale,	88·4	775	328	328
White of egg,	86·3	671	284	244
Milk,	87·0	662	280	266
Apples,	82·0	660	280	273
Cabbage,	88·5	434	184	178

The conditions influencing the quantity of food required are chiefly those of age, climate, and the amount of work to be performed. The relation of food supply to the amount of work has already been fully illustrated. Young animals, including children, require more food in proportion to their body weight than is required by adults, because not only is metabolism more active in their tissues, but growth, or actual increase in bulk, is taking place. Aged persons, on the other hand, require less food, and, *cæteris paribus*, women require less food than men. The following table shows in grammes the average minimum amount of food required at different ages:—

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[1] Frankland, *Philosophical Magazine*, vol. xxxii.

[2] Kilogrammetres are converted into foot-pounds by multiplying by 7·233. 1 kilog. (2·2046 lbs. avoird.) raised 1 metre (3·2808 feet) high = 1 lb. avoird. raised 7·233 feet high.

TABLE X.

	Proteids.	Fat.	Carbo-hydrates.
Child under 1½ years, - - -	20·36	30·45	60·90
,, from 6 to 15 years, - -	70·80	37·50	250·400
Adult man, moderate work, - -	118	56	500
,, woman, ,, - -	92	44	400
Old man, - - - - - -	100	68	350
Old woman, - - - - -	80	50	260

The amount and nature of the food required are also affected by climate. Exposure to a cold bracing atmosphere sharpens the appetite and thus leads to more food being taken. In cold climates, there is a great demand for the production of heat in the body, and both experience and theory point to food rich in carbon as being the most appropriate in these circumstances. Hence in cold climates a large amount of fat is consumed, and by its oxidation, heat is produced. Thus if we compare the chemical composition of stearin, $C_3H_5(O.C_{18}H_{35}O)_3$, with starch, $C_6H_{10}O_5$, we find that 1 grm. of fat will require for its complete combustion over 3 grms. of oxygen and it will only contribute $\cdot\dot{1}$ grm. from its own substance, while 1 grm. of starch requires 1·68 grm. of oxygen, and it contributes about ·5 grm. from the oxygen in the starch. Thus the combustion of 1 grm. of fat produces far more heat than the combustion of 1 grm. of such a carbohydrate as starch.[1]

It must be remembered, however, that a *mixture* of the constituents of food is essential to the formation of a nutritious diet; and, moreover,

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[1] The calculation is as follows :—

$$\begin{array}{llrl} \text{I. } C_3H_5(O.C_{18}H_{35}O)_3. & C_{57} = & 57 \times 12 = & 684 \\ \qquad\text{Stearin.} & H_{110} = & 110 \times 1 = & 110 \\ & O_6 = & 16 \times 6 = & 96 \\ \hline & & & 890 \text{ molecular weight of fat.} \end{array}$$

$890 \div 96 = 9\cdot 4 \;\therefore$ fat contains $\cdot\dot{1}$ ($\frac{1}{9}$th) its weight of O.

(1) $\begin{matrix} C + O_2 = CO_2 \\ 12 + 32 = 44 \end{matrix}$. 12 grms. of C produce 44 grms. of CO_2 ∴ 684 grms. of C produce $44 \times 57 = 2508$ grms. of CO_2. But CO_2 contains $\frac{8}{11}$ths of its weight of O ∴ $2508 \times \frac{8}{11} = 1824$ ∴ 2508 grms. of CO_2 contain 1824 grms. of O.

(2) $\begin{matrix} H_2 + O = H_2O \\ 2 + 16 = 18 \end{matrix}$. 2 grms. of H produce 18 grms. of H_2O ∴ 110 grms. of H produce $18 \times 55 = 990$ grms. of H_2O. But H_2O contains $\frac{8}{9}$ths of its weight of O ∴ 990 grms. of H_2O contain 880 grms. of O. The total O in the products of combustion is therefore $1824 + 880 = 2704$ grms. That is, to burn 890 grms. of fat, 2704

that there must always be a certain amount of *sapidity* or *flavour* in the food. We should turn with disgust from a mess consisting of these constituents, even in proper proportions, if it were not properly cooked, and by cooking, the flavour of meat is developed. Sapidity is also attained by the use of the various condiments. The best example of a natural food is milk. It contains water, albumin in the form of casein or cheese, fat in the form of butter, sugar, and various salts. Hence it is nature's food for all young animals of the mammalian group.

A healthy diet must fulfil the following conditions:—(1) It must contain a due proportion of the various proximate principles found in the body of man. (2) It must be adapted, as regards quantity and quality, to the amount of work done by the individual. (3) It must be adapted, as regards quantity and quality, to the climate, to the age, and in some degree to the sex, and to the digestive powers of the individual. (4) It must be readily digested, as the nutritive value of a food product may theoretically be great while in practice it may be found to be very deficient. (5) It must have a degree of sapidity or flavour which will render it palatable, and thus indirectly aid the digestive process by stimulating the secretion of the various digestive juices.

Interesting observations have been made which show that life cannot be maintained by the use of one proximate principle alone. Majendie fed dogs on sugar, oil, gum, or butter alone, and found that for one or two weeks they did very well, but after that became weak, and died on the thirty-second or thirty-sixth day. When they were fed on white bread and water, they lived fifty days, when on cheese

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grms. of O are required, of which the fat contributes 96 grms., or about $\frac{1}{28}$th part. If 890 grms. require 2704 grms. of O, 1 grm. will require 3·02 grms. : $\frac{2704}{898} = 3{\cdot}02$.

$$\begin{array}{lllll} \text{II. } C_6H_{10}O_5. & C_6 & = & 6 \times 12 = & 72 \\ \text{Starch.} & H_{10} & = & 10 \times 1 = & 10 \\ & O_5 & = & 16 \times 5 = & 80 \\ \hline \end{array}$$

162 molecular weight of starch.

$162 \div 80 = 2 \; \therefore$ starch contains ·5 ($\frac{1}{2}$) its weight of O.

(1) $\begin{array}{c} C + O_2 = CO_2 \\ 12 + 32 = 44 \end{array}$. 12 grms. of C produce 44 grms. of $CO_2 \; \therefore$ 72 grms. of C produce $44 \times 6 = 264$ grms. of CO_2.

(2) $\begin{array}{c} H_2 + O = H_2O \\ 2 + 16 = 18 \end{array}$. 2 grms. of H produce 18 grms. of $H_2O \; \therefore$ 10 grms. of H produce $18 \times 5 = 90$ grms. of H_2O. But 264 grms. of CO_2 contain $\frac{8}{11}$ths of O, that is 192 grms. of O, and 90 grms. of H_2O contain $\frac{8}{9}$ths of O, that is 80 grms. of O. The total O in the products of combustion is therefore $192 + 80 = 272$ grms. Or to burn 162 grms. of starch, 272 grms. of O are required, of which the starch contributes 80 grms., or nearly $\frac{1}{3}$rd. If 162 grms. of starch require 272 grms. of O, 1 grm. will require 1·68 grms. : $\frac{272}{162} = 1{\cdot}68$.

and white of egg, they lived longer, but became feeble, emaciated, and lost their hair. Tiedemann and Gmelin found that dogs fed on cane sugar died in about thirty days, a goose with a sugar diet lived twenty-two days, one with dry starch flour lived twenty-seven days, and one with boiled starch forty-four days. When fed with gum, or fat, such as olive oil, animals lived thirty-six days. A donkey fed with rice alone died after fourteen days. The experiments by Edwards and Balzac have shown that a diet of bread and gelatin is insufficient, producing death after emaciation, without appreciable lesion. The addition of brown soup, however, renders bread and gelatin highly nutritious. Dr. Hammond limited himself to 1½ pounds of gum on one occasion, and a like quantity of starch on another, with water, per day. Hunger, debility, and fever became so great that he was obliged to abandon the first diet on the fourth, and the second on the tenth day. When, instead of these substances, he took 1½ pound of albumin—diarrhœa, albuminous urine, and disgust at the food obliged him to abandon it on the ninth day. A goose fed with boiled whites of eggs lost half its weight by the twenty-sixth day. Dogs fed on gelatin lived only twenty days. The deprivation of saline matters soon injures health. Forster fed a dog with meat, from which all saline matters had been removed, and the dog died in five weeks. Its blood was found to have lost one-fifth of its normal proportion of saline matters. Of all the articles of food, milk appears to be that which contains the proximate principles in the best proportions. A like result may be obtained by combining other articles, such as fat pork with veal, potatoes with beef, and rice with mutton or fowl. Again, stuffing is generally added to ham and veal, bacon to beans, ham to fowls, and so on. The addition of butter to bread forms the almost universal food of the nursery. Mankind have for the most part adopted these rules instinctively. Persons who feed principally on flesh prefer it fat; and those who live largely on vegetables, as potatoes and rice, take considerable quantities of milk.

We shall now advert to some of the facts of importance relating to the various kinds of proximate principles as found in ordinary articles of diet.

1. *Water.*—Water suitable for drinking or for cooking purposes must be clear and without odour. It should also have a fresh, agreeable taste, from the presence chiefly of the carbonic acid and salts held in solution. Distilled water is insipid. Rain water contains traces of carbonic acid, ammonia, nitrous and nitric acids, and is soft owing to the absence of saline matters. Good spring water may contain from 20 to 30 per cent. of its volume of gas derived from atmospheric air, and this gas is richer in oxygen than air, on account of the greater solubility of oxygen than of nitrogen. It is also rich in carbonic acid derived from the soil. The oxygen may exist to the extent of from 8 to 20 c.cm. and the carbonic acid to the amount of from 5 to 30 c.cm. per litre. Artificially aerated water, or the waters of many effervescing springs, may contain as much as from 150 to 1000 c.cm. of carbonic acid gas per litre. The mineral substances in water consist of carbonates, chlorides, and sulphates of the alkalies and alkaline earths, and the amount of residue after evaporation should not exceed ·5 gramme per litre. The quantity of lime and magnesia in water determines its degree of hardness, and this is usually expressed by stating the number of parts of lime (oxide of calcium combined with the mineral acids) in 100,000 parts of water. Thus a good water should not contain more than 20 parts of lime in 100,000—that is, it should not exceed 20 degrees of hardness. Water containing animal organic matter should

never be used for culinary purposes. The microscope may be used to detect the presence of micro-organisms, such as bacteria, monads, etc.,[1] or sterilized gelatin may be inoculated with a drop of the water and the result observed. (See Vol. I. p. 196.)

The quantity of water in the body does not vary much in a state of health, a balance being struck between the amount introduced and that lost by exhalation from the lungs, evaporation from the skin, and by the kidneys and bowels. When the quantity falls below a certain minimum, which will vary much in different persons, and even in the same individual at different times and in different conditions, the sensation of thirst is experienced. The introduction of water into the blood in excessive amount may increase the total amount of saline and other soluble substances eliminated in twenty-four hours by the kidneys. As to the physiological influence of water, see Vol. I. p. 35.

2. *Mineral Matters.*—Mineral substances are indispensable in the food. They are active agents in nutrition, and their presence in the fluids and solids of the body appears to be essential. When an animal is entirely deprived of mineral matters in its food less of these substances appears in the excretions, and the animal quickly falls out of health. The most important salt is *chloride of sodium*, which is found in all the fluids, tissues, and organs of the body, and which is taken as an article of diet, instinctively, both by man and animals. About 20 grammes of common salt are separated by the various excretions in twenty-four hours, and the same amount must therefore be supplied in food. The presence of albumin in the urine has been observed to follow a dietary containing no common salt. Most articles of diet do not contain enough of common salt; indeed, the amount is usually insignificant, and, consequently, most of it is taken directly, either as a condiment, or in salted food. It has been shown that when an animal receives chloride of potassium instead of chloride of sodium in its food, after a certain time the urine does not contain nearly so much of the latter as in normal circumstances, indicating that the blood and the tissues retain it with great tenacity; but it is remarkable that in these circumstances the animal may retain its health for a considerable time. Voit has shown the importance of common salt in the phenomena of diffusion by the following interesting experiment: If albumin alone is injected into the abdomen of an animal, it is not absorbed, but if it is mixed with a little common salt it is taken up with readiness. Common salt is also necessary in the food of herbivora. A part of the chloride of sodium undergoes chemical changes in the body, supplying chlorine to form the free hydrochloric acid of the gastric juice.

The salts of *potash* are also essential in food. They exist in considerable quantity in the blood corpuscles, muscular fibre, and nervous tissue, whilst those of soda are found principally in the fluids. Kemmerich fed two dogs for six weeks with the same quantity of meat entirely deprived of salts. In one case he added to the food a little common salt alone, and in the other case, in addition to the common salt, he gave the salts of potash: at the end of the time the first dog, which received in its food common salt only, was feeble and extremely emaciated; whilst the other, which received salts of potash in addition, was in vigorous health. In small doses they encourage the activity of the circulation by increasing

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[1] The methods followed in the chemical analysis of water are not given in this work, as they pertain more to treatises on hygiene. (See Parkes' *Hygiene.*)

the blood pressure, and augmenting the force and frequency of the cardiac contractions. Beyond a certain point, however, they lessen the activity of the circulation.

The salts of *lime* are required for the nutrition of the textures, more especially for such tissues as bone and teeth. Phosphate of lime, which is the principal salt, is introduced both in articles of food and in water, but the processes by which it is separated from these and incorporated into the tissues, are unknown.

The alimentary importance of salts of *magnesia*, and of *carbonates* and *sulphates* of the alkalies and alkaline earths, although these substances are found in the body, is unknown.

Iron exists in the colouring matter of the blood. (See Vol. I. p. 118.)

The following table shows the percentage composition of the ash of various kinds of food :—[1]

TABLE XI.

IN 100 PARTS OF ASH.	Potash.	Lime.	Magnesia.	Soda.	Common Salt.	Oxide of Iron.	Phosphoric Acid.	Sulphuric Acid.	Silica.
Cow's milk, -	23·46	17·34	2·20	6·96	4·74	0·47	28·04	0·05	0·06
Weak soup, -	43·19	...	...	...	...	...	26·24	2·95	...
Meat extract, -	46·12	0·23	1·96	10·45	...	traces	36·04	0·27	...
Muscle, as in flesh, -	39·40	1·80	3·88	4·86	1·47	1·00	46·74	0·30	...
Brain, - -	34·42	0·72	1·23	10·49	4·74	...	48·17	0·75	0·42
White of egg, -	27·66	2·90	2·70	12·09	39·30	0·54	3·16	1·70	0·28
Yolk of egg, -	10·90	13·62	2·20	1·08	9·12	2·30	60·16	...	0·62
Wheat, - -	27·04	1·97	6·60	0·45	...	1·35	62·59	...	...
Barley, - -	20·91	1·67	6·91	...	...	2·10	38·48	...	29·10
Lentils, - -	34·76	6·34	2·47	13·50	4·63	2·00	36·30	...	...
Potatoes, - -	51·21	3·35	13·58	...	2·41	...	11·91	6·50	7·17
Turnips, - -	37·55	9·76	3·78	12·63	4·91	0·74	8·37	6·34	0·76
Salad, - -	22·37	10·43	5·68	18·50	15·09	2·82	9·39	3·85	11·86

3. *Carbohydrates.*—These consist of starch, cane sugar, grape sugar, gums, and mucilage. *Starch* forms the chief ingredient of potatoes, rice, tapioca, arrowroot. and it exists also in considerable amount in the products of the cereals and of leguminous plants. It exists in the form of small, somewhat oval grains, exhibiting a series of concentric curved markings, as if the grain were built up of layers. These grains are of various sizes, and they also appear to possess different degrees of resistance to the penetration of water, an important point as regards their value in alimentation. A starch grain, after treatment with dilute sulphuric or hydrochloric acids, shows an undissolved portion, retaining the form of the grain, which seems to be a variety of cellulose. The portion dissolved by the acid, and which strikes a blue colour with iodine, is termed granulose. Prolonged boiling in water, the action of dilute acids, and many soluble ferments convert starch into glucose and dextrin.

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[1] Compiled by Beaunis from various authorities. Beaunis' *Physiologie Humaine*, t. i. p. 621.

Cane sugar, familiarly known as obtained from sugar cane or beetroot, exists also in many vegetables frequently used in diet, such as carrot, turnip, parsnip, melon, parsley, cucumber, etc. *Milk sugar* forms an important element of diet, especially in early life. *Grape sugar* is found in fruits, honey, and in such fermented liquids as wine, beer, cider, perry, etc. It is important to note that a substance identical with it may be found after death in the liver, which is probably derived, as will be seen hereafter, from a kind of animal starch, called glycogen, formed in that organ. In the muscles also, more especially in the heart, a small amount of inosite, or *muscle-sugar*, is found. *Cellulose*, $C_6H_{10}O_5$, forming the walls of vegetable cells, is of very little use in alimentation, and the same remark may be made regarding the *gums* and *mucilages*.

All carbohydrates are absorbed into the system in the form of sugar, as the result of the process of digestion. A diet rich in carbohydrates diminishes the amount of urea excreted. They are more readily oxidized than either fats or albumin, and hence after a diet rich in carbohydrates these are used first and the fats and proteids may thus be unconsumed, at all events for a time.

4. *Fat.*—The fat in animal food consists of a mixture of stearin, palmitin, and olein. When the latter predominates the fat is fluid and exists as an oil, but when the former two substances are in abundance the fat is solid, as in lard and butter. When oils are used as articles of diet they are usually derived from plants, such as olive oil, etc. If an animal is fed on fat alone even less urea is excreted than if the animal is starving, showing that the metabolism of proteid matter is diminished by the presence of an excess of fatty matter in a diet.

Animal fats have different melting points. The fat of the horse, the fat of milk (butter), and the fat of dogs have a low melting point, remaining fluid or soft at from 23° to 30° C. The fat of pigs is more consistent and melts at 37° C. Beef suet (the ox) melts between 41° to 48° C., and mutton suet between 43° and 50° C. Fluid vegetable fats contain only olein and palmitin, no stearin.

5. *Proteids.*—As examples of these we have glutin, as found in the cereals, and legumin, which is identical with casein, in peas, beans, haricots, etc. Albuminous matters do not exist to the same amount in plants as in animals. They are met with in animal substances in the form of the myosin of muscle, the casein of milk, the albumin of eggs, the albumin of blood, the fibrin of blood, etc. When we consider the large amount of proteid matter in the blood and tissues it is evident that the proteids must be of great importance in a suitable dietary. They are the seat of active metabolism, the nature of which will be discussed in treating of the nutrition of the tissues.

6. *Accessories to food.*—In addition to water, saline matters, fats, carbohydrates, and proteids which are found, more or less, in every article of diet fitted for the nourishment of the healthy body, various substances are employed by man which may be regarded as *accessories* to food. Such are alcohol, as contained in wines, spirits, beer, etc., vegetable acids, essential oils, condiments, and beverages containing alkaloids, namely, tea, coffee, cocoa, etc.

(*a.*) With regard to *alcohol*, its exact influence, when taken in moderation by those who use it as an article of diet, cannot be precisely stated. It has been asserted by several observers that alcohol is eliminated from the body as alcohol by the various excretory channels. The evidence of this is doubtful, and it is probable that it is split up into simpler compounds. According to Liebig, alcohol may be decomposed in the blood into ethyl aldehyde, acetic acid, oxalic acid, and lastly, into carbonic acid, and water. A small part of the alcohol ingested no doubt is exhaled by the mucous membrane of the lungs and by the kidneys. The odour of the breath depends on the elimination of oxidation products, such as fusel oil. If oxidized, even to a small extent, and the evidence, as already indicated, points to the oxidation of by far the larger proportion of it (95 per cent.), alcohol must be regarded in the scientific sense as a food. No doubt also its ingestion diminishes the metabolism of proteids to the extent of about 6 per cent., as shown by the diminished excretion of urea. Its oxidation will also be attended by the production of heat, but as on the other hand, it lessens the production of heat by interfering with the metabolism in proteid tissues, and also by diminishing the oxidation of carbohydrates and fats, the final result is an actual diminution of bodily temperature. While therefore alcohol must be classed technically as a food, it is in many respects an unsuitable food, and its place can be taken with great advantage by other substances. In small doses it acts as a local excitant of the digestive mucous membrane and afterwards as a diffusible stimulant upon the circulation and central nervous system. In some cases, it may aid the digestive process, but in a state of health it is not only not required, but its use, except in small doses, is positively prejudicial.

The following table gives the percentage of alcohol in the more common kinds of wines, spirits, and malt liquors in use :—

Brandy, -	50 to 60	Port, - -	16 to 23	Hocks, - -	6 to 16
Whisky, -	50 ,, 60	Sherry, -	16 ,, 25	Madeira, -	16 ,, 22
Arrack, - -	50 ,, 65	Champagne,	5 ,, 13	Porter, - -	8 ,, 10
Rum, - -	60 ,, 77	Clarets, -	9 ,, 13	Bass's beer, -	8 ,, 10
Vodka, - -	52	Burgundy, -	7 ,, 13	Lager beer, -	2, 3 or 4
Absinth, -	50 ,, 68	Sauterne, -	14 ,, 16	Bavarian beer,	4
Benedictine, -	52	Marsala, -	20	Table beer, -	2 to 5
Curaçoa, -	55	Tokay, -	17	Sweet ale, -	7 ,, 9
Gin, - -	49 ,, 60				

In addition to alcohol, many wines contain colouring matter, organic acids, such as malic, succinic, acetic, and tartaric acids, tartrate of potash, acetic and œnanthic ethers, and carbonic acid; and the peculiar quality of the wine depends upon the predominance of one or other substance. Wine contains also sugar not changed into alcohol, a trace of proteid matter, and gum. Thus, sherry and madeira contain various ethers and alcohol; port abounds in astringent matter (tannin); hocks contain acids; the sparkling wines, such as champagne, contain ethers, glycerine, saccharine matter, and carbonic acid; and the sweet wines may contain glycerine and inosite. The amount of sugar should never exceed 4 grms. per litre; the amount of glycerine may range from 2 to 6 grms. per litre; and the quantity of phosphoric acid may range from ·15 to ·16 grm. per litre for white wines, and from ·30 to ·33 grm. per litre for red wines.

Brandy contains, in addition to alcohol, œnanthic and other ethers; the aroma of rum depends on butyric ether; gin contains oil of juniper and other aromatics; and whisky, when free from fusel oil, owes its flavour to something derived from malt or from peat smoke. Malt liquors contain alcohol, sugar, dextrin, glutin, various matters extracted from hops, which give bitterness and an aromatic flavour, and various mineral salts. Beer contains from 70 to 90 per cent. of water, 2 to 10 per cent. of alcohol, 2 to 6 per cent. of sugar, 2 to 8 per cent. of dextrin, and ·1 to ·9 per cent. of carbonic acid. The hops which are added to the wort, give to beer its bitter taste, and they add to the beer traces of fat, lactic acid, salts of ammonia, and proteid matter. Certain wines and malt liquors contain a considerable percentage of the salts of potash. Thus the ash of beer has been found to yield in 100 parts 40·8 of potash, 20 of phosphorus, 20 of magnesium phosphate, 2·4 of calcium phosphate, and 16·6 of silica.

(*b.*) The various *vegetable acids* which are taken as condiments in the form of vinegar, acid fruits, lemonade, ginger beer, ginger wine, clarets, etc., excite a gustatory sensation which may for a time relieve thirst and stimulate appetite. When taken in moderation along with food, they stimulate the secretion of saliva and of gastric juice. In passing through the body, these acids are, for the most part, converted into carbonic acid, and consequently appear in the form of carbonates in the urine.

(*c.*) *Stimulating condiments*, such as pepper, mustard, ginger, etc., when taken in small quantity, act as local excitants of the mucous membranes of the mouth and of the stomach. By thus promoting a flow of saliva and of gastric juice, they may assist in the process of digestion; but, at the same time, it is to be remembered that perfect digestion may be performed without their use, and that consequently they are not essential articles of diet.

(*d.*) *Tea, coffee, etc.*—It is remarkable that, in different parts of the world, mankind have for ages been in the habit of drinking infusions of certain herbs, all of which contain essentially the same active substance or alkaloid. Thus the tea of China, the coffee of Arabia and the east, the cocoa of South America, the maté or tea of Paraguay, and the guarana or cocoa of Brazil, have all become valuable beverages, and all contain an alkaloid, represented by the general formula $C_8H_{10}N_4O_2+H_2O$, to which the various names of *thein*, *caffein*, and *guaranin* have been given. *Theobromin*, the alkaloid of cocoa, has the formula $C_7H_8N_4O_2$. To the same group belongs the coca of South America (Erythroxylin coca), yielding the alkaloid *cocain*. All of these alkaloids are related in chemical constitution to xanthin, from which they have been prepared. Tea contains 6 per cent. of thein, and coffee ·3 per cent. of caffein. Infusions of these herbs contain other substances which play an important part in their physiological action. Thus, coffee is rich in aromatic matter; tea contains a considerable amount of tannin (18 per cent. in green tea, and 15 per cent. in black tea); whilst cocoa abounds in fatty matter and vegetable albumin. Tea contains about 3 per cent. of salts of iron, manganese, and soda; and coffee yields 3·4 per cent. of salts, chiefly those of potash. Tea also contains from ·5 to 1 per cent. of an etherial oil, and about 30 per cent. of extractive matter. Tea and coffee stimulate the nervous system without producing any period of after-depression such as follows alcoholic stimulants. They also increase generally the activity of all the secretions; and, they diminish the amount of nitrogenous matter separated by the kidneys, indicating that they lessen the activity of waste of tissue. One of their most remarkable characteristics is the almost instantaneous relief they give to feelings of fatigue, a property which is strikingly manifested in the use of the leaves of coca, which enable those who use it to perform fatiguing marches lasting many hours without food. Cocoa, from the fat and albuminous matter it contains, is a nutritious substance, but is only to a slight extent a nervous stimulant.

It will now be instructive to consider, from a practical point of view, several of the more common articles of diet. First among these is *milk*. Ordinary cow's milk contains, on an average, in 100 parts, 87 of water, 3·4 of proteid matter, 4 of fat, 5 of sugar, and ·6 of salts. The ash of milk yields phosphate of potash, phosphate of lime, and chloride of potassium, with a smaller amount of chloride of sodium, and a trace of oxide of iron. Milk constitutes a model dietary, especially for young animals. These grow and remain in health if fed with milk, but an adult cannot maintain the condition of equilibrium, as regards the amount of nitrogen taken in and given out daily, if fed entirely on milk, even with an allowance of from 2·5 to 3·5 litres per diem. *Butter*, obtained from the cream, contains 85 to 90 per cent. of fats, along with from 7 to 10 per cent. of water, and ·75 per cent. of albumin. It is thus an excellent article of diet, combined with substances that yield proteid matter and carbohydrates, such as bread, potatoes, etc. The milk remaining, after the removal of the butter by churning, *butter-milk*, is less nourishing than ordinary milk on account of the loss of the fat, but as it contains casein, sugar, and salts, it is still a valuable addition to a diet poor in albumin. Hence the value of butter-milk with potatoes. *Cheese* consists of casein and fat precipitated artificially by the ferment of rennet, and contains, on an average, 30 per cent. of proteid matter, and from 7 to 25 per cent. of fat. Hence, if it can be digested, it is a valuable addition to a diet poor in proteid matter and fat, and forms an excellent diet along with potatoes, maccaroni, etc. The *whey* of milk, after removal of the casein and most of the fat, has still a certain nutritious value, as it contains sugar and the phosphates of potash and lime.

Butcher meat consists of the muscles of ruminants, rodents, and pachyderms, and also of birds and fishes, but under the term meat may also be included such soft parts as liver, kidney, spleen, lungs, etc. Ordinary lean meat contains in 100 parts 75 of water, 19 of proteids, 1·5 of gelatinous matter, 1·5 of fat, 1 of carbohydrate (as glycogen and sugar), and 1·3 of salts. Meat ash yields ·75 of acid phosphate of potash, ·078 of earthy phosphates, ·6 of chlorides of the alkalies, and ·01 of oxide of iron. The following table, compiled by Munk,[1] gives the percentage composition of various kinds of meat :—

Table XII.

	Ox.	Calf.	Pig.	Horse.	Fowl.	Pike.
Water, - - -	76·7	75·6	72·6	74·3	70·8	79·3
Solid matter, - -	23·3	24·4	27·4	25·7	29·2	20·7
Proteid matter and gelatin, - - -	20·0	19·4	19·9	21·6	22·7	18·3
Fat, - - - -	1·5	2·9	6·2	2·5	4·1	0·7
Carbohydrate, - -	0·6	0·8	0·6	0·6	1·3	0·9
Salts, - - - -	1·2	1·3	1·1	1·0	1·1	0·8

Meat contains more than four times the amount of proteid matter present in an equal weight of milk. The flesh of birds is richest in proteid matter. Carnivorous animals eat large quantities of flesh to meet the requirements of the body as to carbon. A mixed diet is the one most suitable for man, as by combining meat with substances rich in carbohydrates, smaller quantities of both may be consumed. Finely grated raw meat, as it presents a large surface to the action of the digestive

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[1] Munk, *op. cit.* p. 260.

juices, is almost entirely digested, but the danger of eating raw meat is that of introducing into the body the ova of entozoa, such as *tœnia* and *trichina*. Butcher meat may be prepared by being roasted, stewed, or boiled. Whatever may be the mode of cooking, the internal temperature of the meat ought not to pass 70° C., nor fall below 56° C. When meat is roasted before an open fire, it is acted upon by a strong heat which, by coagulating the albumin, forms a hard layer on the surface, thus preventing the escape of the juices of the meat. By roasting, meat loses, as a rule, about 20 per cent. of its weight. Cold water will dissolve out of meat the saline matters, about 3 per cent. of soluble proteid matters, about 1 per cent. of extractives, such as creatin, xanthin, and hypoxanthin, gelatinous matter, and fat in very small quantity, and a trace of lactic acid. At 45° C. a small part, and at 70° C. the most, of the soluble proteid matter and the hæmoglobin in the meat are coagulated. When beef is boiled in water, about 80 per cent. of the salts are at once dissolved out, and in the fluid various extractive matters, such as creatin, xanthin, etc., are also found. Any gelatin present in the meat is also dissolved. The flesh of young animals contains more of this substance than that of old animals; according to Liebig 1,000 parts of beef yield 6, whilst 1,000 parts of veal yield 50, parts of gelatin. Even after prolonged boiling the meat that remains has considerable nutritious value, as it still contains a small amount of saline matter and about 16 per cent. of proteid matter. The addition of a little fat adds much to its nutritious value. In the preparation of *beef-tea*, the meat should be placed in cold, and not in hot water, and afterwards gradually heated. If placed directly in hot water, a superficial layer of coagulated albumin is formed, which prevents the escape of the juices of the meat and of the soluble substances, and the beef-tea thus obtained is very poor. If beef-tea has been properly prepared, it consists of a solution of gelatin, of salts, and of extractive matters, a little soluble albumin, and any fat which may have been mechanically set free by the process of heating. It may be made more nutritious by the addition of gelatin, bread crumbs, or gravy. There can be no doubt that beef-tea has a certain nutritive value, regarding the exact nature of which, however, considerable controversy has taken place, some supposing that it is due to the extractive matters, whilst others hold that it is really due to the gelatin and salts. The probability is that the stimulating effect produced by a cup of beef-tea after fatigue is due to the extractive matters, creatin, xanthin, hypoxanthin, and that any nourishment obtained from it is owing to the gelatin, albumin, and fat. Good beef-tea contains about ·8 of the total salts of the meat, especially phosphate of potash and chloride of sodium. *Liebig's extract of meat*, largely used in the sick-room, consists chiefly of extractives and of the various salts, and more especially those of potash. This substance should therefore be regarded as a stimulant which acts specially upon a fatigued nervous system, the action being largely due to the salts of potash; but along with meat-juice, bread, or rice, it is an important adjunct to a nourishing diet. Liebig's extract contains about 22 per cent. of water and 78 per cent. of solids, and of the latter 61 per cent. are organic while 17 per cent. are inorganic. *Salt meat* loses portions both of organic and inorganic soluble materials, which pass out into the brine. The amount thus lost is very small. Thus Voit found after 14 days of salting that only ·01 of proteid (albumin), ·14 of the extractives, and ·09 of the phosphoric acid had escaped into the brine. If the meat is kept in brine for several months it loses a proportion of the salts of potash, which are of high alimentary importance. When meat is smoked the surface is hardened by coagulation of the outermost layer, and at the same time certain matters in the smoke, such as creosote, act as antiseptics.

Eggs are highly nutritious substances. Excluding the shell (consisting mainly of carbonate of lime) 100 grms. of hen's egg contain 73·7 of water and 26·3 of solids. The latter consist of egg albumin, vitellin, and nitrogenous extractives to the amount of 12·6 per cent. of fats, such as palmitin and olein, with cholesterin and lecithin, to the amount of 12·1 per cent., and there are traces of grape sugar, along with 1 per cent. of salts, namely, phosphate of potash, chloride of sodium, and oxide of iron. The nutritious value is great also because almost the whole of its substance is readily digested. One hen's egg is equal, according to Voit, to about 40 grms. of fat meat, and to as much as 150 grms. of cow's milk. Hard boiled eggs are readily digested if finely grated so as to present a large amount of surface to the action of the gastric juice; lightly boiled eggs are more easily digested; raw eggs are still more so, especially if the albumin is merely coagulated by dropping the egg into hot water.

Alimentary substances from the *vegetable* kingdom present great differences in their composition. The nutritious matters are enclosed in cells having walls of cellulose, and they are therefore not so easily acted on by the digestive fluids. We also find that the nutritious matters are mixed with a considerable amount of non-nutritious indigestible matters. For this reason the fæces of herbivora are much larger than those of carnivora. Vegetable food also differs from animal food in the character of its saline constituents, the salts of potassium and magnesia (especially the phosphates) preponderating over those of sodium and lime. Vegetable proteid or albumin (sometimes called glutin) does not differ essentially from animal albumin. We find in plants albuminous bodies soluble in water and coagulated by heat, along with globulins which are insoluble in water but are soluble in solution of sodium chloride, such as legumin, conglutin, etc. A vegetable proteid, coagulating spontaneously, is also present and is called vegetable fibrin.

The *cereals*, wheat, rye, barley, oats, maize, rice, and millet furnish valuable articles of food. The following table gives their average chemical composition in percentages.[1]

TABLE XIII.

	Wheat.	Rye.	Barley.	Oats.	Rice.	Maize.	Millet.
Water,	13·6	15·1	13·8	12·4	13·1	13·1	11·0
Albumin,	12·4	11·5	11·1	10·4	7·9	9·9	10·8
Fat,	1·8	1·8	2·2	5·2	0·9	4·6	5·5
Carbohydrates and non-nitrogenous mat'rs,	67·9	67·8	64·9	57·8	76·5	68·4	66 8
Cellulose,	2·5	2·0	5·3	11·2	0·6	2·5	2·6
Ash,	1·8	1·8	2·7	3·0	1·0	1·5	2·4

After removal of the coverings of the grain of wheat, the cellulose cells are burst

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[1] Munk, *op. cit.* p. 264.

by grinding and the contents are reduced to the powder called *flour*. This contains about 65 to 70 per cent. of carbohydrates and 10 to 14 per cent. of albumin. The coverings of the grain still contain some albumin and starch and constitute *bran*, a substance used in the feeding of cattle. The bran of wheat contains 14·1 per cent. of water, 13·5 per cent. of albumin, 2·5 per cent. of fat, 31·6 per cent. of carbohydrates, and 30·8 per cent. of fibrous matter, almost indigestible even by herbivora.

Bread is made by the mixture of wheat flour with water to form dough. This is also mixed with a small amount of yeast and allowed to ferment at a temperature of 30° C. Fermentation changes a portion of the starch first into dextrin and afterwards into carbonic acid, with a trace of alcohol. The evolution of gas makes the dough looser in texture. Further fermentation is arrested by baking the bread in an oven at a higher temperature, and the gas in the bubbles diffused through the dough expands and makes the bread friable, breaking it into irregularly shaped masses, and thus by increasing the surface, making it more readily acted on by the digestive juices. A still higher temperature forms the brown crust by the removal of water. White bread contains in 65 parts about 7·1 of albumin, 1 of fat, 55 of carbohydrates and 1 of salts. An adult would require about 1·6 kilogramme of bread to supply the requisite amount of proteid matter. The quantity may be reduced if the bread is combined with meat and fat or butter. Thus an excellent diet is formed by 350 grms. of meat, 500 grms. of bread, and 100 grms. of butter or fat. Maize and rice are poor in albumin but rich in carbohydrates. They are therefore not so nutritious as wheat-flour, or oatmeal. Barley and oats also furnish excellent food products on account of their combination of albumin and carbohydrates. Oats constitute a good element of diet for horses.

Next to the cereals, *leguminous plants* furnish valuable articles of food. The flour or meal of peas, beans, and lentils contains much albumin, and it is stated that as much as 85 per cent. of this is capable of being digested. Potatoes are less valuable because they contain only a small amount of albumin, and one third of this is undigested. The following table shows the percentage composition of the common leguminous seeds and potatoes :—

TABLE XIV.

	Lentils.	Peas.	Beans.	Potatoes.
Water, - - -	12·5	14·3	14·8	76·0
Albumin, - -	24·8	22·6	23·7	2·0
Fat, - - -	1·9	1·7	1·6	0·2
Carbohydrates, -	54·8	53·2	49·3	20·6
Woody fibre, - -	3·6	5·5	7·5	0·7
Ash, - - -	2·4	2·7	3·1	1·0

As rice and potatoes are so deficient in albumin, it has been estimated that no less than 1·9 kilogramme of rice and 4·5 kilogrammes of potatoes must be consumed to supply to an adult man the necessary amount of albumin. With such a diet, not only is the bulk of the food far too great, but from the preponderance of carbohydrates, acid fermentations may occur in the digestive canal and cause diarrhœa. To form a proper diet with rice or potatoes one must add something containing albumin, such as fish, herring, or cheese or buttermilk.

Garden vegetables cannot be regarded as highly nutritious substances but they are useful adjuncts to diet, and as they are rich in salts of potash they form an excellent combination with salted meats, in which these salts are deficient. Cabbage, turnips, and asparagus contain in percentages 80 to 92 of water, 1 to 2 of albuminous matter, 2 to 4 of carbohydrates, a small amount of sugar, and from 1 to 1·5 of cellulose. The following table by Munk illustrates the principles of dietetics by showing the percentage composition of the green food of herbivora :—

Table XV.

	Grass.	Red Clover.	Meadow Hay.	Common Rye Grass.	Good Rye Straw.
Water,	75·0	78·0	13·0	18·6	13·8
Albumin,	3·0	3·5	9·5	1·5	3·9
Fat,	0·8	0·8	3·1	1·5	1·0
Carbohydrates,	13·1	8·0	40·9	32·4	34·7
Woody fibre,	6·0	8·0	26·7	43·0	40·1
Ash,	2·1	1·7	6·8	3·0	6·5

This table shows that the food of herbivora contains the same proximate constituents as that of carnivora, and it accounts for the large quantities of grass, etc., that must be consumed by a bulky herbivorous animal to supply its body with the requisite amount of the proximate principles. A herbivorous animal receives in its daily food from 5 to 12 times more of salts of potash than of salts of soda. Bunge has shown that this explains the desire all herbivorous animals manifest for common salt. He suggests that carbonate, phosphate, and sulphate of potash at the temperature of the body react on chloride of sodium so as to form carbonate, sulphate, and phosphate of soda and chloride of potassium. This reaction occurs in the blood and the salts of soda thus formed are eliminated by the kidneys. There is thus a daily demand for a larger amount of chloride of sodium than is supplied in the food of herbivora, and the animals therefore instinctively crave for this substance and readily lick blocks of rock salt that may be placed beside them.

Alimentary substances are rarely in a natural condition suitable for consumption, but they require in the first instance to be prepared by *cooking*, which transforms them in such a manner as to render the action of the digestive fluids more easy and certain, while at the same time sapidity or flavour is given to the dish. Water, heat, and condiments are the principal agents employed in the preparation of food. Water softens insoluble matters, whilst it dissolves all those which are soluble, as in soups. Heat affects alimentary matters, and according as it is applied quickly or rapidly, or is obtained from an open fire, from vapour, or from infusion in salted water, food acquires different characters which please the taste and thus promote alimentation. Cooking separates assimilable from non-assimilable matters ; it renders the food more accessible to the digestive fluids ; it fits the salts and other soluble matters of food for rapid absorption ; it may also condense alimentary substances into a small volume, as in concentrated beef-tea; and, finally, the condiments employed in cooking gratify the taste and excite the flow of digestive secretions.

CHAP. III.—HUNGER, THIRST, STARVATION, AND MODIFIED DIETS.

The sensation of *hunger* is referred to the stomach, and it may be at least temporarily relieved by the introduction into that organ of matter that is even not nutritious. Hence it would appear that it depends on an excitation of the sensory nerves of the stomach (the pneumogastrics) and possibly of other portions of the intestinal canal. It is well known that the sensation of hunger may be appeased by the introduction of nutritious food directly into the small intestine by a fistulous opening, by the use of nutritive enemata, and by the ingestion of nutritious substances, such as solutions of peptones, highly concentrated and so small in bulk as to distend the stomach only to a slight degree. The latter facts indicate that hunger may be the result partly of impressions derived from the stomach and partly of a fusion of indefinite sensations caused by impressions from organs partially exhausted from a want of nutritious matter. The sensation must also depend to some extent on the condition of the central nervous organs, as section of the vagi does not remove it. Alcohol, tobacco, and various narcotics diminish and restrain for a considerable time the acuteness of hunger, and it is also well known that certain psychical states have the same effect. In these instances, the influence is probably exerted upon the central, and not the peripheral, origin of the nerves of the stomach. The beginning of the sensation of hunger is termed *appetite*, and is agreeable, but as the sensation increases in intensity it becomes painful, and there are feelings of pinching, torsion, or of ill-defined uneasiness referred to the region of the stomach.

Thirst is a local sensation resulting from a dry condition of the mucous membrane of the posterior wall of the pharynx, which is supplied with filaments from the pneumo-gastric, glosso-pharyngeal, and trigeminal nerves. Division of these nerves, however, does not remove the sensation. When the dry condition is removed even by occasional moistening, thirst is for the time relieved. The dryness may result either from a general diminution of the amount of water of the blood; from the action of certain substances, such as atropine, which arrest secretion from mucous surfaces; or from fear or excitement. The sensation may be removed by the direct injection of water into the blood, or into the alimentary canal, or even temporarily by immersion of the body in water.

The length of time a human being may exist without food or drink cannot be precisely stated, as it is evident that much will depend on the amount of waste going on in the body during the time, the amount of oxygen in the air, the surrounding temperature, and the age of the person. In some circumstances men may pass into a condition somewhat similar to the hybernating state of certain animals, when the amount of waste going on in the body is reduced to a minimum. Thus Indian Fakirs, under the influence of opiates or of Indian hemp, have remained without food, in a state of trance, for even six weeks. Under ordinary circumstances, complete abstinence from food and drink cannot be supported beyond the eighth or tenth day, although there are exceptional cases on record where life was sustained for thirty or forty days with no food, only water being taken. In these exceptional cases the individuals had in a sense acquired a habit of long continued abstinence, and this was aided by the state of mental and bodily quietude in which they spent the time of their voluntary fast. The total deprivation of food in the case of man usually causes death in the third week. Young animals perish sooner than adults; and fat animals will live longer than lean animals. Cold-blooded animals may live without food for many months. Frogs have lived for nine or ten months. With a supply of water, life may be prolonged for a considerable time even with an exceedingly small quantity of solid food, or even with no food, and an animal will live longer upon water alone than on any other proximate principle of food in a dry state. Thus Chossat found that dogs supplied with plenty of water, but without food, lived three times as long as those that were deprived of solids and liquids at the same time.[1] In a confined space saturated with aqueous vapour, men have lived ten days without either food or drink. It is remarkable that supplying the stomach with even a portion of the fluids or solids of the starved animal's body will tend to prolong life. Thus Anselmier preserved the lives of dogs by feeding them with their own blood daily, and life was thus prolonged till the fourteenth day; whereas in Chossat's experiments the animals died in similar conditions on the tenth day.[2] The complete deprivation of water will usually destroy life in eight or ten days, and even after the third day its absence is the cause of horrible distress.

Dogs may live without food or drink for four weeks, and horses and cats for three weeks. It is remarkable that small mammals, such as the guinea-pig and rat, may survive total deprivation of food for only from three to nine days, while

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[1] Chossat, *Sur l'Inanition.* Paris, 1843.

[2] Anselmier, *Archiv. Générale de Médicine*, 1860, vol. i. p. 169.

rabbits may live till the nineteenth day. With a supply of water, horses have been known to survive for four weeks and dogs for nine weeks.

Individuals are met with occasionally who have an excess of appetite, a condition termed *bulimia.* This may occur in certain diseases, as, for instance, in diabetes, and it is frequently seen in the convalescent stage of fevers. In some rare instances it appears to be the normal state of the person. Thus Captain Parry, the celebrated Arctic explorer, narrates an instance of an Esquimaux who, on one occasion, and apparently as a common exploit, in twenty-four hours, devoured 35 lbs. of meat and a number of tallow candles. Twenty pounds of meat in a day is a usual allowance for an Esquimaux, and it is said that the labourer in a Spanish vineyard consumes daily between 8 and 9 lb. avoird. of vegetable food, consisting of bread, onion porridge, and grapes. A still more remarkable case is that of Tarrari, a French soldier, whose appetite was so voracious as to lead to his dismissal from the army. Tarrari's case was one of undoubted disease, and it is remarkable that he died an emaciated miserable man, but he had to the last an undiminished appetite.

On the other hand, the minimum quantity of food required by each individual, in the performance of the active duties of life, cannot be precisely stated, as much depends on idiosyncrasies of constitution and on habit. Many men have led active lives on comparatively small quantities of food, and, judging from the great prevalence of diseases of the digestive organs, it is probable that many persons consume more food than they require. Improper food, excess of food, and irregularity in taking food, are common causes of dyspepsia, and of other forms of gastric derangement.

When an animal or a human being is *starved*, the body loses weight from the rapid using up of certain of the tissues. The organs necessary for the maintenance of life require nutritious matter, and if this is not supplied from without, it is obtained from the tissues of the body itself. Not only does the body lose weight as a whole but those organs in which active nutritive changes occur lose weight more rapidly than those in which such changes are slow. This is illustrated by the following table showing the results obtained by Chossat and Voit. It gives the loss of weight per cent. of different tissues and organs :—[1]

	Chossat.	Voit.
Fat, - - - - - -	93·3	97·0
Blood, - - - - - -	75·0	27·0
Spleen, - - - - - -	71·4	66·7
Pancreas, - - - - -	64·1	50·0
Liver, - - - - - -	52·1	53·7
Heart, - - - - - -	44·8	32·6
Muscles, - - - - - -	42·3	30·5
Kidneys, - - - - - -	31·9	25·9
Bones, - - - - - -	16·7	13·9
Nerve centres (brain, spinal cord),	1·9	9·2

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[1] Beaunis, *op. cit.* t. ii. p. 879.

Fatty matters previously stored in adipose tissue quickly disappear and the emaciated appearance is largely owing to this absorption of fat. No doubt the blood will suffer at an early stage, and as its albumin and other nutritious matters are used up by the tissues, their place is taken by absorption of similar matters from the wasting tissues. The secretions diminish in amount, the urine becomes acid, even in herbivora, from an increased amount of acid phosphates and sulphates, and the amount of urea steadily diminishes; the blood becomes less watery, and the amount of serum albumin is much diminished. Respiratory changes are less active, less carbonic acid is exhaled, tissue oxidations are less active, and, as a consequence, the bodily temperature falls. Chossat found that a warm-blooded animal lost about ·3° C. daily during starvation. The power of the muscular tissues is diminished, and all of these, including the muscular tissue of the heart and of the hollow viscera, become thinner and even undergo fatty changes. The nervous centres are also weakened, producing disorders of intelligence.

A cat that died of starvation on the eighteenth day was found to have lost 48·58 per cent. of its weight, and of this loss 8·26 per cent. consisted of albumin, 5·38 per cent. of fat, and 34·94 per cent. of water. It was also observed in this case that the amount of urine passed diminished to about 13 per cent., the urea to 9 per cent., the saline matters in the urine to 13 per cent., the fæces to 25 per cent., the carbon given off by the lungs to 43 per cent., and the water to about 14 per cent. of the amounts separated at the beginning of the observations.[1]

Such being the general phenomena that follow total deprivation of food, we may now consider the effect of deprivation of one or other of the proximate constituents, or, in other words, the effects of *modified dietaries.* When an animal receives no *water*, the secretions, especially that of the kidneys, are arrested, and, as already pointed out, death will soon occur. The effects following the removal of *saline matters* from the food have already been described (p. 16). If no *proteid matter* is given, one of the most marked effects is a great fall in the amount of urea excreted. This fall is more marked if carbohydrates exist in the diet, with the absence of albumin, than if fats are given. The diminution in the amount of urea shows, that with such a diet, metabolism of albuminous tissue is less active, and it is remarkable that in these circumstances less urea is excreted than if the animal received no food at all. One explanation suggested is that the carbohydrates and fats are readily oxidized and so use up the oxygen supplied to the body that less is available for the proteids, and that as carbohydrates are more

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[1] Bidder and Schmidt, *Die Verdauungssäfte*, 1852. The figures given above have been calculated from those registered by these observers.

easily oxidized than fats, they are used first and protect the proteids to a greater extent than the fats are able to do.

A diet containing *gelatin* alone will not support life. Its ingestion increases the amount of urea in the urine, if an enormous amount is given, but if given alone in small quantity, the amount of urea is diminished. It appears to protect other proteids from oxidation in a manner analogous to carbohydrates and fats. Thus Voit found, in the case of a dog, that on a diet of 500 grms. of flesh with 200 grms. of lard per day the animal lost 136 grms. of weight, but in the same time it only lost 84 grms. with a diet composed of 300 grms. of flesh, 200 grms. of lard, and 100 grms. of gelatin, and it lost only 32 grms. when 200 grms. of gelatin were given instead of 100 grms.

Suppose, in the next place, that no *carbohydrates* are given, and that proteids are alone supplied. In these circumstances, the health of herbivora soon suffers, as their digestive organs are not suited for albuminous food, but carnivorous animals will live in a state of health, for a considerable time, on a pure albuminous diet, along with water. Strictly speaking, even a dog, with a purely albuminous diet, can maintain its body in a state of equilibrium for only a short time. Thus Pettenkofer and Voit kept a dog, weighing 30 kilogs., *in statu quo* for forty-nine hours, on a diet of 1500 grms. of lean meat per twenty-four hours. This was a diet equal to ·05 of its own weight. If fat be supplied, the animal, in such circumstances, will maintain its equilibrium on less albuminous food, and it will keep in sound health.

These statements as to the influence of a diet of albumin, as modified by the presence or absence of *fats*, are well illustrated by the following table showing, in grammes, the results of an experiment by Pettenkofer and Voit, on a dog weighing 30 kilogrammes.

Amount of flesh given.	Amount of fat in food.	Amount of albumin metabolized, calculated from urea, etc., eliminated.	Albumin gained + or lost − by body.	Amount of fat metabolized, calculated from CO_2 eliminated.	Fat gained + or lost − by body.
400	200	449·7	− 49·7	159·4	+ 40·6
500	100	491·2	+ 8·8	66·0	+ 34·6
500	200	517·4	− 17·4	109·2	+ 90·8
800	350	635·0	+ 165·0	135·7	+ 214·3
1500	30	1457·2	+ 42·8	...	+ 32·4
1500	60	1500·6	− 0·6	20·6	+ 39·4
1500	100	1402·2	+ 97·8	8·8	+ 91·1
1500	150	1455·1	+ 41·8	14·3	+ 135·7

A glance at this table shows that when a small amount of fat was given with the albumin, a large amount of albumin was decomposed and the body gained little albumin, or even lost it. On the other hand, when a large amount of fat was given along with albumin, there was a considerable increase in the amount of albumin stored up, and along with this a large increase in the amount of stored-up fat. If fatty acids are given instead of fats, albuminous metabolism is diminished, as if fats had been taken, and it is supposed that, in these circumstances, fat may be formed synthetically in the body, by union of the acids with glycerine. Glycerine does not influence metabolism of proteids in small doses, but in large doses it increases such metabolism. It is partly oxidized into carbonic acid and water, and about 20 per cent. of it may be eliminated by the kidneys.

The results of similar observations by Pettenkofer and Voit, on the influence of carbohydrates on an albuminous diet in the case of the dog, are shown in the following table, which is also very instructive. The figures represent grammes.

Amount of flesh given.	Amount of carbohydrate in food.	Amount of albumin decomposed, calculated from urea, etc., eliminated.	Albumin gained + or lost − by body.	Amount of fat decomposed.	Fat gained + or lost − by body.	Amount of carbohydrates decomposed.
400	250	436	−36	18	−8	210
400	250	393	+7	25	−25	227
400	400	413	−13	25	+45	344
500	200	568	−68	25	+25	167
500	200	537	−37	25	+16	182
500	200	530	−30	25	+14	167
800	450	608	+182	25	+69	379
1500	200	1475	+23	25	+47	172
1800	450	1469	+331	25	+122	379
2500	0	2512	+12	25	+57	0

This table also shows that when a large amount of carbohydrate is given along with albumin, less albumin is decomposed and more is stored up. A large amount of carbohydrate also causes an increased storage of fats.

These facts are of great practical importance although no adequate explanation can yet be offered. They show that a *mixed* diet is the most advantageous for the body. If a certain amount of flesh is given in a diet to meet the requirements of the body, less will be necessary if combined with fat, and still less if combined with carbohydrates.

Chap. IV.—THE GENERAL STRUCTURE OF GLANDS.

Having discussed the nature of food and various questions in practical dietetics, we next proceed to consider the changes which the food undergoes in the process of digestion, and, in the first place, we will take a survey of the histological structure of the digestive canal. As we find in the digestive tract many glands engaged in secreting the digestive fluids, it is important to consider the general structure of secreting organs, and thus avoid repetition in describing the structure of special glands. The internal surface of the intestinal canal, of the respiratory passages, and of certain regions of the uro-genital system is composed of a soft, moist layer, the *mucous membrane*, or *tunica mucosa.* It consists of epithelium and connective tissue. The latter is condensed under the epithelium so as to form a structureless membrane, the *membrana propria*, or *basement membrane*, below which is a looser layer called the *tunica propria*, which gradually merges into the loosely woven connective tissue called the *tunica submucosa.*

Glands are developments of the mucous membrane. They are hollow inversions of the epithelial surface into the underlying connective tissue, and at the beginning of their formation they take the form of simple tubes closed at the inner end. Some glands retain this form, while others become so modified as to have a number of recesses or pouches, termed *acini.* The two chief types of gland structure are the tubular and the racemose (Fig. 1, after Sharpey).

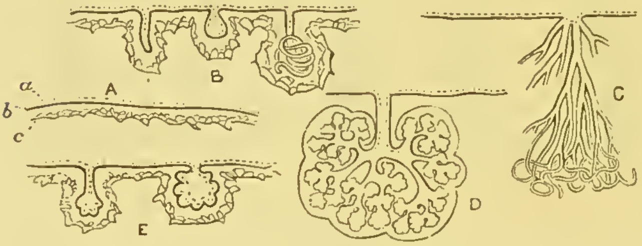

Fig. 1.—Diagram showing the various forms of secreting structures: A, general plan of a secreting membrane; *b*, basement membrane, or membrana propria with cells, *a*, on one side and blood-vessels, *c*, on the other; B, simple *tubular* (gastric glands), *follicular* or *saccular* and *elongated tubular* or *convoluted* glands (sweat glands); C, *compound tubular*, as in kidney; D, *compound racemose*, as in salivary glands, pancreas, etc.; E, simple gland with loculated walls, two forms, as in sebaceous glands of skin, etc.

The *tubular glands* may be (1) *simple tubes*, which are either short blind tubes, as, for example, the glands of Lieberkühn (Fig. 1B), or longer tubes, often coiled at the lower end, as found in the sweat glands of the skin (Fig. 1B). Sometimes also a number of tubes may be connected with one duct, and the tubes may vary much in length, from the short glands of the pylorus to the elongated tubes of the kidney (Fig. 1C).

The *racemose glands* are always ramified, but we may distinguish among them (1) *simple racemose glands*, having few ramifications or acini, as in the glands of the mucous membrane of the nose, and (2) *compound racemose glands*, where there are numerous acini clustered round a duct or ducts, giving rise to an appearance like a bunch of grapes, as in the submaxillary gland.

Some glands have in their walls shallow hemispherical depressions, as seen in Brunner's glands found in the duodenum. These depressions may be regarded as shallow acini, and hence they may be classed among racemose glands, or they may be looked on as very short tubes, and if this view be taken, such glands must be placed among tubular glands.

In the majority of glands, especially those visible to the naked eye, septa of connective tissue penetrate into the gland, dividing it into lobules. These septa support the blood-vessels and nerves. Each gland may be said to consist of the part of the gland in which secretion takes place and of a duct or tube opening on the surface of the mucous membrane.

The *acinus* of a gland consists of a layer of epithelial cells, the *gland* or *secreting cells*, which surround the lumen or central space of the acinus, and rest on a peculiar modification of connective tissue, a *membrana propria*, or basement membrane. On the outer side of this membrane the blood-vessels ramify (Fig. 1). Sometimes numerous stellate nucleated cells may be found outside the basement membrane, or even in place of it, their processes embracing the acini. Between the lumen of the gland and the blood-vessels the gland cells are arranged in a layer, so that on the peripheral side the cells draw from the blood-vessels, or from the lymph-fluid that has exuded from these, materials required for the formation of the secretion, and on the side next the lumen or centre of the acinus they give up the secretion either by a process similar to exudation or by bursting of the cell (Fig. 2). The cells of glands change their appearance according to the stage of the secreting process. (See Vol. I. p. 297.) In some glands all the cells show the same appearances at the same time, but in others, and even in the acinus, they may be found exhibiting different stages, some cells containing secretion, while others are in the resting state (Fig. 4). The cells containing secretion force away from the lumen of the gland those containing none, so that the latter lie on

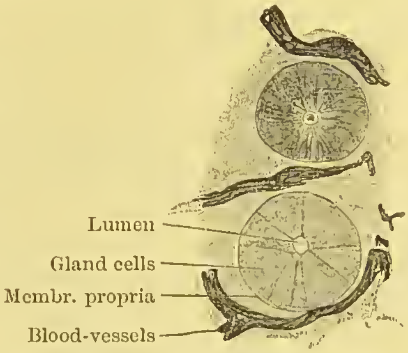

FIG. 2.—Transverse section of two of Lieberkühn's glands from the small intestine of the rabbit, seen from above. × 240 d. [Method No. 1, Appendix.)

the periphery of the acinus, showing halfmoon-like forms, and a group of these compressed cells form a mass called the *crescent* or *lunula of Gianuzzi*, or they may be termed *marginal cells* (Figs. 3 and 4).

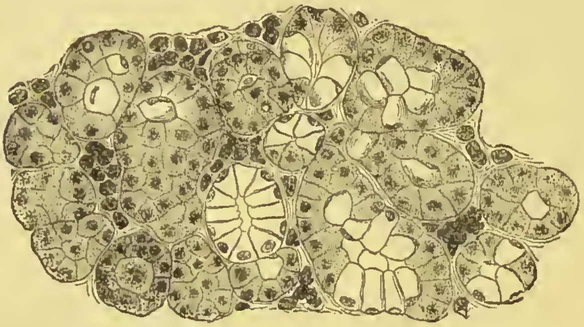

FIG. 3.—Sublingual gland of dog, a mucous gland showing clear cells full of mucigen, and finely granular cells, devoid of mucigen.

The *ducts* of glands contain a kind of epithelium different from that of the gland proper, and these epithelial cells are devoted to the secretion of certain substances, such as saline matter or mucus, which constitute part of the secretion of the gland. Two or more kinds of *duct-cells* may be observed: (1) where the duct, springing from the acinus, is narrow (sometimes called the *intercalary portion*), and lined with clear flattened cells having elongated nuclei; (2) this is succeeded by a still narrower portion lined with cubical cells; and (3) where the duct is wider the cells are more columnar or cylindrical. The part of the cell next the lumen is granular, while the part attached to the *membrana propria* shows a fine longitudinal striation, as shown in Fig. 5. The first portion of the duct has less to do with secretion than the third portion, having cylindrical cells. The

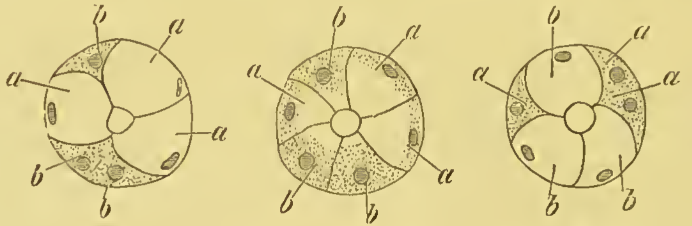

FIG. 4.—Diagram showing the formation of semi-lunar forms. I. Acinus of a mucous gland with gland cells. Three of these contain secretion, *a*, *a*, *a*, and the secretionless gland cells, *b*, *b*, *b*, have been forced from the lumen of the gland towards the periphery. II. The same acinus at a somewhat later stage. The cells *a*, *a*, *a*, have partly discharged their secretion and have become smaller. The cells *b*, *b*, *b*, again begin to form secretion, and as they have become larger they encroach on the lumen. III. The same acinus at a still later stage. The cells *a*, *a*, *a*, are now destitute of secretion, and are forced from the lumen by the growth of the cells *b*, *b*, *b*, now filled with secretion. In I. the cells *b* and in III. the cells *a* are semilunar.

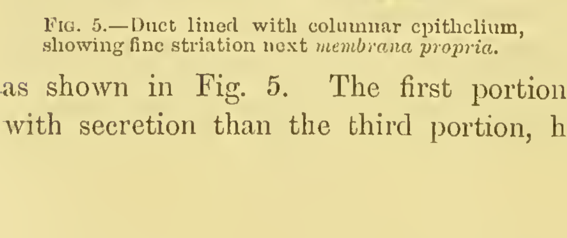

FIG. 5.—Duct lined with columnar epithelium, showing fine striation next *membrana propria*.

larger ducts consist of a layer of simple cylindrical epithelium resting on a layer of connective tissue, in which elastic fibres are interspersed. A fully formed gland may therefore consist (1) of the larger ducts, which divide and subdivide so as to give origin to (2) medium-sized ducts (interlobular), and these are continued onwards into (3) the smallest ducts which open into the acini (intercalary). The distinction to be drawn between mucous and serous glands will be pointed out in treating of the glands of the tongue and the salivary glands.

The nucleated cell of the acinus plays an important part in the process of secretion. It consists, according to Langley, of (1) a framework or network of living protoplasm, (2) a hyaline substance in contact with the framework, and (3) spherical granules embedded in the substance of the hyaline matter.[1] The cell selects matters from the nutritive pabulum supplied by the capillary vessels, and it elaborates these into a more complex substance stored up for a time in the cell. If the cells in a mucous gland have been at rest for some time they may show in their interior a substance somewhat resembling the secretion, but if they are exhausted by excessive stimulation no secreted matters may be found in the cells, and they will therefore present a different appearance from what they do during rest. These facts are illustrated by Figs. 6, 7, 8, and 9, showing the appearances found by Lavdofsky in the orbital gland of the dog at different stages. This gland is a so-called mucous gland because it secretes a fluid rich in mucin. Thus, in Fig. 6 most of the cells in the alveoli are large and clear, and show few granules. They now contain a large amount of mucigen (a substance from which mucin is derived), their protoplasm is not visible, and the nuclei are pushed towards the attached base of the cells. At this stage these cells

FIG. 6.—Orbital gland of dog during rest. Observe the large clear cells containing mucigen, and the dark groups of cells forming the lunulæ of Gianuzzi.

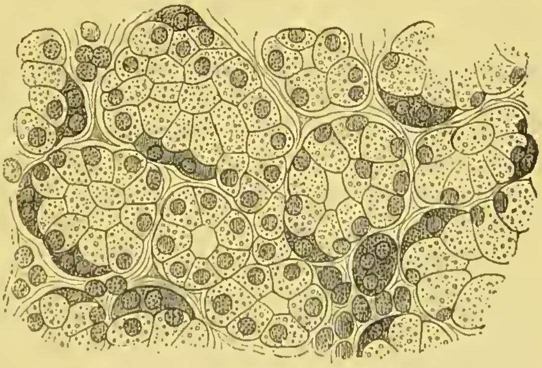

FIG. 7.—Orbital gland of dog, shortly after the beginning of stimulation.

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[1] Langley, "On the Structure of Secreting Cells," *Proceedings of Cambridge Philosophical Society*, vol. v.

do not stain with carmine. Some of the cells in the acinus, however, are not engaged in secretion. These are smaller, darkly granular, and they are pushed to one side by the secreting cells, each group forming a *crescent of Gianuzzi*. Such cells contain no mucigen, and hence their protoplasm stains readily with carmine. If one of the nerves of the gland be now stimulated slightly the cells begin to change as seen in Fig. 7. The mucigen appears to escape, and is then changed into mucin, the cell contracts, its nucleus becomes more rounded, and is now found away from the attached part as if it were moving towards the centre of the cell. Stronger stimulation is followed by the almost entire disappearance of the mucinaginous clear cells, both alveoli and cells are smaller, the protoplasm of the cell is now more apparent, the nuclei are in the centre of the cell, and both they and the protoplasm are stained by carmine. After a long period of stimulation the cells show the appearance seen in Fig. 9; they are now highly granular. If the stimulation ceases, the cells again begin to store up mucigen and gradually regain the appearance depicted in Fig. 6. Stöhr supposes that the granular cells are simply cells which have shed their secretion, while Heidenhain holds that they are developed from the cells forming the crescents of Gianuzzi. The view taken by Langley seems the most consistent with fact. From observations made on the cells of the pancreas, Langley concludes that the formation of secretion, the growth of protoplasm, and the discharge of the secreted product from the cell may go on at the same time. He observed that during the secretion of a gland that forms a fluid containing albuminous matter (a so-called serous or albuminous gland, like the parotid or the pancreas), the cells became very granular, and that the granules were apparently dissolved off the border of the cell next the lumen, and thus contributed to the secretion. During active secretion the three elements of the gland cell, according to Langley, undergo changes; the granules decrease in size and in numbers, the hyaline matter increases, and the protoplasmic network also increases. The hyaline matter increases most in the outer or attached region of the cells. The granules disappear from this region. Thus there is seen an inner and an outer granular zone. The meshes of the network in the outer zone are filled with

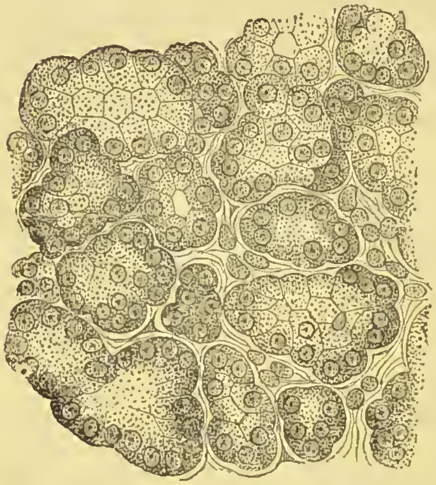
FIG 8.—Orbital gland of dog after stronger stimulation and a period of activity.

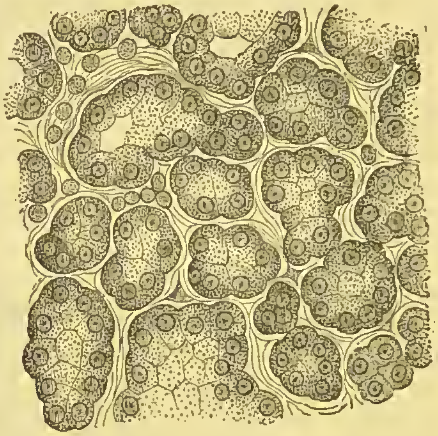
FIG. 9.—Orbital gland of dog after still stronger stimulation. The cells have now become exhausted.

hyaline matter, while those of the inner (next the lumen) contain granules. In tracing the appearances of the glands in a number of animals, many intermediate conditions are found indicating a transition from the protoplasmic network to the hyaline matter. It is probable that the protoplasm forms the hyaline matter, and that this in turn gives rise to the granules. After long continued action the granules disappear, and the substance of the cell is clear and transparent. There is thus a marked optical difference between what occurs in a serous from that which happens in a mucous gland. In the mucous gland the secretion renders the cells clear and transparent, while after prolonged stimulation and discharge of the secretion the cell is granular; but in the serous the cell becomes more granular near the free border during activity, and is only transparent after prolonged stimulation. The difference, however, depends on the nature of the substance found in the cell during secretion, and not on any fundamental difference in the process. In both classes of cells new matter is formed at the expense of the protoplasm of the cell, and in the one case the matter assumes a granular form, while in the other it is clear and transparent. Langley regards the granules as *mesostates*—"that is, substances stored in the cell and destined to give rise to the organic substances of the secretion."

CHAP. V.—THE MOUTH, TEETH, AND TONGUE.

The mucous membrane of the cavity of the mouth consists (1) of epithelium, (2) of a *tunica propria*, and (3) of submucous tissue. The *epithelium* is formed of stratified layers of pavement epithelium. The *tunica propria* contains bundles of connective tissue, richly intermingled with elastic fibres. The bundles of the uppermost layer are fine and form a dense fretwork, so dense as to be almost homogeneous. On the upper surface of the *tunica propria* we find numerous papillæ, usually simple (Fig. 10), the length of which varies in different parts of the mouth. The longest (·5 mm.) are found on the margin of the lips and gums. The *tunica propria* merges into the *submucous tissue*, which is formed of broader bundles of connective tissue, containing few elastic fibres. The submucous tissue is firmly connected with the periosteum only on the hard palate and on the gums. In this tissue we find numerous glands. These are racemose mucous glands from 1 to 5 mm. in breadth. Their duct (Fig. 10, 2) is wider at its lower end, and it is lined through the greater part of its length with stratified epithelium. The smaller branches springing from it are lined by stratified cylindrical epithelium, and the smallest branches have a single layer of cylindrical cells. We also sometimes find the chief duct receiving the ducts of small accessory glands of the mucous membrane (Fig. 10, 3). The structure of the acini will be described along with the mucous glands of the tongue. The *vessels* in the mucous membrane of the mouth are found in two networks, one, the coarser, in the submucous tissue, and the other, more delicate, in the *tunica propria*. From the latter loops pass up into the papillæ. *Lymphatic* networks also exist in the submucous tissue, and a few lymphatic vessels are found in the *tunica propria*. A wide meshed network of medullated *nerve fibres* is found in the submucous tissue, and from these meshes delicate nervous twigs pass into the *tunica propria*. These end in Krause's end bulbs, or, after losing the white substance of Schwann, they penetrate into the epithelial layer, where, after repeated divisions, they end as free fibres.

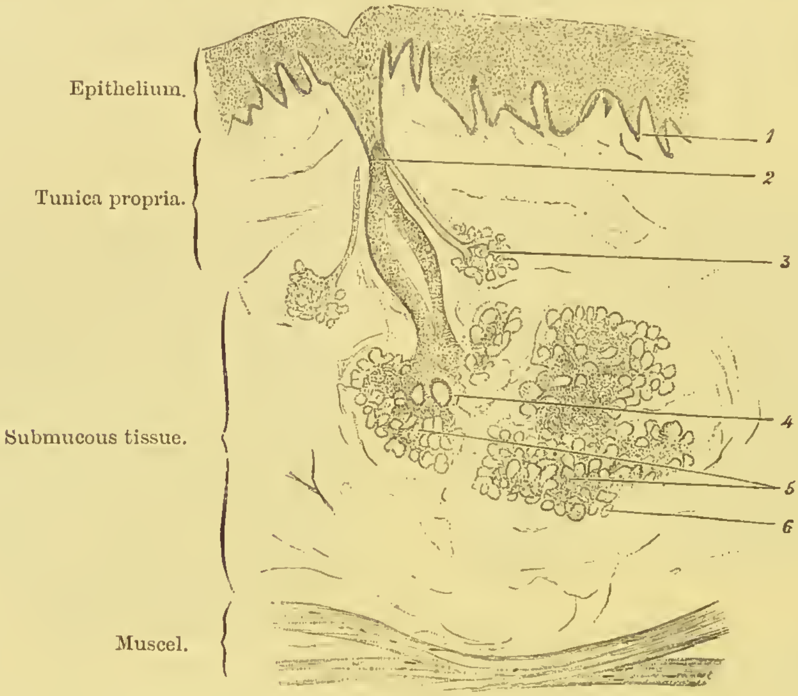

FIG. 10.—Vertical section through the mucous membrane of the lips of an adult man. × 30 d. (1) Papillæ. (2) Duct of gland. (3) Accessory gland. (4) Transverse section of a small duct. (5) Gland divided into lobules by connective tissue. (6) An Acinus. (Method No. 2, Appendix.)

A. THE TEETH.

The teeth in man are developed in two sets, a first, known as the temporary, deciduous, or *milk* teeth, and a second set, called the *permanent* teeth. The formulæ for the two sets are as follows—

Milk Teeth, $M.\,\frac{2}{2}\quad C.\,\frac{1}{1}\quad I.\,\frac{4}{4}\quad C.\,\frac{1}{1}\quad M.\,\frac{2}{2} = \frac{10}{10} = 20$

Permanent Teeth, $M.\,\frac{3}{3}\quad Bic.\,\frac{2}{2}\quad C.\,\frac{1}{1}\quad I.\,\frac{4}{4}\quad C.\,\frac{1}{1}\quad Bic.\,\frac{2}{2}\quad M.\,\frac{3}{3} = \frac{16}{16} = 32$

in which *M.* represents molars, *Bic.* bicuspids, *C.* canines, and *I.* incisors.

The following table gives the dentition of some of the domestic animals—

	I.	C.	Bic.	M.
Dog, - - -	12	4	4	24
Cat, - - -	12	4	...	14
Pig, - - -	12	4	4	24
Horse, - - -	12	4	...	24
Ruminants, - -	8	...	...	24

Among horses, only stallions have canine teeth. In ruminants, the 8 incisor teeth exist in the lower jaw, and there are no incisors in the upper jaw.—(Munk.)

Each tooth shows a portion above the gum termed the *crown*, a part in the gum, the *fang*, and at the junction of these there is a constricted portion called the *neck* or *cervix*. The incisor teeth have their wide chisel-shaped crowns, convex in front and sometimes furrowed. The canines have long pointed crowns, convex in front and hollowed behind, and the upper canines, or eye teeth, are larger and longer than the lower ones. The canines are very large and prominent in feline animals. The bicuspids, sometimes called pre-molars, show two pointed cusps or tubercles in the crowns. The molars have a large cuboidal crown showing four cusps in the case of the upper molars, and five cusps in that of the lower molars. By these cusps a grinding or triturating surface is formed. The row of teeth in each jaw forms the dental arch, and in man the upper overlaps the lower dental arch when the jaws are brought together. In man there is no hiatus or gap in the row of teeth.

The milk teeth begin to appear about the seventh month, and they have all cut the gum by the end of the second year. The milk teeth appear in the following order—the lower middle incisors appear first, about the seventh month, the upper incisors in the ninth month, the anterior molars in the twelfth month, the canines in the eighteenth month, and the posterior molars in the twenty-fourth month. The teeth of the lower jaw usually appear before the corresponding teeth of the upper jaw. The milk teeth are succeeded by the permanent teeth in the following order—the central incisors from the fifth to the seventh year, the anterior molars also from the fifth to the seventh year, the lateral incisors from the seventh to the ninth year, the anterior bicuspids from the eighth to the tenth year, the canines from the ninth to the twelfth year, the posterior bicuspids from the tenth to the twelfth year, the middle molars from the twelfth to the fourteenth year, and the posterior molars, or wisdom teeth, from the seventeenth to the twenty-fifth year. When a child is five years of age, the jaw contains more teeth than at any other period of life, for at that time all the permanent teeth, except the wisdom teeth, are developed in addition to the milk teeth.

We shall next consider the structure of a tooth. It consists of certain hard materials surrounding a cavity, the *pulp cavity*, filled with a soft mass, the *tooth pulp*. The hard parts are formed (1) of *dentine*, (2) of *enamel*, and (3) of *cement* or *crusta petrosa*. The dentine forms the chief mass of the tooth and determines its form, it surrounds the pulp cavity and also a canal in the fang of the tooth through which blood-vessels and nerves pass to the pulp. The dentine is covered with a cap of enamel, while the *crusta petrosa* clothes the fang, so that dentine is not freely exposed to view (Fig. 11).

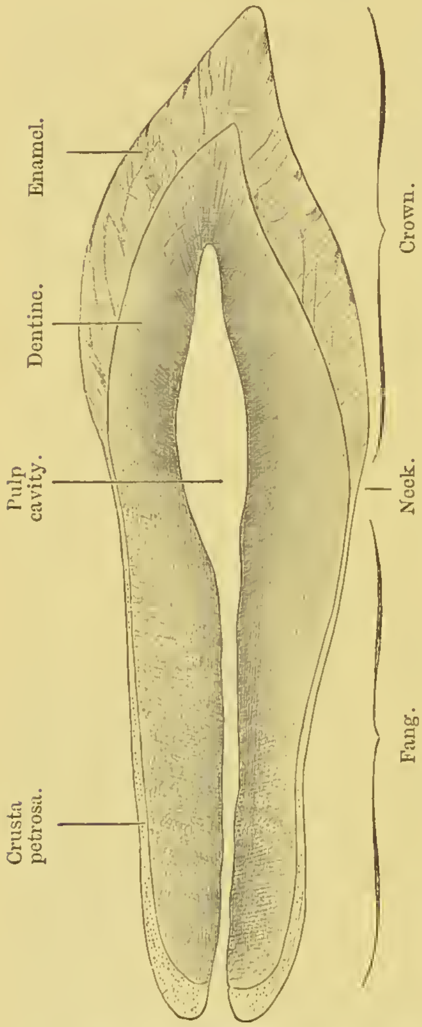

FIG. 11.—Longitudinal section of a human incisor tooth. × 4 d. (Method No. 3, Appendix.)

Dentine is a white opaque matter harder than bone. It consists of a homogeneous matrix, which is traversed by numerous small canals, the dentine tubes (Fig. 12, 2). These begin on the surface of the dentine next the pulp cavity with a diameter of 25 μ, and they radiate outwards towards the outer surface of the dentine. At the beginning of their course the tubes divide once or twice, and, much diminished in calibre, they end either in delicate tubes at the boundary of the enamel, or they bend round and end in neighbouring canals, so as to form a loop. Throughout their course they give off delicate lateral branches which anastomose with those of adjacent tubes. The matrix immediately surrounding the canals is very dense and forms sheaths to the tubules, and the lumen of the dentine tubes is filled during life with soft fibres, termed the *fibres of Tomes*. Towards the outer periphery of the dentine, where it abuts against enamel or *crusta petrosa*, there are irregular inter-globular spaces (Figs. 12 and 13). These are gaps varying in size and containing a soft substance. Opposite these gaps the dentine forms conical or hemispherical prominences.

The *enamel* is harder than dentine and it is formed of hexagonal prisms or bands (Fig. 12, 1), termed *enamel prisms.* The upper surface of the enamel is covered by a thin homogeneous hard layer or membrane, termed *Nasmyth's membrane*, or the membrane of the enamel, found only in the teeth of young animals.

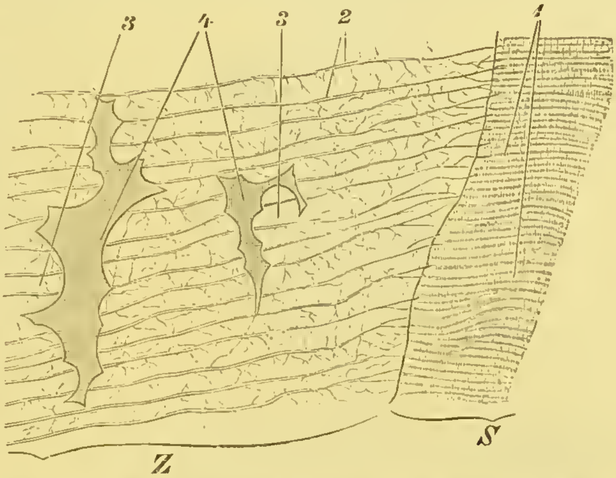

Fig. 12.—From a longitudinal section of the lateral portion of the crown of human molar tooth. × 240 d. S, enamel. Z, dentine. (1) Enamel prisms. (2) Small dentine tubes. (3) Dentine prominences or bosses, projecting into, (4) The interglobular spaces. (Method No. 4, Appendix.)

The *crusta petrosa* resembles bone in its structure in having lacunæ and canaliculi, but it does not show series of concentric lamellæ, and Haversian canals are only occasionally found in the teeth of old persons. The lacunæ do not exist near the neck of the tooth.

The space between the root of a tooth and the alveolus of the jaw is occupied by the periosteum which is firmly connected with the outer surface of the *crusta petrosa.* The *pulp* is formed of a soft delicate connective tissue, the cell elements of which lie mostly on the surface, and are termed *odontoblasts.* These are elongated nucleated cells having, especially on one side, long processes, some of which run into the pulp while others pass into the dentine tubes. The latter constitute the dentine fibres already mentioned (Fig. 14, *f*). The blood-vessels and nerves are confined to the pulp and do not pass into the dentine.

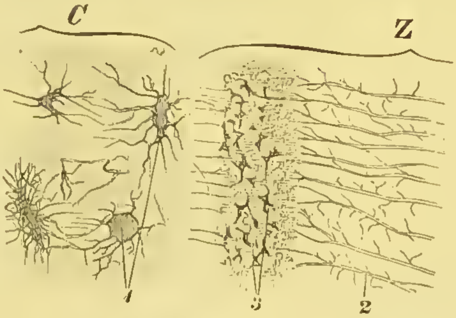

Fig. 13.—From a longitudinal section of the fang of a human molar tooth. × 240 d. Z, dentine. C, *crusta petrosa.* (1) Lacunæ containing bone corpuscles with radiating processes. (2) Small dentine tubes, separated from the *crusta* by a granular layer in which many small interglobular spaces may be seen. (Method No. 5, Appendix.)

We shall now consider the *development of teeth.* This begins in man towards the close of the second month of intra-uterine life, and is first shown as an exuberant growth of the entire mucous membrane covering the jaw. This thickening of the membrane forms a prominence termed the *dental ridge.* Next, a furrow appears running along the ridge, the *dental furrow* (Fig. 15, *Zf*), the edges of which now form the dental ridges, (Fig. 15, *Zw*). The epithelium now undergoes rapid proliferation, that is the cells increase in number, so that they not only fill up the dental furrow but the mass of cells penetrates into the underlying connective tissue. This mass or strip of cells is termed the *enamel germ*, (Fig. 15, 2, *Sk*), and it consists of cylindrical cells (Fig. 16, 3), which come from epithelial cells lying deepest in the stratum. While the enamel germ becomes thicker at its lower end (Fig. 15, 3), in the *tunica propria* underneath, a number of spherical papillæ corresponding to the number of milk teeth, make their appearance (Fig. 17, 4). These *papillæ* are formed of connective tissue cells. The enamel germ and the papilla approach each other and ultimately the germ forms a cap over the summit of the papilla (Fig. 15, 4), and the under surface of the enamel germ now constitutes the *enamel organ* (Fig. 15, 4, *So*).

Fig. 14.—Six odontoblasts having (*f*) dentine fibres connected with them. (*h*) Processes passing into pulp. From the pulp of the tooth of an infant. (Method No. 6, Appendix.)

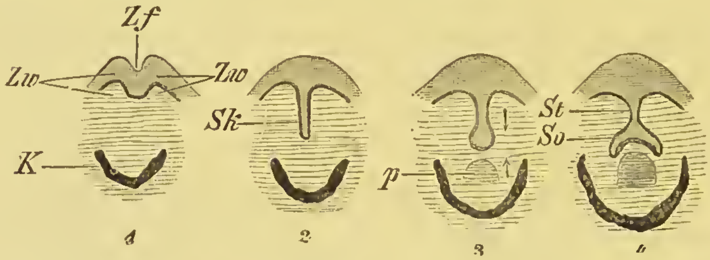

Fig. 15.—Diagrammatic representation of the development of a tooth, showing four transverse sections of an embryonic lower jaw. The epithelium is shown by dots, and the connective tissue by transverse lines. 1, *Zf*, dental furrow. *Zw*, dental ridge. *K*, bone of lower jaw, black. 2, *Sk*, enamel germ. 3, *p*, papilla. 4, *So*, enamel organ. *St*, neck or shaft of enamel organ.

The portion of the enamel organ that does not undergo any subsequent change into enamel is termed the neck or shaft (Fig. 15, *St*). The deeper cells of the enamel organ now form elongated cylinders resting in the papilla, and they become calcified into enamel prisms. They are termed *germ cells* (Fig. 17, 3, *c*). The peripheral cells (Fig. 17, 3, *a*), on the other hand, become much flattened, and the intermediate cells (Fig. 17, 3, *b*) grow into stellate cells, the processes of which anastomose. The latter constitute the enamel pulp.

The connective tissue surrounding the young tooth at an early period becomes firm and forms a sac. At a later stage, two layers may be distinguished in the wall of this sac, an inner loose (Fig. 18, 1, *b*), and an outer thick firm layer (1, *a*). The shaft of the enamel organ now disappears and the formation of dentine follows. The cells already mentioned as *odontoblasts* grow or collect on the upper surface of the papilla. These are concerned in the formation of dentine. The *crusta petrosa* is formed after birth, just before the eruption of the tooth from the periosteum of the alveolus. The enamel membrane, according to some, is a product of the germ cells, while others think that it comes from the peripheral cells of the enamel organ (Fig. 18, 2, *c*). The permanent teeth are formed in the same way as the milk teeth. Their enamel germs grow out laterally from the shafts of the enamel organ of the milk teeth, forming, in the language of Goodsir, cavities of reserve. The fully formed permanent tooth pushes into the cavity of the milk tooth and partly by pressure and partly by the action of special large multinuclear protoplasmic cells called *odontoclasts* (which eat away the fang), the

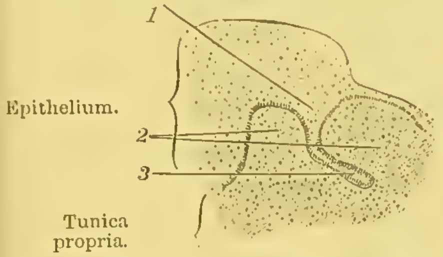

FIG. 16.—From at ransverse section of the lower jaw of the embryo of a sheep. × 40 d. 1. Dental furrow. 2. Dental ridge. 3. Enamel germ. (Method No. 7, Appendix).

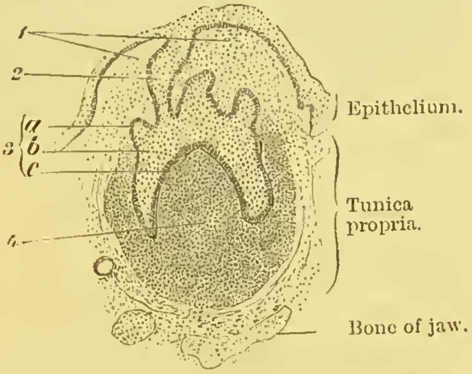

FIG. 17.—From a transverse section of the lower jaw of a human fœtus of four months. × 40 d. 1. Dental ridge. 2. Shaft of enamel organ. 3. Enamel organ; *a*, peripheral cells; *b*, germ or enamel pulp; *c*, cylindrical cells bearing enamel prisms. 4. Papilla. (Method No. 8, Appendix).

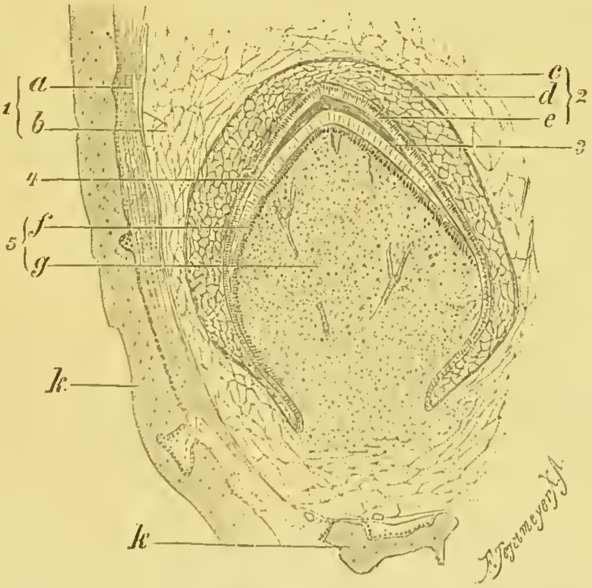

FIG. 18.—Transverse section of the lower jaw of a puppy dog. × 40 d. 1. Dental sac, shown only on left side; *a*, outer, *b*, inner layer. 2. Enamel organ; *c*, peripheral flat cells; *d*, enamel or germ *pulp*; *e*, enamel cells. 3. Enamel. 4. Dentine. 5. Papilla; *f*, odontoblasts; *g*, blood-vessels; *k*, bone of lower jaw. The tissues originating from connective tissue are seen on the left and those springing from epithelial cells on the right side. (Method No. 9, Appendix).

root of the milk tooth is destroyed. The crown then drops out of the gum and the place of the milk tooth is soon occupied by the permanent tooth. Thus a complete tooth is formed partly from epithelium,—the enamel,—and partly from connective tissue,—the dentine and the pulp and the *crusta petrosa* is an accessory formation yielded by the neighbouring periosteum.

Chemically considered, teeth consist of an organic matrix infiltrated with earthy salts. Aeby gives the following percentage analysis of the teeth of oxen :—

	Enamel.	Dentine.
Organic matter,	3·60	27·70
$3C_3P_2O_8$,	93·35	91·32
CaO,	0·86	5·27
$CaCO_3$,	4·80	1·61
$MgCO_3$,	0·78	0·75
Fe_2O_3.	0·09	0·10
$CaSO_4$,	0·12	0·09

There are also traces of calcium fluoride.

The functions of the teeth will be considered in treating of mastication, and will be deferred till a description has been given of the tongue.

B. The Tongue.

The tongue is a muscular structure covered with mucous membrane. Its *muscles* are intrinsic and extrinsic. The *extrinsic* muscles pass into the tongue and connect it to neighbouring parts. We find connected with each half of the tongue, supposing it to be divided equally by an antero-posterior septum, four muscles, the *hyo-glossus*, the *genio-hyo-glossus*, the *stylo-glossus*, and the *palato-glossus.* The *hyo-glossus* arises from the hyoid bone, and passes upwards to be inserted between the *stylo-glossus* and the *lingualis,* one of the intrinsic muscles. This muscle depresses the tongue and draws it backwards. When both muscles contract the dorsum of the tongue becomes convex. Beneath the *hyo-glossus,* we find the *genio-hyo-glossus* arising from the inner surface of the anterior part of the lower jaw, and its fibres spread out like a fan, the lower passing to the hyoid bone, a few going to the pharynx, and the rest entering the entire length of the tongue. When the anterior fibres of this muscle contract, the tip of the tongue is drawn backwards, but the posterior fibres tend to protrude the tongue. The middle fibres depress it. When the two muscles act, the tongue is protruded in a straight line, and when one acts the tongue is protruded and the tip is turned towards the side of the inactive muscle, as in some cases of paralysis. Sometimes the tongue may be the seat of fibrillar contractions. The *stylo-glossus* springs from the styloid process of the temporal bone and passes to the side of the tongue, one set of fibres blending with the *lingualis* and the other decussating with the fibres of the *hyo-glossus.* The *stylo-glossus* draws the tongue backwards and raises its base. When it acts along with the *genio-hyo-glossus,* the back of the tongue becomes concave. The *palato-glossus,* found in the anterior pillars of the fauces, passes into the upper surface of the tongue, and its fibres are lost among those of the *stylo-glossus.* It is concerned in the movements of deglutition.

The *intrinsic* muscles consist of certain well-defined bundles of fibres situated in the substance of the organ. They are (1) the *superior lingual* consisting of longitudinal fibres, situated below the mucous membrane, and running from the tip of the tongue back towards the hyoid bone; (2) the *inferior lingual* formed of fibres running longitudinally along the under surface, between the fibres of the *genio-hyo-glossus* and those of the *hyo-glossus* muscle; (3) the *transverse* muscle composed of fibres passing transversely from a fibrous septum in the median plane to the dorsum and sides of the tongue, and (4) the *vertical* fibres passing in a curved direction outwards towards the dorsum and under surface of the border of the tongue. It is by the action of these muscles, assisted by the extrinsic muscles, that the tongue assumes manifold forms in articulate speech and in the movements of mastication and deglutition.

The *septum* separates the muscular masses into a right and left half. It attains its greatest height about the middle of the tongue and gradually shades off towards the tip. It never reaches the surface, ending about 3 mm. below the epithelial layer. The septum consists of connective tissue.

The nerves of the tongue are three: (1) the *lingual* or gustatory branch of the fifth nerve distributed to the mucous membrane of the anterior two thirds of the organ, and conferring sensibility on that part; (2) the lingual branch of the *glosso-pharyngeal,* distributed to the posterior third, also sensory; and (3) the *hypoglossal* or ninth nerve, distributed to the muscles, and motor as regards its function. In addition to these nerves, filaments from the *sympathetic* accompany the blood-vessels of the tongue. The *arteries* come chiefly from the lingual, and there are a few small branches from the facial and ascending pharyngeal. The *veins* pass into the internal jugular vein.

The *mucous membrane,* like that lining the mouth, consists of epithelium, *tunica propria,* and submucous tissue, but it differs from it by having numerous papillæ on its surface. We find three forms of papillæ: (1) *papillæ filiformes,* (2) *papillæ fungiformes,* and (3) *papillæ circumvallatæ.* The *papillæ filiformes* (Fig. 19) are cylindrical or conical elevations of the *tunica propria,* on the upper end of which there are from five to twenty small secondary papillæ. They consist of fibrous connective tissue, in which a few elastic fibres are interspersed, and

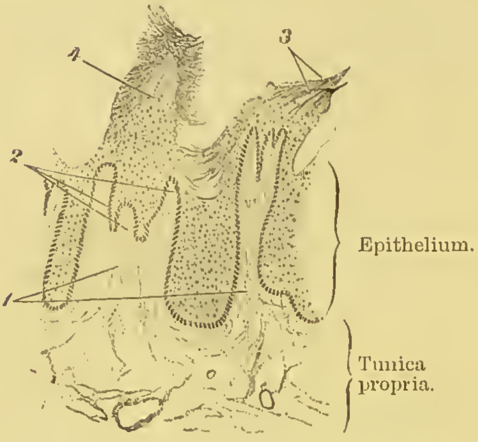

Fig. 19.—Longitudinal section of the mucous membrane of the central part of the human tongue. × 30 d. 1, Section through papillæ filiformes, each of which bears three secondary papillæ; 3, a double; and 4, a single process of epithelium, covered with masses of loosely adhering flat epithelial cells. (Method No. 10, Appendix.)

they are clothed with a layer of flat epithelial cells. Sometimes these cells form simple thread-like or divided processes, covering the secondary papillæ. These papillæ occur in large numbers, and their length varies from ·7 to 3 mm. The *papillæ fungiformes* (Fig. 20) are prominences of a spherical form, rising from the *tunica propria* by a narrower stem, and their upper surface is covered by secondary papillæ. They consist of a network of connective tissue fibres and a few elastic fibres. The epithelium covering them consists of thin flattened cells, not so horny in character as those on filiform papillæ. They are not so numerous as the filiform variety, but they occur on all parts of the surface of the tongue, and they are detected by the red colour caused by their vascularity. Their length varies from ·5 to 1·5 mm. The *papillæ circumvallatæ* (Fig. 21) resemble broad and flattened fungiform papillæ, and they are cut off from the surrounding mucous surface by a deep furrow. One side of the furrow is formed by the papilla, and the other side, called the ridge, by the neighbouring mucous membrane. Each papilla is formed of connective tissue. Secondary papillæ occur only on the upper surface of the papilla, and not on its sides. Among the epithelium cells of the lateral surface of the papilla and on the ridge forming the other side of the furrow we find the end organs, called *taste buds* or *taste goblets*, connected with the sense of taste. From eight to fifteen circumvallate papillæ are found. Their height ranges from 1 to 5 mm., and their breadth from 1 to 3 mm.

Fig. 20.—Longitudinal section of the mucous membrane of human tongue. × 30 d. 1, Secondary papillæ covering; 2, a fungiform papilla; 3, shaft or stem of a fungiform papilla; 4, small filiform papilla. (Method No. 11, Appendix.)

The term *papilla foliata* is applied to a number of parallel folds of mucous membrane, situated one on each side of the postero-lateral margin of the tongue of some animals. They are well seen in the rabbit. They contain end organs of taste.

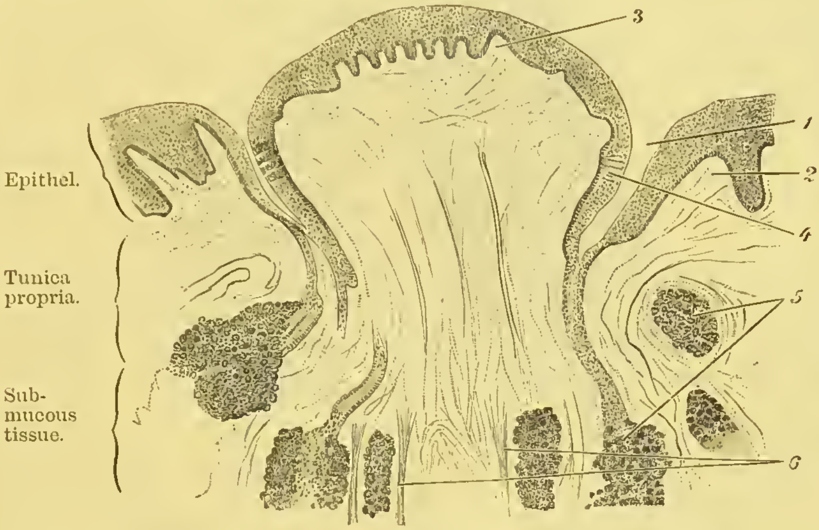

FIG. 21.—Vertical section through a circumvallate papilla of man. × 30 d. 1, Furrow ; 2, ridge ; 3, secondary papillæ ; 4, taste end organs in the epithelium ; 5, serous glands ; 6, muscle fibres. (Method No. 12, Appendix.)

Behind the circumvallate papillæ, the mucous membrane of the human tongue is raised into a number of spherical masses, from 0·11 to 4 mm. in breadth, by the development underneath of adenoid tissue. These are visible to the naked eye. In the centre of these elevations a small opening may be observed passing into a shallow cavity. This cavity is surrounded by adenoid tissue, and this again by a layer of compact connective tissue. The cavity is lined by stratified epithelium. These spherical masses of adenoid tissue are similar in character to the solitary follicles in the small intestine, which, when grouped together, form a Peyer's patch. During life, numerous leucocytes pass from the adenoid tissue through the epithelium into the cavity, and thus they reach the mouth, appearing in its secretion as mucous and salivary corpuscles. The epithelium on this part of the tongue is infiltrated with leucocytes. The *tonsils*, situated between the anterior and posterior pillars of the fauces, show a similar type of structure (Fig. 22). They consist of spherical masses of adenoid tissue grouped round a central cavity, and beyond this we find a layer of connective tissue. The ducts of small mucous glands open into the central cavity, and there are large lymphatic channels situated in the vicinity of the tonsils.

Two varieties of glands, mucous and serous, are found in the mucous membrane, among the upper layers of the muscular fibres of the tongue.

The *mucous* glands resemble those of the mouth. They are found along the margins of the tongue, especially near its root, and their ducts are lined by cylindrical epithelium. The wall of each acinus consists of a structureless membrane lined by cylindrical epithelial cells. The appearance of these cells varies according to the state of their function when examined. During rest, the protoplasm is finely granular, and the nucleus, situated midway between the centre of the cell and the side of the cell attached to the membrane, is oval, its long diameter being parallel with the membrane (Fig. 23, I. *b*). During secretion, the cell becomes clear and the nucleus is pressed flat against the wall of the cell

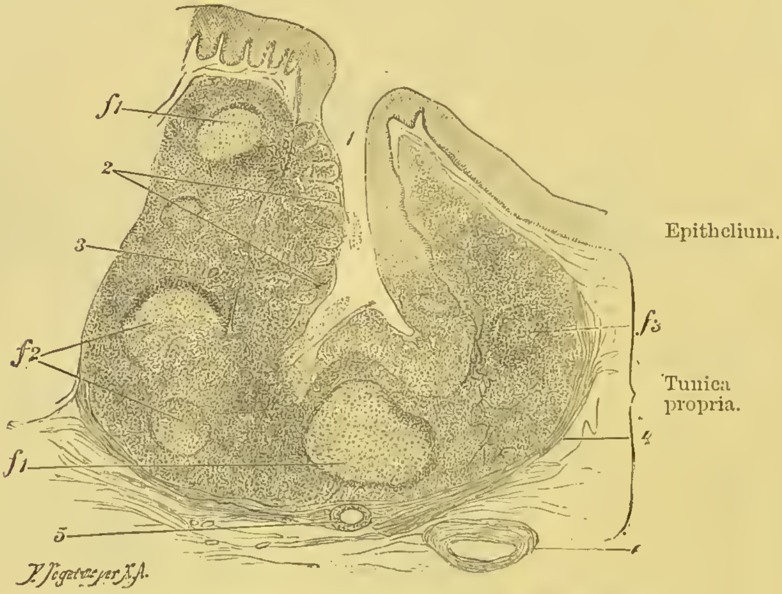

FIG. 22.—Vertical section of human tonsil from a young subject. × 20 d. 1. Cavity of tonsil containing emigrated leucocytes. 2. Epithelium lining the cavity penetrated on the left and beneath with wandering leucocytes. On the right side the epithelium has not been affected. 3. Adenoid tissue containing noduli or masses of germinal tissue. *f* 1. Sections of nodules; *f* 2. Sections of nodules; *f* 3. Partial section of nodule. 4. Fibrous layer surrounding adenoid tissue. 5. Section of duct of mucous gland. 6. Blood-vessel. (Method No. 13, Appendix.)

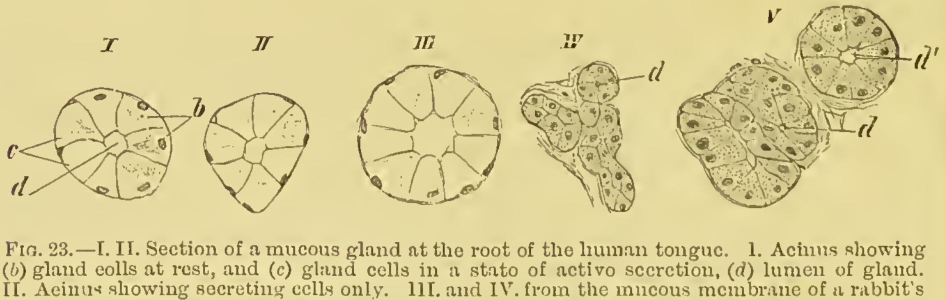

FIG. 23.—I. II. Section of a mucous gland at the root of the human tongue. I. Acinus showing (*b*) gland cells at rest, and (*c*) gland cells in a state of active secretion, (*d*) lumen of gland. II. Acinus showing secreting cells only. III. and IV. from the mucous membrane of a rabbit's tongue. III. Acinus of mucous gland. IV. Several acini in a serous gland, showing at *d* the lumen very small. V. Several acini in a serous gland in human tongue with lumen wide at *d'*, and narrow at *d*. × 240 d. (Method No. 14, Appendix.)

(Fig. 23, I. *c*, II.). In man, one and the same mucous gland and even one and the same acinus may show gland cells in different stages of activity. Two small glands, known as Nuhn's gland and Blandin's gland, found at the tip of the tongue, are organs of this description.

The *serous* or albuminous glands are found only near the circumvallate and foliated papillæ, their ducts opening into the furrow or groove. The ducts are lined by cylindrical epithelial cells. The small acini consist of a delicate *membrana propria*, lined with short cylindrical or conical cells. The protoplasm of the cells is darkly granular and a spherical nucleus exists near the centre of the cell (Fig. 23, IV. and V.). The lumen of the acini, d^1 and d, is very narrow.

The *blood-vessels* of the mucous membrane form extended networks from which twigs pass into the papillæ, sometimes even reaching the secondary papillæ. At the base of the tongue the nodules of adenoid tissue already referred to are richly supplied with vessels. The acini of the glands have also a capillary network surrounding them.

The *lymphatics* of the tongue are in two layers; a deeper network consisting of larger lymphatics and a superficial network of very fine vessels. Minute vessels pass from the latter into some of the papillæ. Near the root of the tongue the lymphatics are very richly developed.

The *nerves* of the mucous membrane show in their course small groups of ganglion cells, and they terminate either in the form of delicate filaments passing between the epithelial cells and probably ending free, or by uniting with the end organs of taste (See Sense of Taste), or in the end bulbs of Krause which have to do with tactile impressions (See Sense of Touch).

CHAP. VI.—THE SALIVARY GLANDS.

These glands consist of three pairs—the parotid, the submaxillary, and the sublingual. The *parotid* gland is the largest of the salivary glands. It is situated on the side of the face between the ear and the lower jaw and its duct, termed the *duct of Steno*, about 60 mm. in length, passes forwards over the masseter muscle, runs obliquely through the buccinator muscle, and enters the mouth by a narrow opening opposite the second upper molar tooth. The *submaxillary* gland lies beneath the horizontal part of the inferior maxilla and its duct, known as the *duct of Wharton*, 50 mm. in length, opens in the floor of the mouth at the side of the frænum of the tongue, and close to the duct on the opposite side. The *sublingual* gland, the smallest of the three, is found beneath the tongue, and it discharges its secretion by a number of small ducts (from 8 to 20), termed the *Rivinian ducts*, some of which, along with one larger one called the *duct of Bartholin*, unite with the duct of Wharton.

The salivary glands are either serous or mucous glands, or both. We distinguish :—(1) *mucous salivary glands*, in the sublingual of man, the rabbit, the dog, and the cat, and in the submaxillary of the dog and the cat ; (2) *serous salivary glands*, in the parotid of man, the rabbit, the dog, the cat, and the submaxillary in the rabbit; and (3) *mixed* or *muco-serous glands*, in the submaxillary of man, the ape, the guinea pig, and the mouse.

(1) *The Sublingual Gland.*—The duct of Bartholin is formed of a wall of connective and elastic tissue, lined by a single layer of short cylindrical epithelium cells. Nearer the gland, the small ductlets, sometimes called *interlobular ducts*, as they pass between the lobules, are lined by large cylindrical epithelium cells having the part of the cell next the lumen granular in appearance, while the part attached to the *membrana propria* shows a longitudinal striation (Fig. 5). The next part of the duct, passing into the acinus, is called the intermediate or *intercalary* portion, and it is lined by a single layer of flattened cells, each having an oval nucleus, and the acini consist of a *membrana propria* lined with mucous cells. The *membrana propria* is formed of nucleated connective tissue cells. The mucous cells present appearances varying according to the state of the secretory process, but semilunar forms are very common. Numerous leucocytes are found in the connective tissue surrounding the acini.

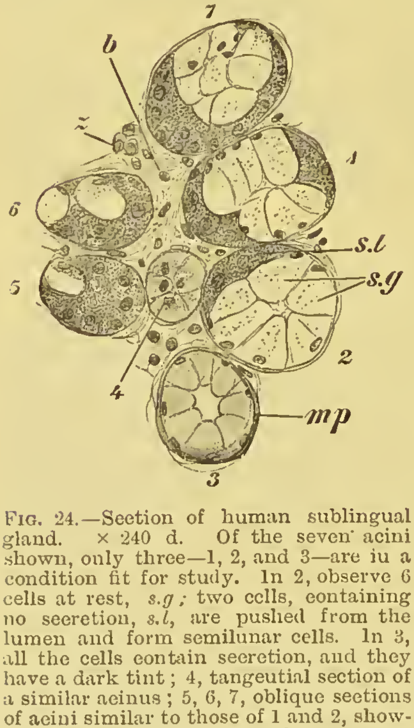

FIG. 24.—Section of human sublingual gland. × 240 d. Of the seven acini shown, only three—1, 2, and 3—are in a condition fit for study. In 2, observe 6 cells at rest, *s.g* ; two cells, containing no secretion, *s.l*, are pushed from the lumen and form semilunar cells. In 3, all the cells contain secretion, and they have a dark tint ; 4, tangential section of a similar acinus ; 5, 6, 7, oblique sections of acini similar to those of 1 and 2, showing semilunar forms and no lumen ; *mp*, *membrana propria* ; *b*, connective tissue with numerous leucocytes, *z*. (Method No. 15, Appendix.)

(2) *The Parotid Gland.*—The duct of Steno is lined with columnar epithelium. Nearer the gland, in the smaller ducts (interlobular) we find cylindrical cells showing a delicate striation, and in still smaller ducts in the substance of the gland (intercalary) the cells are spindle shaped. The ducts lined with spindle shaped cells end in the acini, and these consist of a delicate *membrana propria* lined with cubical albuminous or serous cells. When resting they are small, and show a finely granular dark appearance, and when filled with secretion, they become larger and clearer (Fig 25).

(3) *The Submaxillary Gland.*—The duct of Wharton agrees in structure with the ducts of the parotid and sublingual glands. Near the acini, the ductlets are lined by cubical epithelium. The acini have their *membrana propria* lined either with serous gland cells, like those of the parotid, or mucous gland cells, with semilunar forms similar to those of the sublingual gland (Fig. 26).

The capillary *blood-vessels* of the salivary glands form a dense network round the acini. Spaces occur between the acini which are probably *lymph paths.* *Nerve fibres,* both medullated and non-medullated, are found in considerable quantity, and small groups of ganglion cells occur in their course.

FIG. 25. — Portion of human parotid. × 240 d. *s*, portion of small duct ending in acinus, and lined with cubical epithelium. Narrow lumen of acinus seen at *l*. The other acini have been cut obliquely. (Method No. 16, Appendix.)

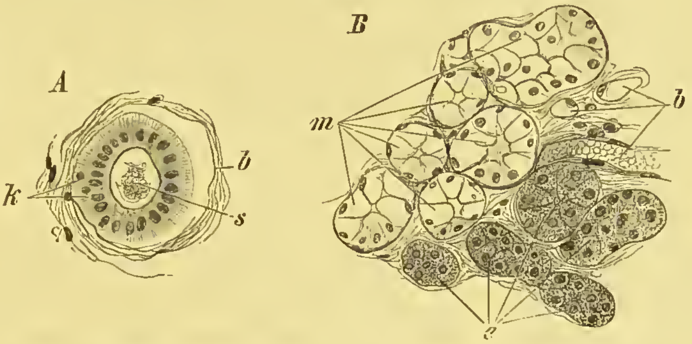

FIG. 26.—Section of human submaxillary gland. × 240 d. *A*. Transverse section of duct. The epithelial cells on the right have been detached from the surrounding connective tissue at *b*. Observe the striation of the cells; *k*, wandering leucocytes; *s*, secretion. *B*, *m*, acini with mucous gland cells; *e*, acini with serous gland cells. In group *m* the lumina of four acini may be seen, but the lumina of all acini filled up in group *c*. *b*, blood-vessel cut lengthways, and containing coloured blood corpuscles. (Method No. 17, Appendix.)

CHAP. VII.—PROCESSES IN THE MOUTH.

Some animals introduce food into the mouth by the action of the tongue (ox), or by the mobility of the lips (horse), or by a proboscis or trunk (elephant), or with the aid of the fore paws (squirrels and monkeys). Man carries food to the mouth with the hand. Fluids may be poured into the mouth, and thence pass directly into the pharynx, and through it, by a process of deglutition, into the stomach. Fluids are sucked into the mouth by aspiration. When we drink from a cup, with lips immersed, the air is removed from the mouth by inspiration, and the fluid flows in under atmospheric pressure; when the lips are not entirely immersed, some air rushes in with the fluid, and a gurgling sound is produced. When a child sucks at the breast, the mouth acts as a kind of pump, of which the tongue is the piston. The lips are applied hermetically round the nipple, the isthmus of the fauces is closed by the base of the tongue touching the soft palate, and the anterior part of the tongue is placed below the nipple. When these arrangements are made, there is muscular action of the cheeks, lips, and tongue, which aids the pressure of the atmosphere on the breast in forcing the milk into the cavity of the mouth. No respiratory effort requires to be made, and hence a child breathes quietly while the mechanism of suction is in action.

After food has been introduced into the mouth, it is there subjected to two processes which are carried on simultaneously. It is broken down by the triturating movement of the jaws, and it is mixed with a fluid poured into the mouth by the various glands already described.

1. **Mastication.**—The food is divided by the incisor and the canine teeth, and is then triturated between the superior and inferior molars. The hard surfaces of the teeth, formed of enamel, enable the teeth to act forcibly, even on very hard substances, without much risk of injury, while the sensibility of the teeth enables us to graduate the amount of pressure required.

The incisors are used in biting off morsels of food, the canines in tearing, and the molars in crushing. The lower jaw may be moved either from above downwards or horizontally. The first movement approximates or separates the dental arches, whilst the second produces a to-and-fro movement of trituration. These movements depend on the form of the articulation between the condyle of the lower jaw and the glenoid cavity of the temporal bone. In carnivora, the form is such as to permit chiefly of vertical movements, and these animals do not masticate their food, but swallow it in lumps. A different form of articular surface, permitting of gliding movements in the horizontal direction, exists in herbivora, so as to render possible the extensive lateral movements of the lower jaw in chewing the cud. Man, who is omnivorous, possesses a mechanism admitting, within certain limits, of both kinds of movements. The lower jaw may be pulled down by the *genio-hyoid*, the *mylo-hyoid*, and the anterior belly of the *digastric*, all of which are muscles passing from the lower jaw to the hyoid bone, which is fixed during the movement in question by the *omo-hyoid*, *thyro-hyoid*, and *sterno-hyoid* muscles. The lower jaw is raised by the *masseter*, the *temporal*, and the *internal pterygoid*. The jaw is protruded by the *external pterygoids* and retracted by the *internal pterygoids*. The *external pterygoids* act alternately on the two sides, each muscle drawing forwards the condyle of the jaw, and thus causing a horizontal movement of the lower jaw. The *orbicularis oris* muscle keeps the mouth closed. The *buccinator* muscle prevents the food from collecting outside the dental arches. In the monkey large quantities of food may be retained in pouches between the cheeks and the teeth, and the animal may be seen to push with the paws the contents of the pouch into the mouth. Some animals chew more on one side than the other, and they then move the lower jaw from right to left and from left to right by the action of the *external pterygoid* and the *internal pterygoid* of one side, and the *masseter* muscle of the other side. Lateral movements are greatest in ruminants, while forward and backward movements are characteristic of rodents.

In mastication, the food is rolled backwards and forwards, and from side to side, by the movements of the tongue, an organ which, by the action of its extrinsic muscles, may be moved as a whole in all directions, while its intrinsic fibres permit of a change of form to suit every varying condition. The tongue also assists in the process as a tactile organ, as by it we become conscious of the position of the bolus of food with reference to the teeth, and also by it we obtain the knowledge that the food is in a fit state for deglutition.

Mastication is assisted by the food becoming mixed with the fluids in the mouth (mixed saliva), especially if the food is very dry. Thorough mastication prepares the food for the action of the digestive fluids, and dyspepsia may occur when this mechanical process is imperfectly carried out. The horse masticates very thoroughly, crushing the cellulose walls of the cells in its food that contain nutritious matter. The first mastication of ruminants is hastily and imperfectly done, but in the second mastication the food is thoroughly comminuted.

The *motor* nerves concerned in mastication are: (1) the motor branches of the inferior maxillary branch of the fifth, supplying the muscles of mastication, the buccinator, and the anterior belly of the digastric; (2) the hypo-glossal, governing the movements of the tongue by its extrinsic and intrinsic muscles, and supplying, by the *descendens noni* nerve, also the *omo-* and *sterno-hyoid*, and the *sterno-thyroid*; special branches of the hypo-glossal also supply the *genio-hyoid* and *thyro-hyoid*; and (3) the facial supplying the posterior belly of the digastric, the *stylo-hyoid*, *platysma*, and the muscles of the lips, and also, along with twigs from the inferior maxillary branch of the fifth, the buccinator muscle. The *sensory* nerves belong to the fifth, and the glosso-pharyngeal to the tongue; and the *centre* for reflex movements is in the *medulla oblongata* and *pons Varolii* associated with the nuclei of the fifth, facial, hypo-glossal and glosso-pharyngeal nerves.

2. **Insalivation.**—During the process of mastication, the food is mixed with a fluid, termed the *saliva.* The union of the secretion of the glands, along with a small quantity of fluid supplied by the glands in the lining membrane of the lips, cheeks, and tongue, constitutes the *mixed saliva.*

(1) *General Physical and Microscopical Characters of Mixed Saliva.*—This is a transparent or slightly opalescent fluid, which deposits a small amount of sediment. When a small portion of the sediment is examined

with a magnifying power of 350 d., it is found to contain squamous epithelium cells, derived from the mucous membrane of the mouth, and globular nucleated cells. The latter are termed *salivary corpuscles,* and may show active molecular, and sometimes amœboid, movements. In addition to these, larger masses of protoplasm, exhibiting amœboid movements, are sometimes met with. The specific gravity of saliva ranges between 1004 and 1009.

FIG. 27.—Drop of saliva, showing, *a,* pavement or squamous epithelium from mouth; and *b,* salivary corpuscles.

(2) *Chemical Characters of Mixed Saliva.*—Mixed saliva is alkaline, from the presence of alkaline sodium phosphate. The average alkalinity of fifty-one samples of human mixed saliva, expressed as sodium carbonate, was found by Chittenden to be ·08 per cent. It contains from 5 to 10 parts per 1000 of solid matter. The solids consist of *inorganic salts,* namely, carbonate of lime, alkaline chlorides, phosphates of lime and magnesia, and sulphocyanide of potassium. Carbonic acid, one of the gases in the saliva, holds carbonate of lime in solution, and when the gas escapes, as it does in the mouth, carbonate of lime may be deposited so as to form a coating on the teeth, or if the process occurs in the glands, a salivary concretion may be formed in a duct.

The sulphocyanide of potassium strikes a blood red colour with a solution of perchloride of iron. Saliva also contains a little oxygen and nitrogen. Külz extracted from 100 c.cm. of human saliva 1 c.cm. of O, 2·5 c.cm. of N, and 3·5 c.cm. of CO_2. In addition, he estimated that 50 c.cm. of carbonic acid were locked up in carbonates.

The organic matters consist chiefly of a substance called *ptyalin,* first discovered by Leuchs in 1831, along with a small amount of albumin. Mixed human saliva contains about ·139 per cent. of albumin and ptyalin.

When ptyalin is obtained pure by precipitation with lime water added to saliva, acidulated with phosphoric acid, it is a greyish-white powder, readily soluble in water. To obtain a glycerine extract, the procedure is to cover a minced salivary gland with absolute alcohol for twenty-four hours. The alcohol is then poured off, and the gland substance is allowed to macerate in strong glycerine for several days. The ptyalin may then be precipitated from the glycerine extract by the addition of alcohol.

Ptyalin belongs to the class of amylolytic ferments, and it transforms starch into maltose with great rapidity. Saliva also contains, as already mentioned, a trace of albumin, along with mucin and globulin. Mucin may be readily demonstrated in saliva by the addition of a drop of acetic acid, which coagulates the mucin, so that the saliva becomes viscid and molecular in appearance. The following table shows the results of the analyses of various kinds of saliva.[1]

	Human Mixed Saliva.			Dog's Mixed Saliva.	Human Parotid.	Dog's Sub-maxillary.	Dog's Parotid.	Horse's Parotid.
	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Water, - - -	994·6	995·1	994·1	989·6	985·4	994·4	991·5	990·0
Solids, - - -	5·3	4·8	5·9	10·3	14·6	5·6	8·4	10·0
Mucin and Epithelium,	?	1·6	2·1	?	9·0	2·4	1·5	4·0
Soluble Organic Matter,	3·2	1·3	1·4	3·5				
Sulphocyanide of Potassium, - - -	?	·06	·01	?	0·3	...	...	...
Salts, - - - -	1	1·8	2·2	6·8	5·0	3·8	6·2	6·7

I., Herter; II., Jacubowitsch; III., Frerichs; IV., Schmidt and Jacubowitsch; V., Mitscherlich; VI., Herter; VII., Herter; VIII., Lehmann.

In 1000 parts of human saliva, Jacubowitsch found 1·82 of mineral matters, and this amount consisted of ·51 of phosphoric acid, ·43 of soda, ·03 of lime, ·01 of magnesia, and ·84 of alkaline chlorides. Sulphocyanide of potassium is not present in the mixed saliva of the dog and horse.

(3) *Characters of Special Salivas.*—The secretions of the various salivary glands have been collected by introducing canulæ into the ducts. The *parotid* saliva is fluid, limpid, and clear as water. Its reaction is alkaline, but less so than that of the submaxillary gland. It contains ptyalin, and it may show a trace of urea. When exposed to the air in a vessel, it becomes milky from the deposition of carbonate of lime. Carnivorous animals have small parotid glands, while herbivora have them largely developed. When we consider that the food of carnivora contains about 75 per cent. of water, and that of herbivora is often dry, we see that the parotid saliva will be useful merely for moistening the food. The *submaxillary* saliva is much more viscid, from the amount of mucin it contains. It contains ptyalin and sulphocyanide of potassium. The more special characters of this saliva will be presently described. The fluid obtained from the *sublingual* gland is transparent and extremely viscid from the presence of a large amount of mucin. It is strongly alkaline.

The saliva of newly born children contains only a small amount of

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[1] Compiled from Hoppe-Seyler's *Physiologische Chemie* and Maly's article, Chemie der Verdauungssäfte under der Verdauung in Hermann's *Handbuch der Physiologie*, vol. v.

ptyalin, and this is supplied by the parotid alone. The ferment appears in the saliva of the submaxillary gland about two months after birth. After this period, and especially during the eruption of the teeth, saliva is copiously secreted.

(4) *Action of Saliva upon Starch.*—Saliva acts upon one proximate principle of food only, namely, starch, which it converts into maltose and a form of dextrin. Thus—

$$\underset{\text{Starch.}}{20(C_6H_{10}O_5)} + 8H_2O = \underset{\text{Maltose.}}{8(C_{12}H_{22}O_{11})} + \underset{\text{Achroodextrin.}}{2(C_{12}H_{20}O_{10})}.$$

The amount of starch changed in the mouth into sugar, in ordinary mastication, does not exceed 53 per cent. The transformation quickly occurs at a temperature of 35° C. When the temperature is lower, the action is retarded; at 40° C. the amylolytic action reaches its maximum, and when it rises above 60° C. the action is retarded. It may act slightly at 65° C., and at 70° C. it is arrested. The diastase of germinating grain, which affects a similar transformation in starch, requires a higher temperature than ptyalin. Ptyalin may act slightly even at 20° C. It would appear from the observations of Chittenden and Martin that the action of increased heat is on the ferment and not on the molecule of starch. The action is much more rapid with boiled than with raw starch.

If we mix a solution of boiled starch, thick enough to form a paste, with filtered saliva, at a temperature of 35° C., the paste soon becomes fluid, and the solution now contains soluble starch or *amidulin*, which still gives a blue colour with iodine. About a minute thereafter, the fluid will not give this blue reaction with iodine, but a reddish colour, indicating the presence of *erythrodextrin*, and, at the same time, by Fehling's solution, the presence of a substance capable of reducing cupric oxide to cuprous oxide can be demonstrated. This substance is chiefly *maltose*, $C_{12}H_{22}O_{11} + H_2O$, only a very small amount of ordinary grape sugar being formed. Maltose crystallizes in white silky needles, is less soluble in alcohol than grape sugar, and it rotates the plane of polarization about three times more strongly to the right than grape sugar,—glucose being $[a]_D = +52°·85$, and maltose $[a]_D = +155°$. Three parts of maltose reduce the same amount of cupric oxide as is reduced by two parts of grape sugar. In addition to erythrodextrin, another modification of dextrin, termed *achroodextrin*, exists in the fluid. This may be precipitated by alcohol, and it is not further altered by the ptyalin. Saliva acts best in a neutral solution. Strong acidity arrests the action, but it will act slightly in weak acid or weak alkaline solutions. As shown by Chittenden, ptyalin is destroyed by the action of pepsin and hydrochloric acid, and thus the process is soon arrested in the stomach. Sir W. Roberts has shown that infusion of tea arrests the action, while coffee and cocoa have only a very slight effect.

Various observers, and more especially Chittenden and Ely, Langley and Eves, Chittenden and Smith,[1] and Grützner, have investigated the action of ptyalin in various conditions, and though differing on not a few points, the following may be regarded as the more important general conclusions:—

(1) The diastatic action is most effective when the dilution of the saliva in the digestive mixture is as 1 to 50 or 1 to 100. When diluted to the extent of 1 to 2000 or 1 to 3000, a small amount of sugar may still be formed, but when a certain degree of solution has been reached, the action of the small amount of ferment in contact with a large amount of starch is devoted exclusively to converting granulose into soluble starch, or other non-reducing body. On the other hand, diminishing the amount of starch in largely diluted saliva increases the amount of sugar formed. (2) The diastatic action of neutralized saliva is greater than that of normally alkaline saliva. (3) Sodium carbonate retards the diastatic action of ptyalin in proportion to the amount of alkaline carbonate present. (4) The presence of proteid matter in the form of neutral peptone tends to increase the rate of action of ptyalin. (5) Small percentages of acid proteids retard, and large percentages almost completely destroy the action of ptyalin. (6) Free hydrochloric acid to the extent of ·003 per cent almost completely stops the action of ptyalin, and from ·005 to ·010 per cent. destroys ptyalin altogether. Langley arrived at the same conclusion independently. Thus, when the fluid in the stomach contains free hydrochloric acid, ptyalin will be destroyed, but as this does not occur at the beginning of digestion, there is a short period during which the conversion of starch into maltose may go on. As acid proteids are formed, the action will become less and less until it ceases.

The saliva of man, monkeys, rabbits, mice, squirrels, and guinea-pigs has a strong diastatic action, while that of the dog, cat, bear, and pig is almost inactive. The saliva of the horse is powerful, and the saliva of oxen and sheep is remarkably active, even on unboiled starch. Saliva that is inactive serves the function of moistening the food, thus preparing it for being swallowed. The amount of saliva secreted in twenty-four hours varies in animals according to the nature of the food. Thus the amount secreted by man is from 500 to 800 grammes, while horses may secret 40,000, and oxen even 60,0000 grammes, that is, from ·083 to ·1 of the weight of the body. Animals living on dry food and drinking little water secrete a large amount of saliva. Thus, in

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[1] Chittenden and Smith, *Studies from the Laboratory of Physiological Chemistry, Yale College, U.S.A.*, p. 33. References to other papers are here given. See also Langley and Eves, *Journal of Physiology*, vol. iv. No. 1 ; *ibid.*, vol. iii. No. 3.

the horse, Colin found that when fed with hay and straw, the amount of saliva secreted was four times, with barley flour twice, with oats about equal, with wet hay about half, the weight of the bolus of food, and when the horse was fed with barley flour mixed with water, no saliva was secreted. The secretion of saliva is increased by the movements of the jaws in speech, by the sense of flavour, and even by the imagination of a savoury dish.

3. **Influence of the Nervous System on Salivary Secretion.**—The influence of the nervous system on glandular secretion has been so clearly elucidated in the case of the *submaxillary gland of the dog*, as to merit the careful attention of the student at this period of his physiological studies. Although the anatomical arrangements are not the same in the dog as in man, the physiological mechanism is probably identical.

This gland in man receives fibres from two sources, namely, from the facial, by the *chorda tympani*, and from the sympathetic. The *chorda tympani*, arises from the facial nerve at the lower end of the aqueduct of Fallopius, passes through a minute canal which opens on the posterior wall of the tympanum, crosses the tympanum, and then leaves this cavity by an opening near the inner end of the Glasserian fissure, and passing down on the inner side of the internal lateral ligament of the

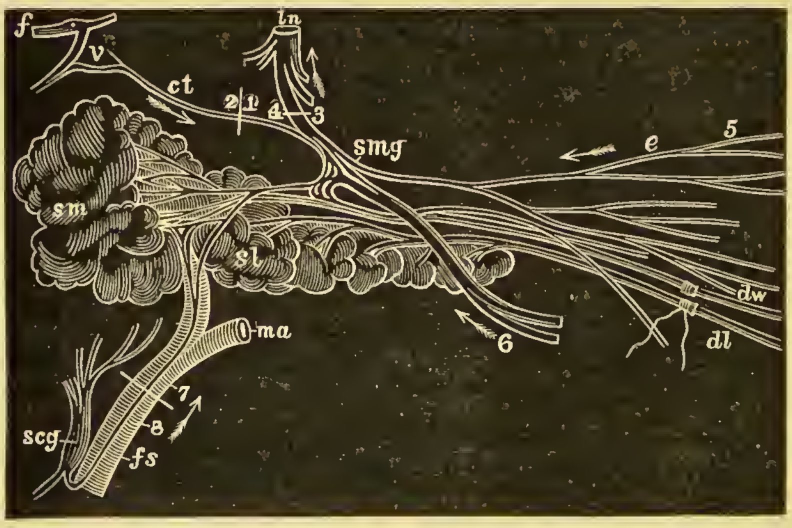

FIG. 28.—Diagram showing the nervous arrangements of the submaxillary glands of the dog: *sm*, submaxillary gland; *sl*, sublingual gland; *dw*, Wharton's duct, from the submaxillary gland; *dl*, duct of the sublingual gland; *f*, facial nerve; *v*, vidian nerve; *ct*, chorda tympani, joining the lingual branch of the fifth *ln*; *smg*, submaxillary ganglion; *scg*, superior cervical ganglion of the sympathetic; *fs*, filament from the sympathetic, passing upwards to join the submaxillary ganglion *smg*; *e*, sensory branches of the lingual, distributed to the mucous membrane of the mouth; *ma*, deep maxillary artery. The figures refer to the points of section of the various nerves, and the arrows indicate the normal direction of the nerve current.

jaw, joins the trunk of the lingual nerve, and passes on with it to the submaxillary ganglion and the tongue. In the angle which it thus forms with the lingual lies the submaxillary ganglion. The submaxillary ganglion in man is connected by anterior and posterior roots with the lingual branch of the fifth nerve. The posterior root conveys fibres to the ganglion from the *chorda tympani* and the inferior maxillary nerve and the ganglion is also joined by delicate fibres from the sympathetic derived from the plexus on the facial artery. Five or six small nerves pass from the ganglion to the submaxillary gland and a few run forwards to the mucous membrane of the mouth and to Wharton's duct.

When a canula is placed in the duct of the submaxillary gland, there flows from it a turbid, whitish fluid. On applying weak acids to the tongue, the saliva becomes limpid, whilst, on applying alkalies, it is turbid, white and viscous. It has been found that these characters may be more or less changed according to the nerve stimulated. Thus—

1. If the *chorda* is divided and then irritated at 1 (the distal end), the arteries of the gland dilate, the stream of blood through them becomes more rapid, the veins pulsate, and the saliva discharged from the duct is copious and watery. This variety may be termed the *saliva of the chorda tympani.* It contains very few histological elements, and consists principally of water, holding in solution a small quantity of the various salts.

2. When the sympathetic fibres are excited, the arteries contract, the stream of blood becomes slower, the veins contain very dark blood, and the secretion, called *saliva of the sympathetic*, is ropy, viscous, opaque, and contains histological elements, such as salivary corpuscles, the protoplasmic masses already alluded to, and mucin. After prolonged stimulation of the sympathetic, the secretion becomes watery and resembles chorda saliva, showing that the two kinds of saliva are not specifically distinct, a statement supported by the fact observed by Langley that in the cat the sympathetic saliva is less viscid than that of the chorda. A latent period of from 1·2 to 24 seconds may elapse between the moment of stimulation and the modification of secretion, and this applies both to the chorda and to the sympathetic, but especially to the latter.

3. If the lingual is divided at 4—3, and a stimulus applied to the end next the brain, there is a copious secretion, but this is not the case if the *chorda tympani* has been previously divided at 1. This would indicate that thero is a nervous arc, consisting of sensory filaments in the lingual, a nerve centre in the encephalon, and secretory filaments

in the chorda,—an example of what is termed a reflex excito-secretory action. If, after division of the lingual, the chorda, and the sympathetic, stimulants are applied to the mucous membrane of the mouth, there is still an increase of secretion, a fact which can only be explained by supposing that the submaxillary ganglion acts as a subsidiary reflex centre. In ordinary circumstances the saliva of the submaxillary gland is watery, that is to say, it is chorda saliva, and the action of the chorda is excited by stimulations affecting the nerves of taste (glosso-pharyngeal and lingual of the fifth), or the sensory branches of the fifth distributed to the mucous membrane of the mouth and tongue, or the olfactory nerves, or the sensory branches of the vagus distributed to the stomach. Thus a sapid substance, the mechanical irritation of the mouth produced by masticatory movements or by rolling a marble about with the tongue, an odour of food, or the entrance of food into the stomach, or irritation of the stomach, will all cause a flow of watery saliva.

The chief reflex centre is in the *medulla oblongata*, near the origin of the seventh and ninth cranial nerves, and according to some, although this is doubtful, the sympathetic fibres concerned in the process also originate here. This centre may be excited by impressions reaching it from the cerebrum, as occurs when the thought of savoury food may cause the mouth to "water," or it may be inhibited, that is to say, restrained from acting, as may occur in states of mental excitement, when the mouth may become dry or even parched.

Ludwig was the first to show that the increased secretion produced by excitation of the chorda is dependent on increased activity of the function of the secreting elements of the gland, and not on changes in the blood-vessels; in other words, that in the submaxillary gland the process of secretion is not a filtration, but is effected by changes which go on within the gland itself, of such a nature as to determine a current from the circulating blood towards the duct. This conclusion was based by Ludwig on the observation that if the duct be constricted, secretion will continue,

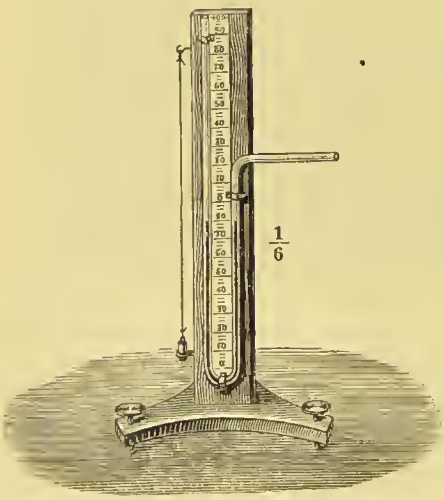

FIG. 29.—Manometer such as is used in physiological experiments.[1]

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[1] It consists of a U-shaped glass tube, having one limb shorter than the other, and attached to a wooden or metallic frame bearing a scale, graduated usually

notwithstanding that the pressure in the interior of the gland becomes greater than that in the arteries. Thus the pressure in Wharton's duct, as measured by a manometer (Fig. 29), may be twice as great as the pressure in the carotid or in the arteries of the gland. Secretion may even continue after the circulation has ceased, as when the head has been severed from the body, a fact which clearly shows that secretion depends on the activity of the cells, and is not a mere filtration of fluid from the blood. Pflüger asserts that the terminations of nerves may be traced into direct connection with the protoplasm of the salivary cells, and even with their nuclei (Fig. 30). (See also Fig. 318, Vol. I. p. 484). Although it cannot be said that these observations have been corroborated, and although the appearances seen by Pflüger may receive other explanations, it is highly probable that the nerve terminations are connected with cells. Kupffer has observed such a connection in the salivary cells of the cockroach (*Blatta*), and Maccallum believes he has traced nerve endings into the cells of the liver. It has also been ascertained that the chorda contains two kinds of fibres, one influencing secretion directly, and the other having an inhibitory action on the blood-vessels. Thus, atropine paralyzes the secretory fibres without having any effect on the other kind. Stimulation of the chorda after the administration of atropine is followed by dilatation of the vessels, but there is no secretion, that is to say, the *vaso-secretory* fibres have been paralyzed by the drug, but it has not affected the *vaso-dilator* fibres.

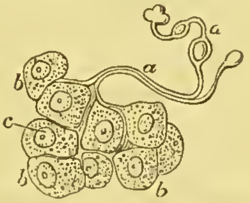

FIG. 30.—Nerves terminating in a cluster of cells in a salivary gland: *a*, nerve; *b*, *b*, *b*, cells; *c*, nucleus; *d*, small swellings on nerve fibres.

About twenty-four hours after the chorda has been divided, even supposing the sympathetic to be intact, a thin watery fluid, begins to flow from Wharton's duct. This secretion, called *paralytic secretion*, increases slowly till the seventh or eighth day, and then it diminishes, with accompanying degeneration of the glandular tissue. It is curious that section of *one* chorda is followed by a watery secretion from both glands, and Langley restricts the term *paralytic* to the saliva secreted by the gland on the side of the divided nerve, and gives the name *antilytic* to that on the opposite side. The paralytic secretion is probably chiefly owing to the action of the venous blood increasing the excitability of a local centre in

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into millimetres. Mercury is placed in the tube. The shorter limb is connected by leaden or thick-walled india rubber tubing to a canula inserted, in the experiment described in the text, into Wharton's duct. The pressure depresses the mercury in the shorter limb and raises it in the longer, and the amount of pressure is measured by doubling the height through which the mercury is raised in the longer limb. In the Fig. the mercury stands at 80; suppose the pressure raised it to 140, then the pressure would be 120 mm.

the gland. Langley has shown that the gland cells assume the resting appearance during the flow of a paralytic secretion.

During secretion the temperature of the gland rises by 1·5° C., and the venous blood flowing from the gland may be hotter than the arterial blood flowing to it. The chemical changes in the gland also are the cause of certain electrical phenomena, observed by Bayliss and Bradford. At rest the living gland gives a current, and it can be shown that the hilum of the gland is positive to other parts. On irritating the chorda, the hilum becomes first more positive and then it becomes negative, whereas, on irritating the sympathetic, the hilum becomes less positive, that is to say, there is a negative variation. Atropine destroys the chorda variation, but it only lessens the sympathetic variation.

From these facts we draw the following conclusions regarding secretion: (1) secretion may be increased by the direct action of nervous energy on the protoplasm of secreting cells; (2) secretion may be increased or diminished according to the supply of blood sent to the gland; (3) secretion does not depend simply on filtration of fluid from the blood, but also on cellular activity; (4) the supply of blood to a gland may be under the control of two antagonistic sets of nerve fibres, the one so acting as to increase, while the other diminishes, the supply of blood; (5) the nervous arrangements of secretion may be under the control of a reflex centre or centres in proximity to the gland, or in the cerebro-spinal axis; and (6) secretion is attended with an increase of temperature, and is thus one of the sources of animal heat.

The sublingual gland is supplied by numerous nerves derived from the lingual branch of the fifth and from the sympathetic. It probably also receives filaments from the submaxillary ganglion, and through it from the chorda, but its innervation has not been satisfactorily worked out.

The parotid gland receives nerve filaments, corresponding in physiological action to those of the chorda, from the glosso-pharyngeal nerve, through the lesser superficial petrosal nerve and the otic ganglion, the fibres ultimately reaching the gland by a branch of the auriculo-temporal. The tympanic branch of the glosso-pharyngeal, termed the nerve of Jacobson, passes from the petrous ganglion of the glosso-pharyngeal to the inner wall of the tympanum, through a foramen in the bone between the carotid foramen of the petrous portion of the temporal bone and the jugular fossa. Running along the inner wall of the tympanum, it leaves that cavity at its upper and fore part, and then becomes the small superficial petrosal nerve. This nerve appears on the upper surface of the petrous portion of the temporal bone, external to the *hiatus Fallopii*, then runs downwards and joins the otic ganglion. This ganglion, Arnold's ganglion, receives filaments from the inferior maxillary branch of the fifth, from the sympathetic by branches from the plexus on the middle meningeal artery, and from the glosso-pharyngeal by the small superficial petrosal nerve. As the latter nerve, in its canal, receives a filament from the geniculate ganglion of the facial nerve, it is probable that filaments from the facial, similar in function to those of the chorda, reach the otic ganglion by this route. Two or more filaments pass from the otic ganglion to the roots of the auriculo-temporal nerve, and the parotid branches of the latter ultimately reach the parotid gland. Experimental investigation on the nervous supply of the parotid gland, owing to the deep-seated position and complicated connections of the nerves, have not yielded results comparable in accuracy with those on the nerves of the submaxillary gland, but enough has been accomplished to show that the nervous secretory mechanism is of the same kind. Thus Langley has found that stimulation of Jacobson's nerve caused a secretion, and that if the sympathetic nerve was stimulated *after* stimulating Jacobson's nerve, considerable secretion followed, showing that the sympathetic nerve contains secretory fibres for the parotid gland, at all events in the dog.[1] Previous observers had obtained no secretion, or only an extremely scanty secretion, after stimulating the sympathetic.

To explain the apparently antagonistic action between the fibres of the chorda and those of the sympathetic, Heidenhain has advanced an ingenious theory.[2] Remembering that in a gland cell we find two substances, namely, the protoplasm engaged in metabolism, and the matter secreted, he supposes that each cell may be influenced by two sets of nerve fibres, physiologically distinct—the one, *trophic*, exciting chemical processes in the protoplasm, and the other, *secretory*, having to do with the separation of the secreted products. The cranial nerves, of which the chorda is a branch, contain many secretory fibres and few trophic fibres, and hence the secretion excited by such nerves is copious and watery. On the other hand, the sympathetic contains numerous trophic fibres and few secretory fibres, and hence the secretion following its irritation is scanty and rich in formed elements. Strong or long continued stimulation acts on the secretory fibres, the secretory matters are used up, and thus the percentage of organic matter in the saliva diminishes, even in the case of sympathetic saliva. But as stimulation, more especially if gentle and intermittent, tends to increase the amount of protoplasm, by calling it into moderate action, the character of the cells undergoes changes, so that the central cells of the acinus disappear, and their place is taken by the rapidly growing cells of the periphery. This theory is certainly in the direction indicated by other lines of inquiry, as it points to two kinds of processes occurring in a gland cell, the one, anabolic, concerned in the up-

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[1] J. N. Langley on the "Physiology of the Salivary Secretion." *Journal of Physiology*, vol. x. No. 4.

[2] Heidenhain. Hermann's *Handb. d. Physiolog.* 1880, Bd. v.

building of protoplasm, and the other, katabolic, having to do with the decomposition or splitting up of complex substances. It is easy to conceive that each of these processes may be governed by a specific nerve filament. Recent investigations by Langley tend to show that the influence of the one nerve is not so independent of that of the other as was at first supposed. Thus stimulation of the cerebral nerve of the submaxillary, the sublingual, or of the parotid, increases the irritability of the gland for influences conveyed to it by the sympathetic.[1]

Chap. VIII.—DEGLUTITION.

After the food has been crushed into fragments or into pulp by the teeth, and mixed thoroughly with the saliva, it is moulded into a globular mass or bolus, and this is carried to the stomach by a complicated series of muscular movements, termed deglutition. The portions of the alimentary canal through which the bolus is carried are the pharynx and œsophagus.

The *pharynx* is a muscular bag or sac about 112 mm. in length, extending from the base of the skull to the lower border of the cricoid cartilage. It is continuous below with the œsophagus, and it has apertures in front communicating with the nose, mouth, and larynx. The *velum palati* projects backwards into it. The muscles of the pharynx are the superior, middle, and inferior constrictors, the *stylo-pharyngeus*, and the *palato-pharyngeus.* The three constrictors form an outer layer of muscular fibres, and these fibres pass more or less in a transverse direction, and the *stylo-pharyngeus* and *palato-pharyngeus* form an inner layer, having the fibres running longitudinally. The *velum palati*, or soft palate, is a curtain passing backward from the hard palate, and it shows a conical process, the *uvula*, in the centre, and two folds at the sides termed the *anterior* and *posterior pillars of the fauces*, having the tonsils lodged between them. The *isthmus of the fauces* is the constricted passage between the anterior pillars. The anterior pillar contains the *palato-glossus* muscle, while the posterior pillar is occupied by the *palato-pharyngeus* muscle. The soft palate is raised by the *levator palati*, and it is held tense against pressure from below and against the action of the *palato-glossi* and *palato-pharyngei*, which are depressors of the palate. The *azygos uvula*, situated in the uvula, raises and shortens that process. Lastly, we have to remember that seven openings lead into the pharynx—the two posterior openings of the nares, the two Eustachian tubes, the isthmus of the fauces, the opening of the larynx, and the passage into the œsophagus.

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[1] Langley, *op. cit.*

The wall of the pharynx is formed of three layers—mucous membrane, muscular layers, and fibrous or connective tissue layers. The mucous membrane of the portion opposite the fauces is covered with stratified pavement epithelium, and it contains numerous mucous glands. It also shows papillæ or foldings of the *membrana propria.* The epithelium of the upper portion is columnar and ciliated, even as low as the base of the uvula, although the boundary line is not always the same. Lymphoid or adenoid tissue is found below the mucous membrane in large quantities. This tissue forms the chief substance of the tonsils, as already explained (see p. 47), and it also forms a mass on the posterior wall stretching between the orifices of the Eustachian tubes. This is sometimes termed the pharyngeal tonsils. From this adenoid tissue numerous leucocytes migrate and form salivary corpuscles. The muscular tissue is of the striated variety, and the connective tissue layers consist of ordinary white fibrous tissue, intermingled with elastic tissue.

The *œsophagus*, or gullet, is the passage leading from the pharynx, at the base of the cricoid cartilage, and opposite the sixth cervical vertebra, to the stomach, passing through the diaphragm and entering the stomach opposite the tenth dorsal vertebra. Its length is about 237 mm. In a state of rest the lumen of the œsophagus is not that of a circle or oval, but it is star-shaped, owing to the mucous coat being thrown into longitudinal folds. The wall consists of three coats—an outer, muscular, a middle, composed of connective tissue, and an inner, mucous. The mucous membrane consists of a layer of stratified pave-

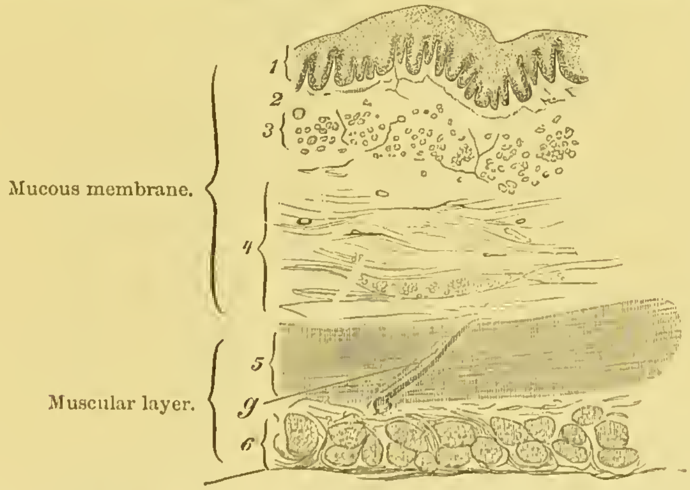

FIG. 31.—From a transverse section of the middle of the human œsophagus. × 10 d. 1, pavement epithelium; 2, tunica propria; 3, muscularis mucosæ; 4, submucous layer; 5, circular layer of muscular fibres; 6, longitudinal layer of muscular fibres; *g*, blood-vessel. (Method No. 18, Appendix.)

ment epithelium (Fig. 31, 1), and of a *tunica propria* bearing papillæ (2). Below this we find a layer of involuntary muscular fibres running longitudinally, termed the *muscularis mucosæ.* In the submucous coat, formed of connective tissue, there are numerous racemose mucous glands. These are most abundant near the lower end of the œsophagus, and in man the cells of these glands are columnar in shape. The œsophagus in the embryo is lined by columnar ciliated epithelium. The muscular layers in the upper part of the œsophagus present a red colour and consist of striated muscle, but lower down, the tissue is paler and the fusiform cells of involuntary muscle appear. At the lower end the tissue is composed entirely of involuntary muscle. In some animals striated muscle forms the greater part of the layer through the whole length of the œsophagus. Thus in the horse voluntary fibres may be found as low as opposite the base of the heart, and two spiral turns, of figure of 8 loops, pass round the layer of involuntary fibres as far as the end of the œsophagus. The movements of

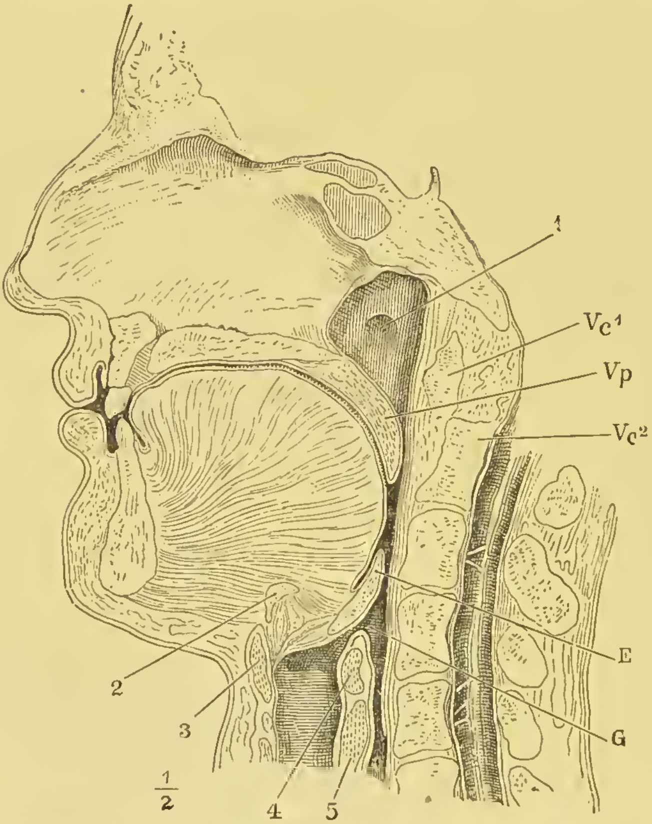

FIG. 32.—Median section through the head, showing the parts concerned in deglutition in a state of rest. Vc^1, Vc^2, first and second cervical vertebræ; Vp, velum palati; E, epiglottis; G, lower part of pharynx; 1, opening of Eustachian tube; 2, hyoid bone; 3, thyroid cartilage; 4, section of arytenoid muscle; 5, cricoid cartilage. (S. Mayer after Henle.)

striated fibres rise quickly to a maximum amount and then go quickly off again, while those of involuntary muscle reach the height of contraction slowly, and gradually go back to a state of rest. Hence in the œsophagus, the movements of the upper part are quick and of the lower part slow. The fibres are arranged in two layers, an inner circular and an outer longitudinal. The submucous layer is formed of connective tissue, with elastic fibres. The layers of the œsophagus are richly supplied with blood-vessels, and lymphatics are found both in the mucous and submucous coats. A small amount of adenoid tissue exists in the submucous coat. Between the muscular coats there is a network of nerve fibres, having here and there small masses or ganglia containing ganglionic nerve cells. A nervous plexus is also found in the submucous coat.

The process of deglutition may be divided into three periods. During the first, the bolus is carried through the isthmus of the fauces; in the second, it passes through the pharynx; and, in the third, it is carried through the œsophagus. The position of the parts at rest is shown in Fig. 32.

When the bolus arrives at the isthmus of the fauces, an involuntary and reflex movement commences, which it is impossible to stop. The tongue is carried backwards and its central portion elevated by the contraction of the *stylo-glossi* muscles; and, at the same time, by the action of its intrinsic fibres, the tongue changes its form, and pushes the bolus from before backwards, against the soft palate. The bolus then passes through the isthmus of the fauces, and the anterior pillars, by the contraction of the *palato-glossi* muscles, approximate behind it, so as to prevent its return into the mouth.

The bolus having now reached the pharynx, a series of simultaneous movements occurs, with the object, on the one hand, of preventing its entrance into the nose, and into the respiratory passage, and, on the other, of carrying it into the œsophagus. The position of parts is illustrated by Fig. 33.

(*a*) *Movements of the Pharynx.*—The lower jaw, having been fixed by the muscles of mastication pressing the dental arches against each other, or against a bolus of food, the pharynx is drawn upwards, and somewhat forwards, by the action of the *palato-pharyngei*, *stylo-pharyngei*, the constrictors, and the muscles passing from the lower jaw to the hyoid bone. The ascension of the pharynx is accompanied by a similar movement of the larynx, as may be observed by putting the tip of the finger on the larynx during the act of swallowing. At the same time, the constrictor muscles of the pharynx contract from above downwards, pressing the bolus against the soft margins of the palate and the root of the tongue, and so carry the bolus towards the œsophagus.

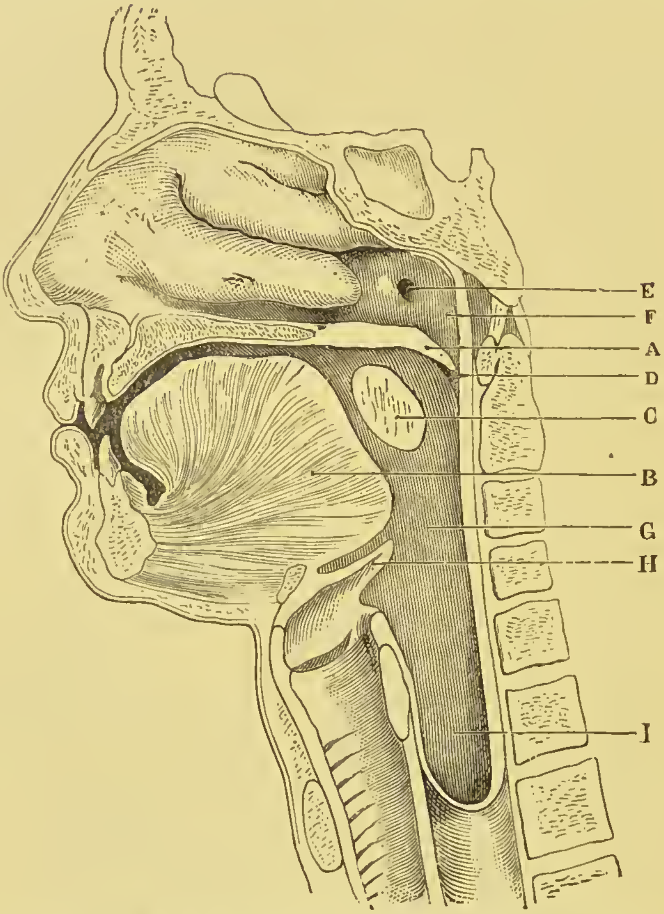

Fig. 33.—Median section through the head showing the position of parts during deglutition. E, Eustachian tube; F. upper part of pharynx shut off from lower part G by A, the velum palati; D, tip of uvula touching posterior wall; C, bolus of food; B, tongue; H, epiglottis; I, œsophagus (S. Mayer after Henle).

(*b*) *Closure of the Pharyngo-nasal Cavity.*—With the view of preventing the regurgitation of the food into the nasal openings, the soft palate is raised by the *levator palati* and made tense by the *tensor palati* muscles, the posterior pillars of the fauces are almost completely approximated by the action of the *palato-pharyngei*, and the small chink left between them is closed by the uvula, containing the *azygos uvulæ.* The posterior border of the soft palate is thus directed almost horizontally backwards, and nearly touches the posterior wall of the pharynx (Fig. 33).

According to Kronecker and Falk, by the energetic contraction of the mylo-hyoid muscles diminishing the cavity of the mouth suddenly, the bolus is propelled rapidly (in ·1 of a second) through the pharynx and œsophagus, and actually reaches the stomach before the muscular structures of these cavities begin to act. The contractions of the walls of the pharynx and œsophagus are, according to these observers, for the purpose of sweeping into the stomach any fragments left behind.

(*c*) *Closure of the Respiratory Passage.*—This is effected by closure of the glottis from close approximation of the true vocal cords and by depression of the epiglottis. These movements may be readily observed with a laryngoscope. The hyoid bone is carried forwards and upwards by the genio-hyoid, the mylo-hyoid, and the anterior belly of the digastric, and the larynx is pulled towards the hyoid bone by the thyro-hyoid. The larynx is thus brought below the root of the tongue, the vocal cords are approximated by the lateral crico-arytenoids, and the epiglottis is closed, like the lid of a box, over the *rima glottidis* by the pressure of the bolus and by the contractions of the aryteno-epiglottidean muscles.

Any remains of the food after the first sudden piston-like action of swallowing are carried downwards by the contractions of the pharynx into the œsophagus. When the bolus reaches the œsophagus, the pharynx falls downwards, the orifices of the mouth, nasal openings, and glottis, are opened, and the remains of food or fluids are carried from above downwards in the œsophagus by a series of successive contractions. The movement in the œsophagus is wavelike, as may be seen in the neck of a horse drinking water from a trough. Such movements are termed peristaltic. After all the food has entered the cardiac orifice of the stomach, the circular fibres round this orifice contract like a sphincter. This is the last act in the deglutition process.

According to most authorities, the Eustachian tube is opened during deglutition by the action of the *tensor tympani* muscle, but Cleland holds that it is closed during this act "by the thickening which accompanies the contraction of the *levator palati*, pressing up the membranous floor of the canal against the upper and outer wall, so as completely to obliterate the opening."[1]

The movements above described are excited by the action of a stimulus, such as a morsel of food or a few drops of liquid, touching the posterior parts of the tongue and the anterior parts of the fauces. They are facilitated by the food being slightly moistened, as it will be found almost impossible to swallow a perfectly dry powder. Thus Magendie found in the horse that when the flow of saliva into the mouth was prevented the time of swallowing dry food was much increased, and the movements were performed with difficulty. It is also to be noted that it is extremely difficult to perform the movements with the mouth open.

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[1] Cleland, *Journal of Anatomy*, iii. p. 97.

Kronecker and Meltzer found that the total duration of the movements of deglutition was about 6 sec., and that about half of that period was occupied by the movements of the lower part of the pharynx and of the œsophagus. Strictly speaking, according to the new views promulgated by Kronecker, Falk, and Meltzer, these movements really follow the rapid movement of true deglutition.

If the closure of the respiratory passage is not complete, as sometimes happens in rapid eating and drinking, particles of matter enter the larynx, and instantly give rise to a feeling of irritation or of choking. Several strong expiratory efforts are immediately made, and by the sudden puff of air the foreign particles may be expelled. The epiglottis is of great importance in the mechanism. If destroyed, fluids readily pass into the larynx and cause distressing symptoms of violent coughing.

Nervous Arrangements of Deglutition.—Deglutition affords an excellent example of a *complex reflex action.* Many muscles are involved in the process, and it is evident that they must be co-ordinated, both as regards time and amount of contraction, with the greatest nicety. The *sensory* nerves are branches of the fifth supplying the palate and tongue; of the glosso-pharyngeal, distributed to the tongue and pharynx; and the superior laryngeal of the pneumo-gastric, for the upper orifice of the larynx. The *centres* are situated in the *medulla oblongata* and *pons Varolii.* They are as follows:—(1) Motor nucleus of 5th below the lateral angle of the 4th ventricle; (2) nucleus of the 7th (facial) immediately behind the nucleus of the 5th, and deeply placed in the substance of the *pons;* (3) the nucleus of the pneumo-gastric and glosso-pharyngeal in the base of the posterior cornu in the lower part of the *medulla oblongata;* and (4) the hypoglossal nucleus in the base of the anterior cornu in the lower part of the *medulla oblongata.* It is to be observed that these nuclei of grey matter, containing nerve cells, are in close proximity to each other. The *motor* supply of the various muscles concerned in deglutition is as follows:—(1) The *thyro-hyoideus, genio-hyo-glossus, hyo-glossus,* and *stylo-glossus* muscles, and the intrinsic muscles of the tongue by the hypoglossal or ninth cranial nerve; (2) the elevators of the hyoid bone, namely, the anterior belly of the digastric and the mylo-hyoid by the mylo-hyoid branch of the inferior maxillary division of the fifth nerve, the posterior belly of the digastric and the stylo-hyoid by branches of the facial nerve, and the genio-hyoid also by the hypo-glossal; (3) the three constrictors of the pharynx, the *palato glossus* and *palato-pharyngeus,* by the pharyngeal plexus formed by the pharyngeal branch of the vagus, the glosso-pharyngeal, and the sympathetic—the inferior constrictor also receiving twigs from the external laryngeal branch of the superior laryngeal branch of the vagus; (4) the *stylo-pharyngeus* by a branch from the glosso-pharyngeal; (5) the *tensor palati* by a twig from the otic ganglion of the fifth; (6) the *levator palati* and *azygos uvulæ* by the facial through the petrosal branch of the Vidian; and (7) the lateral crico-arytenoid and the aryteno-epiglottidean muscles by the inferior laryngeal branch of the vagus.[1]

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[1] The relation between the movements of deglutition and of respiration will be discussed in treating of the nervous arrangements of respiration.

CHAP. IX.—STRUCTURE OF THE STOMACH AND INTESTINES.

A. THE STOMACH.

The general form and appearance of the *stomach*, along with its blood-vessels, is shown in Fig. 34. When moderately distended, it measures in length from 250 to 300 mm., and in breadth from 100 to 125 mm.

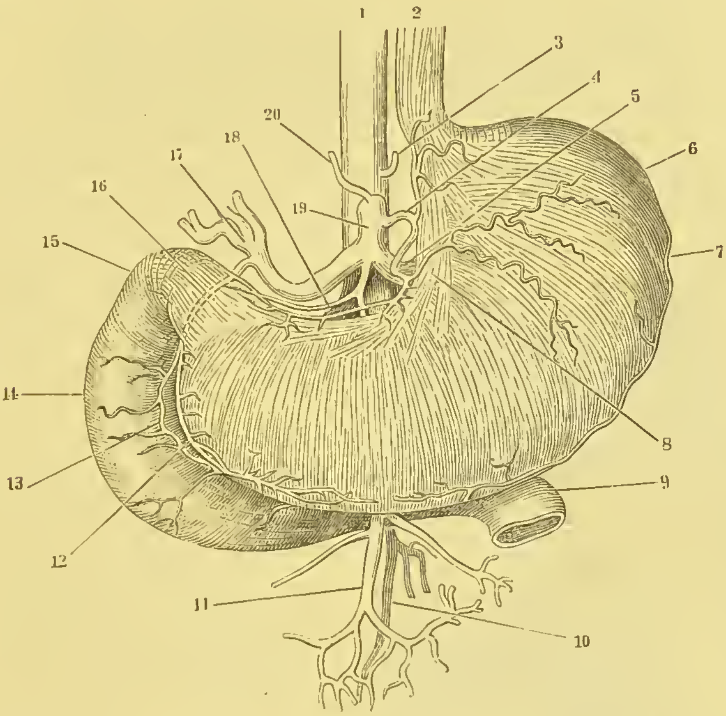

FIG. 34.—Front view of the stomach and duodenum. The organ has been distended, and its peritoneal covering dissected off. Quarter natural size. 1, descending aorta; 2, œsophagus; 3, left coronary artery to the lesser curvature (an occasional branch); 6, great cul-de-sac or fundus; 7, left gastro-epiploic artery, a branch of the splenic, passing along the greater curvature; 8, longitudinal muscular fibres of œsophagus radiating over the stomach and passing over to the pylorus; 9, end of the lower horizontal portion of the duodenum cut across; 12, right gastro-epiploic artery, a continuation of the gastro-duodenal, which is a branch of the hepatic, passing along great curvature; 14, descending portion of the duodenum; 15, upper horizontal part of the duodenum; 16, gastro-duodenal artery, passing behind the pylorus, and then continued as 12; 18, right coronary artery, a branch of the cœliac axis, passing to the lesser curvature. (Krause.)

The wall of the stomach, from 2 to 3 mm. in thickness, is formed of three layers, (1) the mucous membrane, (2) the muscular coat, and (3) the serous coat. The mucous membrane, sharply differentiated by its reddish-grey colour from the pale, almost white, lining of the œsophagus, is formed of epithelium, *membrana propria* or basement membrane, *muscularis mucosæ*, and a submucous coat (Fig. 36). The epithelium consists of simple cylindrical (columnar) cells which secrete mucus.

We can distinguish (Fig. 35) in each cell an upper portion *s*, containing mucin, and a lower protoplasmic portion *p*, containing a nucleus. The extent of the cell containing mucin varies according to the state of the cell. Certain cells from which the secretion has escaped are called cup or goblet cells. Between these cells at their base small round cells are found, which are either young epithelial cells or leucocytes. The *membrana propria* is formed of fibrillated connective tissue, so as to produce a network, and numerous leucocytes are found in the meshes. In the mucous membrane we find glands, the basement layer running up between them, in some places so as to form only a very thin layer; but in others, as near the pylorus, the glands are wide apart, and are separated by a thick layer of the tissue forming the *membrana propria*.

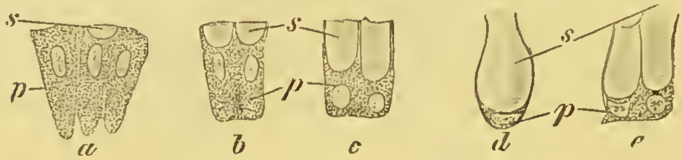

FIG. 35.—Secreting epithelial cells, from the mucous membrane of the human stomach. × 560 d. *p*, protoplasm; *s*, secretion; *a*, two cells in a resting state. The cell situated between these shows the beginning of the mucous metamorphosis; *e*, the upper wall of the cells on the right has burst, the contents have escaped, the granulated protoplasm has again increased, and the nucleus has again become round. (Method No. 18, Appendix.)

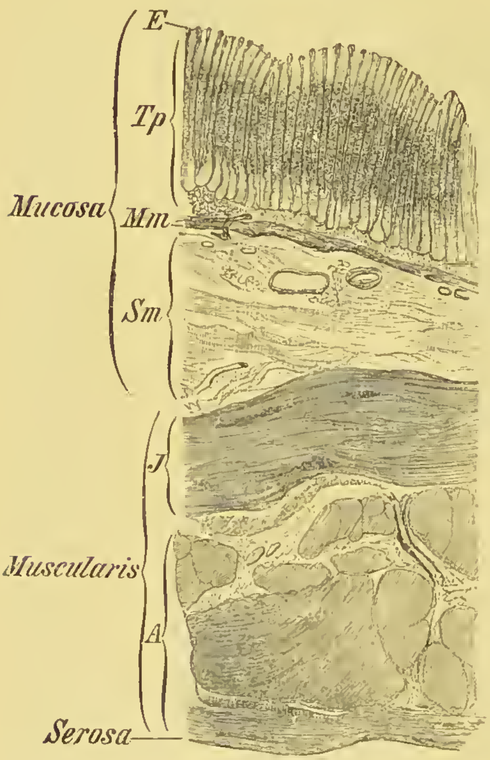

FIG. 36.—Vertical section through the wall of the human stomach. × 15 d. *E*, epithelium; *Tp*, tunica propria containing tubular glands, closely packed, so that they are best seen at their ends. *Mm*, muscularis mucosæ; *Sm*, submucous tissue showing sections of vessels; *J*, inner circular layer of muscular fibres; *A*, outer layer of muscular fibres showing transverse or oblique sections of bundles. (Method No. 19, Appendix.)

Two kinds of glands are found: (1) glands of the fundus, cardiac glands, or oxyntic glands,[1] and (2) glands of the pylorus. Both are simple or furcated tubes, closed at the deeper end, and they either singly or in groups open into small saucer-shaped

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[1] Oxyntic, from ὀξυς, acid, a name given by Langley because they contain the cells that secrete the hydrochloric acid of the gastric juice.

depressions on the free surface of the mucous membrane. Each gland consists of three portions—a neck near the surface of the mucous membrane, a body deeper down, and a blind end or cul-de-sac, and each gland shows a basement membrane lined with secreting cells. The *glands of the fundus* show cells of two kinds, *principal* or *central* or *adelomorphous*[1] cells, and *parietal*, *border*, *delomorphous*, or *oxyntic* cells. The principal cells are clear, cylindrical, or cubical cells, having some granular protoplasm (due, according to Klein, to a network of fine fibres) surrounding a globular nucleus. These cells disappear quickly, and after death they soon lose their normal appearance. The border or marginal cells are large, dark, and irregularly angular, almost globular cells, having finely granular protoplasm surrounding a globular nucleus (Fig. 37). They are readily stained, especially with the aniline dyes. The principal cells line the tube, and the marginal cells, irregularly distributed, abound chiefly in the neck and body. In the body of the gland they form almost a continuous layer, but they are pushed to the side of the gland by the principal cells (Fig. 39 *c*). The *glands of the pylorus* are lined throughout with cylindrical (columnar) cells, having a round nucleus near the attached end of the cell, and in the intermediate zone between the gastric proper and the pyloric regions of the stomach, a few cells may be found resembling marginal cells. In the region of the pylorus also, in the dog, peculiar dark cone-shaped cells have been found, the nature of which has not been ascertained. During digestion, both classes of cells become darker and more granular, and the nuclei of the cells near the pylorus are found near the middle of the cell.

FIG. 37.—Lower half of an isolated gland of the fundus from stomach of rabbit. × 240 d. *B*, border or marginal cells. The sharp line *M* represents the *membrana propria*. (Method No. 20, Appendix.)

Heidenhain has traced the changes in the glands of the fundus from their condition during fasting to that seen after digestion has begun. During fasting the tubules are shrunken, and the marginal cells do not bulge from their sides. An hour after receiving food, they bulge from the side and are much increased in size, and the central cells are also very granular. A little later, as the digestive period comes to a close, the cells again shrink in volume. According to Langley, the principal cells, which are very granular while the gland is at rest, become differentiated into two zones when the gland is active. Some of the granules are dissolved and discharged with the secretion, and the others crowd towards the lumen, so that the outer third or half of the cell, next the basement membrane, becomes clear and transparent. After digestion has ceased, the cells again become granular.

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[1] Adelomorphous, ἄδηλος, hidden, a name given by Rollet.

The *muscularis mucosæ* consists of two or three layers of smooth (involuntary) muscular fibres, interwoven together, and sending delicate branches among the tubular glands. The submucous coat is formed of loose connective tissue, intermingled with elastic tissue, and containing here and there groups of fat cells.

As regards the *muscular coat*, it is only in the pyloric region that two distinct layers are apparent. There are a strong internal circular layer and a weaker external layer. In other regions, the arrangement of the fibres is very complicated, chiefly on account of the longitudinal fibres of the œsophagus passing obliquely over the other coats. Bundles of muscular fibres are thus found running in all possible directions. The serous coat is formed of peritoneum.

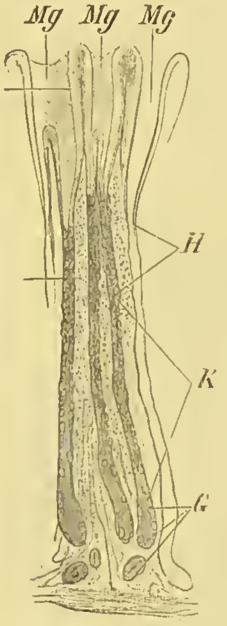

FIG. 38.—Vertical section through the mucous membrane of the human stomach. × 50 d. The very narrow lumen of the glands of the fundus is not visible. *Mg*, Alveolar depressions on surface of mucous membrane. In these the surface epithelial cells of the mucous membrane may be seen from the side and also from above. Into the middle depression (*Mg*, in centre) two glands open, and into the left depression, one gland. *H*, neck; *K*, body; *G*, bottom of gland. (Method No. 21, Appendix.)

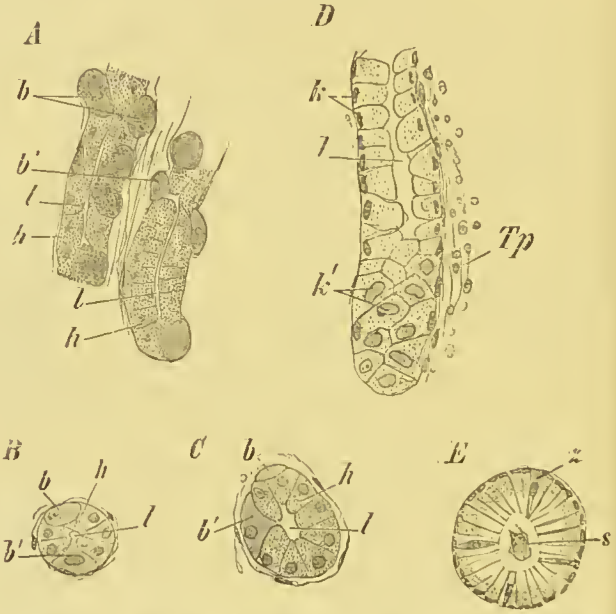

FIG. 39.—*A*, longitudinal, and *B*, transverse section of a fundus gland in a cat. *C*, transverse section of a fundus gland in man, near the bottom of the gland. × 240 d. *b*, marginal cells; *h*, principal cells; *l*, lumen of gland; *bb*¹, marginal cells reaching the lumen. *D*, Longitudinal section of gland in pyloric end of human stomach, × 240 d, showing lower end of gland, its upper part beginning exactly in the middle of the illustration. Observe in the upper part the lumen, *l*, and the position of the nuclei of the gland cells, *k*. The lower part of the gland has been cut near the periphery, so that we see on the surface the flat nuclei, *k*¹, of the gland cells. *Tp*, tunica propria containing numerous leucocytes. *E*, Transverse section of gland from pyloric portion of stomach of dog; *s*, secretion in lumen; *z*, dark cells with large nucleus. × 240 d. (Method No. 22, Appendix.)

B. The Intestines.

These consist of the small and the large intestines. The small intestine commences at the pylorus and terminates at the junction of the ileum with the great intestine. In an adult man, the length of the small intestine is about 6 metres. It is divided into (1) the duodenum, ·3 metre, (2) the jejunum, 2·280 metres, and (3) the ileum, 3·420 metres in length. The great intestine extends from the termination of the ileum to the anus. Its length in an adult is about 1·8 metre, and it is divided into (1) the cæcum, ·062 metre, with the vermiform appendix, (2) the colon, 1·538 metre, and (3) the rectum, ·200 metre in length.

The ratio of the length of the intestines to the length of the body varies much in different animals. Thus in the cat it is as 4 : 1, in the dog as 5 : 1, in man as 9 : 1, in the horse as 12 : 1, in the pig as 16 : 1, in the ox as 20 : 1, and in sheep and goats as 26 : 1. These figures show that the relative length of the canal is much greater in herbivora than in carnivora. Although the horse, which is herbivorous, has a comparatively short canal, the capacity of its intestines is very great. The capacity of the intestinal canal of an ox (exclusive of the stomach) is about 80 litres, while that of a horse is 200 litres; but the capacity of the stomach of the ox is about 200 litres, and that of the horse, only from 10 to 18 litres, so the total capacity of the whole intestinal canal of an ox is much greater than that of a horse. As the capacity of a dog's intestine is about 8 litres, the contrast with that of a herbivorous animal is striking. The capacity of the intestine of omnivorous animals is indicated by that of the pig, 27 litres. The human intestine of an adult has a capacity of about 20 litres. According to Munk the surface of the intestinal mucous membrane, amounts, in the ox, to 15, in the horse, to 15·5, in the pig, to 3, and in the dog, to ·5 square metres.

The wall of the intestine, like that of the stomach, is composed of (1) mucous membrane, (2) muscular layers, and (3) a serous layer. The mucous membrane consists of epithelium, resting on a *tunica propria*, a *muscularis mucosæ*, and of a submucous coat. The *epithelium* is formed of cylindrical cells, showing on their free surface a band or border of denser matter than the rest of the cell. (See Fig. 147, p. 301, Vol. I. 3.) The protoplasm of the cell is granular and often shows small refractive globules of fat. The lower end of the cell is often bifurcated or pointed and extends into the tissue of the *tunica propria*. If the cells undergo mucous degeneration, they give rise to cup or goblet cells, seen in Fig. 35, *d*, and presenting an appearance like a cup with a circular mouth. (See also Fig. 40.) Numerous leucocytes are found between the epithelial cells, and young epithelial cells exist in the *tunica propria*. The *tunica propria* is formed of reticulated connective tissue, containing leucocytes. It forms a thin layer along the bases of the glands found in the mucous membrane and it runs up between the glands. It is also, in the small intestine, elevated into numerous cylindrical processes, about 1 mm. in height, which project from the mucous membrane. These are termed intestinal *villi.* The free end of a villus is shown diagrammatically in Fig. 42. They exist in immense numbers—10 to 18 in a sq. mm. in the duodenum, and from 8 to 14 in a sq. mm. in the ileum. Krause states that their total number is about 4,000,000. Numerous connective tissue cells occur in villi, more especially at the upper end, between the lacteal and the base of the epithelial cells. The glands found in the *tunica propria* are known as *Lieberkühnian glands or crypts* (Fig. 43). They are simple tubular glands lined throughout with cylindrical cells, serous in character in the small, and mucous in the large, intestine. In the small intestine the mouths of these glands are sometimes arranged like a wreath round the bases of the villi. The *muscularis mucosæ* consists of an inner circular and of an outer longitudinal layer of involuntary muscle, and from it fibres pass into the villi, running nearly to their tips. Transverse muscular fibres are also found in the villi of man, and by the contraction of these longitudinal and transverse fibres, the forms of the villi are

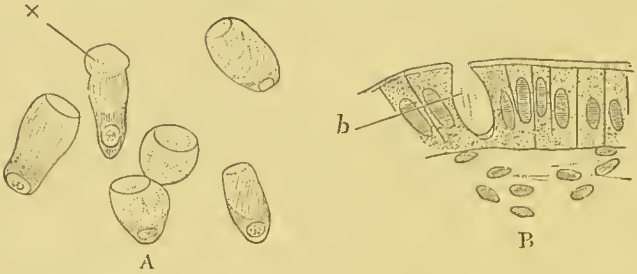

Fig. 40.—Goblet cells, × 560 d. A, from a rabbit; ×, mucus escaping; B, from man; *b*, a goblet cell between cylindrical cells.

Fig. 41.—A villus in a state of contraction, from the small intestine of a rabbit. × 70 d.

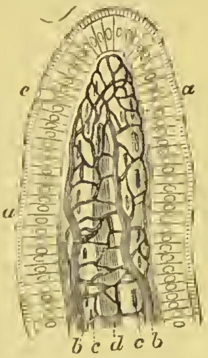

Fig. 42.—Diagrammatic view of the upper portion of a villus. *a a*, columnar or cylindrical epithelium; *c*, goblet cell; *b b*, artery and vein; *c*. nuclei of connective tissue; *d*, lacteal.

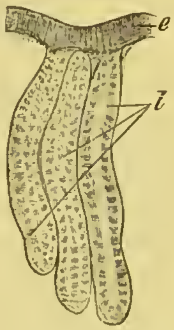

Fig. 43.—Three Lieberkühnian glands from the intestine of a rabbit. × 80 d. *e*, epithelium on upper surface. *l*, the glands. (Method No. 23, Appendix.)

altered. The *submucous coat* is formed of loose fibrillar connective tissue. In this coat and in the region of the upper half of the duodenum only, we find small racemose glands, known as *Brunner's glands* (Fig. 44, *br*). The duct of each Brunnerian gland, lined by cylindrical cells, passes through the *muscularis mucosæ* and runs in the *tunica propria* parallel with Lieberkühn's glands, above described. The acini of the glands are formed of a structureless *membrana propria* lined with cylindrical cells. The absorptive surface of the small intestine is much increased by numerous reduplications of the mucous membrane passing transversely, termed *valvulæ conniventes.*

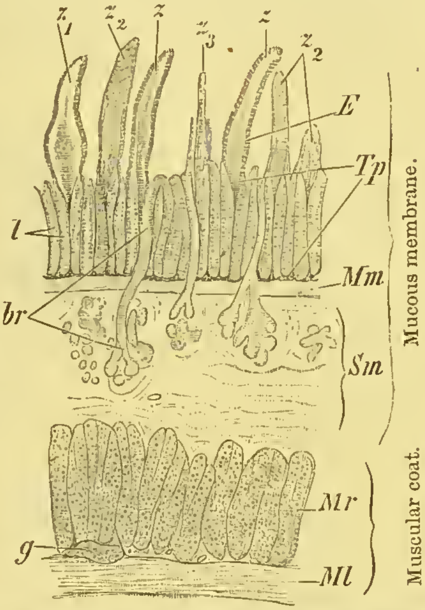

FIG. 44.—Section through the duodenum of a cat. × 30 d. *E*, epithelium. *Tp*, tunica propria. *Mm*, muscularis mucosæ, consisting in the cat of a longitudinal layer only. *Sm*, submucous coat. *Mr*, circular band of muscular fibres cut transversely. *Ml*, longitudinal layer of muscular fibres. *br*, Brunnerian glands. *g*, ganglion cells in Auerbach's plexus. *z*, villus cut along its axis; z_1, villus showing the epithelium raised from connective tissue; z_2, villus cut obliquely; z_3, epithelium has fallen off the villus, showing the connective tissue naked. (Method No. 24, Appendix.)

The *lymphoid tissue* of the intestine requires careful attention. Throughout the whole length of the bowel numerous leucocytes are found in the *tunica propria.* They may be either sparsely distributed, or they may be found in little masses, from ·5 to 2 mm. in diameter. These masses may be collected apparently at one spot so as to form nodules, and these nodules, if found single, are termed the *solitary* glands of Peyer, and if there are groups of nodules, they constitute an *agminated* gland of Peyer, or a *Peyer's patch.*

A few *solitary* glands are found in the stomach, but they abound in the intestines in considerable numbers. They are round or oval masses in the *tunica propria,* and at an early period of development, their upper surface is immediately under the epithelium while the lower surface rests on the *muscularis mucosæ.* With advancing growth they burst through the *muscularis mucosæ* and penetrate into the submucous tissue. The part in the submucous tissue soon assumes a globular form and becomes of greater size than the portion in the *tunica propria.* The complete form of a gland is thus like that of a pear, with the narrower end directed towards the epithelial surface. No villi cover the solitary gland, and as the gland grows it presses the Lieberkühnian glands to the side. The gland consists of adenoid tissue. In the centre of each we find protoplasmic matter forming a germ centre, and the leucocytes formed in it pass into the neighbouring lymphatics or wander through the epithelial cells, and some of the latter covering the surface of the gland often contain leucocytes which have been captured during their transit.[1]

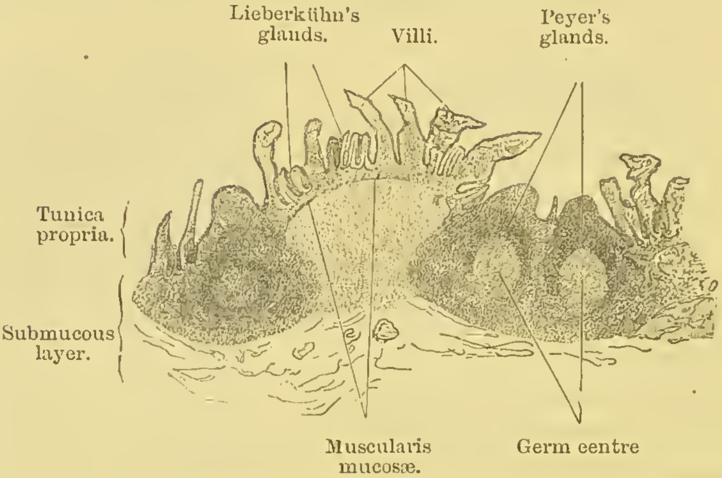

FIG. 45.—Vertical section of mucous membrane of intestine of man. × 20 d. Showing three glands of a Peyer's patch. The one on the left has been cut exactly through the middle. The submucous tissue between the glands contains numerous leucocytes. (Method No. 25, Appendix.)

A *Peyer's patch* is a group of from 10 to 60 nodules, each of which alone would form a solitary gland. These lie side by side, never above each other, and by pressure each gland may be flattened, instead of being globular or pear-shaped. Such groups are found chiefly in the lower part of the small intestine, the ileum. Sometimes, instead of individual glands, broad irregularly shaped masses of adenoid tissue may be found in this part of the bowel, and the same arrangement may be met with in the *appendix vermiformis*, in man.

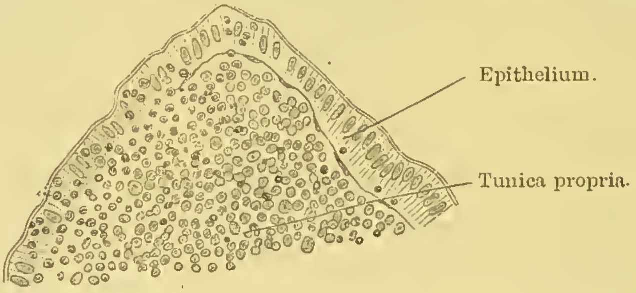

FIG. 46.—From a vertical section of the small intestine of a kitten seven days old. × 240 d. Summit of a solitary gland. On the left the epithelial cells contain leucocytes, and on the right three leucocytes may be seen in the cells. (Method No. 26, Appendix.)

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[1] P. Stöhr, Ueber die Lymphknötchen des Darmes. *Archiv. für Mikroskop. Anatomie.* Bd. xxxiii.

The *muscular coats* of the intestine consist of an internal circular and of an external longitudinal layer of involuntary muscle. The circular coat is considerably thicker and stronger than the longitudinal coat. In the great intestine, the external longitudinal layer is not uniformly distributed round the tube but exists in three bands, each of which, however, is very thin.

The opening from the small into the large intestine is guarded by the *ileo-cæcal valve*, consisting of two segments. The upper segment is horizontal, the lower somewhat oblique, with a narrow slit-like aperture between them. When the cæcum is full, the folds come into apposition, so that no matters can pass back into the ileum, while they may pass freely from the latter into the great intestine. Each segment is a fold of mucous membrane, containing some muscular fibres belonging to the circular coat. Villi exist only on the ileac surfaces of the segments.

C. Special Features in the Physiological Anatomy of the Stomach, Intestines, and Peritoneum.

1. The Blood-Vessels of the Stomach and of the Intestine.—The vascular arrangements of the stomach and of the great intestine resemble each other, and those of the small intestine are somewhat modified by the presence of villi. The small branches of the arteries ramify on the serous coat, then penetrate the muscular layers, which they supply, and finally spread out into a capillary network in the submucous coat. From this, delicate branches pass through the *muscularis mucosæ* to the *tunica propria* and form a network near the base of the glands. Delicate capillaries (4·5 to 9 μ in diameter) pass from this network, run in a spiral manner round the tubular glands, and form another network of wider capillaries (9 to 18 μ) surrounding the mouths of the glands. From these wider and superficial capillaries small veins originate which descend between the tubules to a venous network in the *tunica propria*.

In the small intestine, only the minute arteries distributed to the Lieberkühnian glands have the arrangement above described. The arteries supplying the villi (Fig. 47, *a*) form a capillary network in the villus, close under the epithelium. At the point of the villus these capillaries unite to form the radicle of a small vein (Fig. 47, *v*), which then receives, as it descends perpendicularly, the small capillaries spirally surrounding the mouths of the glands, or rather the small veins originating from these. The veins then pass on to the plexus in the *tunica propria*, as already described. Brunner's glands are surrounded by a capillary network supplied by the submucous blood-vessels. A capillary network surrounds the solitary and agminated glands, out of which minute vessels pass into the interior of the gland, but these do not always reach the centre, so that a non-vascular area is found in the middle of the gland.

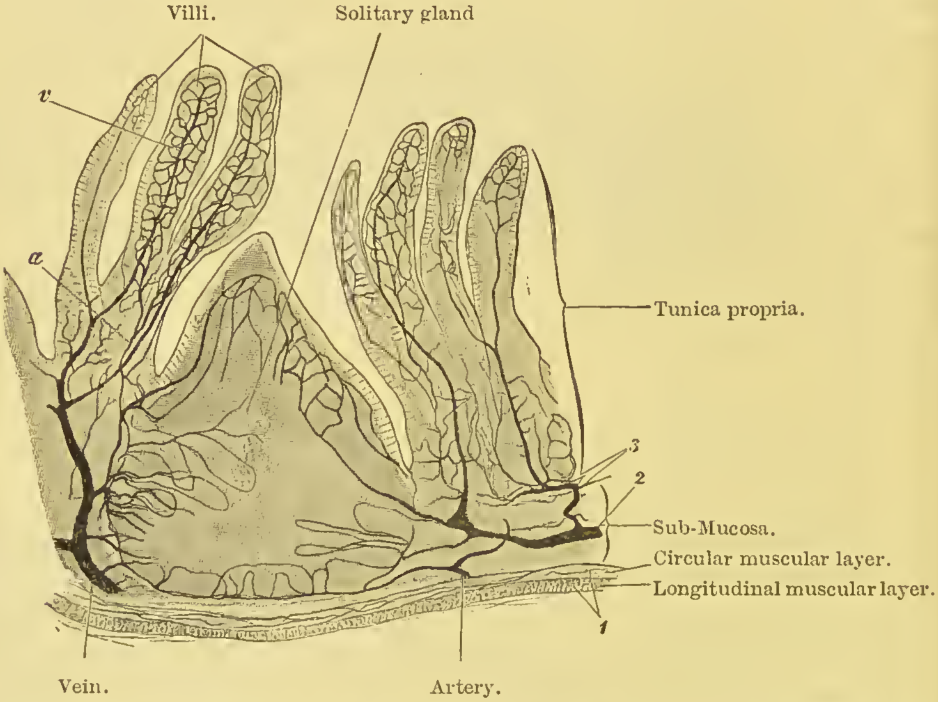

FIG. 47. Transverse section of injected small intestine of rabbit. × 50 d. The solitary gland is so divided that in its upper half the minute capillaries entering the gland are seen. The Lieberkühnian glands are not seen in a thick section of this kind. 1, network in the muscularis mucosæ; 2, in the submucous coat; and 3, in the *tunica propria*. (Method No. 27, Appendix.)

2. **The Lymphatics of the Stomach and Intestine.**—These begin in the stomach and great intestine as delicate vessels, closed at the upper end, and about 30 μ wide, descending between the tubular glands. In the small intestine, a small vessel termed a *lacteal* is found in the centre of each villus, from 27 to 36 μ in width. These lacteals join a narrow meshed network of lymphatics (lacteals) at the base of the tubular glands, and this network is united to a deeper wide-meshed network in the submucous coat. Lymph vessels, furnished with valves, spring from this, penetrate the muscular coats, and here they receive the vessels of a network of lymphatics between the circular and longitudinal layers. The muscular tissue is richly supplied with lymphatics. The lymph vessels, which have thus collected lymph (or chyle, the term given to the fatty-albuminous matter absorbed by the lacteals in the villi) from all parts of the coats of the intestines, run along the serous coat as far as the attachment of the mesentery, and

then they pass between the layers of this membrane to the mesenteric glands. The Peyerian glands have a network of lymphatics surrounding them, but none of these penetrate the gland. In the small intestine of the rabbit large lymph sinuses are found between the glands forming a Peyer's patch.

3. **The Nerves of the Stomach and of the Intestines.** The stomach is supplied by the pneumo-gastric nerves, and by branches of the sympathetic derived from the solar plexus. The nerves of the small intestine come from the superior mesenteric plexus, formed from branches of the pneumo-gastric nerve, the semilunar ganglion, and the cœliac plexus. The branches follow the divisions of the superior mesenteric artery. The large intestine is supplied by branches of the inferior mesenteric and hypogastric plexuses. The numerous nerve filaments, consisting chiefly of non-medullated fibres, form a network under the serous coat, then penetrate the longitudinal layer of muscular fibres, and spread out so as to form a plexus between the muscular layers. This plexus between the longitudinal and circular coats is called the *plexus myentericus*, or *Auerbach's plexus*. Small nervous nodules, or ganglia, containing multipolar ganglion cells, occur at the points where the fibres join to form a meshwork. The meshes are either angular or round in form.

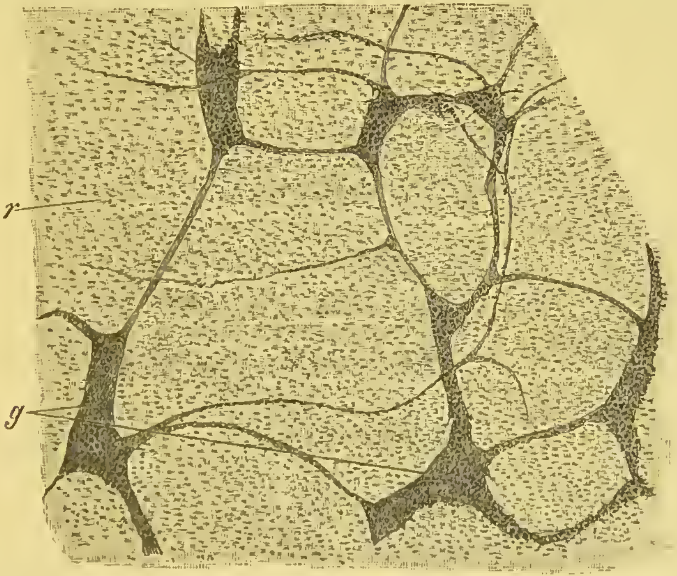

FIG. 48. Auerbach's plexus from a young dog. × 50 d. *g*, group of ganglion cells. *r*, circular muscular layer, recognizable by the oval nuclei. (Method No. 28, Appendix.)

From this plexus numerous non-medullated fibres issue, some of which terminate in the involuntary muscular fibres, while others pass through the circular muscular coat and form another, and more delicate, plexus in the submucous coat, known as *Meissner's plexus*, in which both the ganglion cells and the meshes are smaller than in the plexus of Auerbach. Fibres pass from Meissner's plexus to the glands, but the mode of their termination is unknown (Figs. 48 and 49.)

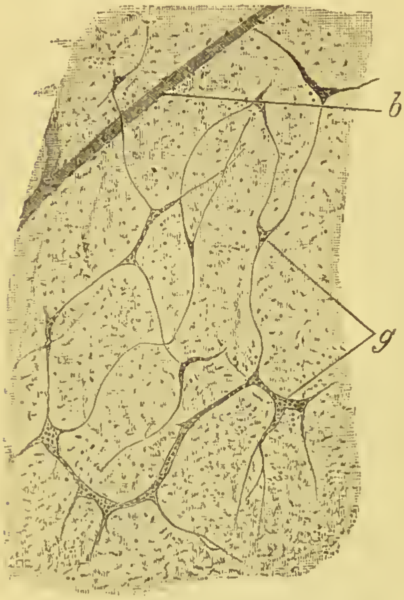

FIG. 49. Meissner's plexus from a young dog. × 50 d. *g*, group of ganglion cells; *b*, blood vessel. (Method No. 29, Appendix.)

The Peritoneum.—The outer covering of the stomach and intestines, termed the peritoneum, consists of bundles of connective tissue and of numerous elastic fibres. It is covered by a single layer of flat polygonal epithelial cells. The connective tissue bundles are stronger in the layers of the peritoneum forming the mesentery and lining the parietes of the abdomen, than those forming the layer covering the viscera, and they run in all directions so as to form a network. In the middle of the great omentum we find meshes of very regular form. A few connective tissue corpuscles are found among the fibres, and they are more numerous in young animals. The elastic fibres are numerous, more especially in the parietal layer. The subserous coat consists of connective tissue, having elastic fibres intermingled. On the outer surface of the intestine and on the surface of the liver, this coat is so thin as to be scarcely seen, but it is thicker where the serous coat can be caused to glide on the deeper coats. It contains lymphatics and capillary vessels. A few delicate nerve fibres terminate in Vaterian or Paccinian corpuscles.

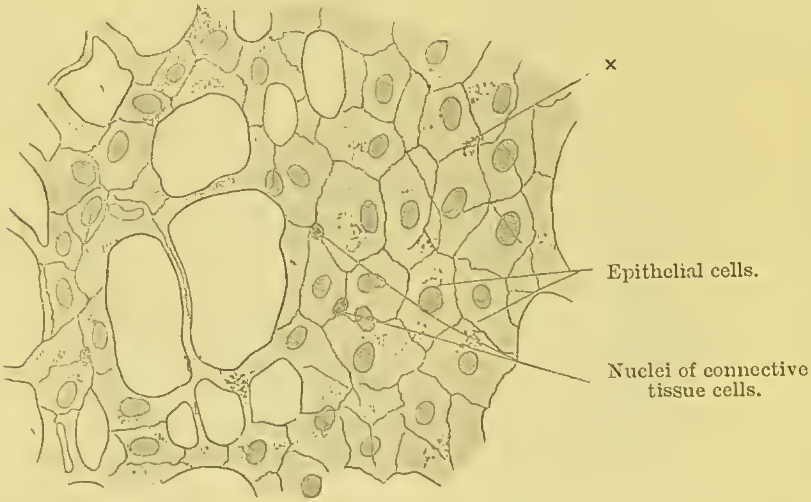

FIG. 50.—From the great omentum of a rabbit. × 240 d. Connective tissue bundles form the meshes. At × indication of epithelial cells on the other side of the omentum. (Method No. 30, Appendix.)

CHAP. X.—DIGESTION IN THE STOMACH.

When the food reaches the stomach it is subjected to the action of a juice secreted by the glands in the mucous membrane of that organ. It is also moved in the stomach, so as to bring it into intimate contact with the juice, and as portions are successively digested they are expelled into the duodenum. These movements are effected by rhythmic contractions of the muscular layers in the walls of the viscus.

1. **The Movements.**—When the stomach is empty, its greater curvature is directed from above, downwards, but when it is filled, the stomach rotates on its horizontal axis, so as to cause the greater curvature to look forwards and the lesser to look backwards. By this arrangement, the stomach dilates in the direction of least resistance, that is, towards the anterior abdominal wall. The food is directed from the cardiac end in two streams, one along the great cul-de-sac and along the greater curvature to the pyloric opening, and the other along the lesser to the same opening. At the pyloric opening, the two streams join to form another current, which passes back to the cardiac opening almost through the central part of the cavity. There is thus a rotatory movement imparted to the contents of the stomach. Such movements are not continuous. They occur at short intervals of time and last for a few minutes. The stimulus exciting the movements is the mechanical contact of the food with the mucous membrane, and probably also the gastric juice, now being secreted, may act as a chemical stimulus. By these movements the food is thoroughly mixed with the fluids poured into it from the mucous membrane of the stomach. During digestion, the pyloric orifice is firmly closed by the contraction of a strong band of fibres forming a sphincter, which relaxes occasionally so as to permit the passage of digested matter from the stomach into the duodenum. The movement necessary for emptying a portion of the contents into the duodenum is of a different kind from that already referred to. It has more of the character of a sudden active contraction, and it is most marked near the pylorus. These movements of ejection occur soon after a meal, and they are repeated at intervals of 15 or 20 minutes, until the meal has been digested and the stomach emptied. The nerves which supply the stomach are the pneumo-gastric and the sympathetic (splanchnic). Stimulation of the sympathetic nerve does not excite movements. whereas, when the pneumo-gastric is stimulated, vigorous movements occur in the cardiac end, especially if the stomach is distended. As such movements persist for a time, after division of both nerves, there

can be no doubt that ganglionic centres exist in the nervous plexuses in the wall of the organ. Sometimes spontaneous contractions occur near the pylorus, and they are arrested when the splanchnics (more especially the left splanchnic), are irritated. It would thus appear that movements of the wall of the stomach depend primarily on local centres, that impressions travelling along certain fibres of the vagus may stimulate such movements, or make them more active, and that filaments in the splanchnics exert an inhibitory or restraining influence. If the wall of the stomach be struck sharply with a blunt edge, or if induction shocks be applied to a portion of it, local circular contractions will appear, and the movement may be propagated in a wave-like manner along a short extent of the wall of the organ. In this experiment the long latent period characteristic of involuntary muscle is very evident.

Closely connected with the mechanisms just described is the act of *vomiting*, which occurs so frequently in disease as to merit attention. Vomiting may be caused: (1) by the introduction into the stomach of an irritating substance, which may act either directly on the stomach itself, or by being absorbed into the blood, may influence reflex centres associated with the movements of the stomach and allied organs (foreign bodies, undigested food, worms, bile, such emetics as mustard, sulphate of zinc, sulphate of copper, etc.); (2) by the action of poisonous substances introduced into blood-vessels or absorbed by the skin, which may influence the stomach directly or the reflex centres above alluded to (injection of tartar emetic into vessels or absorption by inunctions of emetine, apomorphia, ipecachuana, etc.); (3) by irritations occurring in other organs which appear to influence the reflex centres (pregnancy, abdominal tumours, calculi, passage of gall-stones, etc.); (4) by irritations in the neighbourhood of reflex centres themselves (inflammatory actions at base of brain, as in acute tubercular meningitis); and (5) by psychical conditions, such as feelings of loathing and disgust either on seeing a disagreeable object or even remembering an object which previously excited those feelings. The peculiar kind of vomiting and nausea known as sea-sickness is associated with disturbance of the sense of equilibrium.

Vomiting is usually preceded by a sensation called *nausea*, and by a flow of saliva into the mouth. The first event is a deep inspiration. The diaphragm descends, the lungs are filled with air, and the glottis is closed. The contracted diaphragm affords a fixed surface against which the stomach may be pressed, either by its own contractions, or by pressure of the abdominal muscles. Sometimes there is an escape of gas from the œsophagus or stomach immediately before vomiting. The cardiac orifice of the stomach is then opened by contraction of the longitudinal fibres of the œsophagus, and the walls of the stomach contract spasmodically, so as to force the food into the œsophagus, as it cannot escape through the pyloric orifice, in consequence of the sphincter remaining firmly contracted.

In the *horse*, the cardiac and pyloric orifices are not far apart, so that when the stomach is compressed pressure acts almost equally on the two orifices. The cardiac orifice is also guarded by a flap of mucous membrane, the sphincter at the pyloric orifice is so weak as to offer little resistance in this direction, and, lastly, in this animal the stomach does not touch the abdominal wall. By these anatomical arrangements, vomiting becomes almost impossible, and when the walls of the stomach contract strongly, the contents of the stomach are driven into the small intestine, and there may be a dejection of excrement, but no vomiting upwards. In carnivora, on the other hand, as in the dog, the cardiac sphincter is weak and the pyloric sphincter strong, and when the walls of the stomach and the abdominal walls contract strongly, there is vomiting upwards, because the cardiac orifice opens, and often a dejection from the bowel at the same time, as the contents of the intestine, when submitted to pressure, cannot escape upwards, owing to the firmly shut pylorus. The greater the size of the fundus of the stomach, the more difficult is it to empty the organ by vomiting. Hence children, in whom the fundus is not greatly developed, vomit more easily than adults.

The matters thus ejected into the œsophagus are carried upwards into the pharynx by an anti-peristaltic movement; sometimes the orifices of the larynx and the nasal passages are closed by the same mechanism as has been described in deglutition, but frequently, in consequence of the violence of the action, matters may be forced into these openings. In violent vomiting, the stomach is forcibly squeezed against the diaphragm and vertebral column by contractions of the abdominal muscles.

Regurgitation of food from the stomach occurs as a normal act in ruminants, and human beings are sometimes met with who have this power. It is then termed *merycism*. *Eructation* is a violent expulsion of gas from the stomach, and causes a sound in the upper part of the œsophagus.

The nervous centre concerned in vomiting is in the *medulla oblongata*, and is closely associated with the deep origins of the glosso-pharyngeal and the pneumo-gastric nerves. There is no reason for supposing that a special centre for vomiting exists. The various mechanisms are brought into play by the irritation of centres connected with deglutition, the movements of the stomach, the movements of the muscles of the abdomen, and the movements of respiration, and the peculiar disturbances in the rhythm of these movements that occur in vomiting probably are caused by the streaming out of nervous impulses from one centre to the other. Almost any strong afferent impulse, from any organ of the body, may stimulate these centres so as to cause the movements of vomiting.

2. **The Action of the Gastric Juice.**—For purposes of experimental investigation, gastric juice has been obtained in various ways. Thus Spallanzani and Reaumur caused animals to swallow a small perforated metallic sphere, in which a bit of sponge was inserted, and which could be withdrawn from the stomach by a thread, or expelled by vomiting. Again, cases have occurred in human beings in which a fistulous opening through the walls of the abdomen into the stomach has become permanent. Permanent fistulous openings have been established in animals. The method of making such openings was first practised by Bassow in 1842. Investigations into the digestive process have also been conducted outside of the body by the use of an artificial gastric juice, obtained by treating the mucous membrane of the stomach of the dog or pig, first with alcohol, and afterwards with glycerine, and acidulating the fluid with hydrochloric acid. Eberle, in 1834, was the first to study digestion outside the body by the use of an artificial juice.

The most famous case of gastric fistula that ever occurred, inasmuch as observations made by means of it laid the foundation of our knowledge of the process of digestion, is that of Alexis St. Martin, a Canadian, eighteen years of age, who, when in good health, was accidentally wounded by the discharge of a musket on June 6th, 1822.

> "The charge," says Dr. Beaumont, who, after conducting the case to a successful issue, so far as the life of his patient was concerned, took the man into his employment and conducted a careful and elaborate series of investigations, "consisting of powder and duck shot, was received in the left side, at a distance of one yard from the muzzle of the gun. The contents entered posteriorly, and in an oblique direction, forward and inward, literally blowing off the integuments and muscle to the size of a man's hand, fracturing and carrying away the anterior half of the sixth rib, fracturing the fifth, lacerating the lower portion of the left lobe of the lung, the diaphragm, and perforating the stomach."

From this injury he recovered; but, twelve months after the accident, a perforation into the stomach, two and a half inches broad, still remained. Subsequently, a small fold of the mucous membrane of the stomach appeared, and increased in breadth till it filled the aperture and acted as a valve, opening from without inwards. Cases of gastric fistula in the human being are rare, but up to 1859 forty-seven had been recorded.

Physical Characters of Gastric Juice.—When obtained pure, it is a limpid colourless fluid with an acid reaction, having an odour somewhat like that of old vinegar. Its specific gravity in man is from 1002 to 1003, and in the dog from 1005 to 1009. Under the microscope it exhibits no well-defined histological elements. It rotates the plane of the vibrations of polarized light to the left.

Chemical Composition of Gastric Juice.—The gastric juice of man contains about ·5 per cent., while that of the dog may amount to 2·5 per cent., of solid matter. A free *acid* always exists, namely, hydrochloric acid. Gastric juice of the human being contains from ·1 to ·17 or even ·3 per cent., and that of the dog ·3 per cent. The mineral salts are chiefly chlorides, about ·2 per cent., namely, alkaline chlorides, chloride of ammonium, chloride of calcium, the alkaline and earthy phosphates, and traces of iron. It contains usually a small amount of albuminous matter, as indicated by the opalescence caused by the addition of bichloride of mercury. The principal organic constituent is *pepsin,* a substance belonging to the class of ferments, which, as usually seen, is a greyish white, amorphous powder, slightly soluble in water, but readily soluble on the addition of acid to the water.

Formation of Gastric Juice.—The blood is brought, as already described, to the glands of the fundus and of the pylorus, fluid plasma oozes out of the capillaries so as to bathe the *membrana propria* and the cells situated on it, and from this plasma, the glandular cells secrete the elements of the juice. The principal cells of the pyloric glands are the seat of the formation of pepsin. In a starving animal, the principal cells are clear and far outnumber the marginal cells, but when secretion begins, the marginal cells rapidly increase in number, and the principal cells, although for a short time they increase in size, soon decrease in size. Towards the close of digestion the principal cells again increase in size and become clear, while the marginal cells decrease. The inference is that the marginal cells are formed out of the principal cells, chiefly during secretion. The marginal cells have to do with the formation of the hydrochloric acid. Heidenhain, with antiseptic precautions, succeeded in separating a portion of the fundus of the stomach of dogs from the rest of the organ, and, while leaving its vascular attachments to surrounding parts, so as not to interfere with its blood supply, he made an opening into the portion of the stomach thus shut off, and stitched its margins to the edges of the fistulous opening in the abdominal wall. A cul-de-sac of the fundus, opening externally, was thus formed. By a similar operation on another dog, a cul-de-sac of the pyloric end was formed. (Three out of seven animals survived the operation.) He found that the cul-de-sac of the fundus secreted a juice containing pepsin and hydrochloric acid. The pyloric cul-de-sac yielded a viscid alkaline juice which quickly digested fibrin after the addition of ·1 per cent of hydrochloric acid. It therefore contained pepsin. Now, as principal cells are found in both the glands of the pylorus and the glands of the fundus, and marginal cells only in the glands of the fundus, it follows that pepsin must be secreted by the principal cells, and hydrochloric acid by the marginal cells. Brücke showed that the deep portion of the glands of the fundus is neutral or slightly alkaline, while acidity is found only near the mouth. This fact indicates that the acid is expelled at the moment it originates in the gland cell. Brücke's observation has been corroborated by a beautiful experiment carried out by Claude Bernard. He injected a solution of ferrocyanide of potassium into one vein of an animal, and lactate of iron into another vein. These substances strike a blue colour only in the presence of a free acid, and accordingly he found, on killing the animal, that only the surface of the mucous membrane of the stomach was stained by Prussian blue.

There is no satisfactory explanation of the curious fact of the formation of free hydrochloric acid from an alkaline fluid, the blood. It is evident we must look to the chlorides, and especially to sodium chloride, as the source of the acid, but the difficulty is to explain the decomposition of these by any acid, so as to set free the chlorine, which, by combining with hydrogen, forms hydrochloric acid. The only acid present in the blood is carbonic acid, and it has been supposed that the chlorides may be decomposed by it. This is a very unlikely supposition. Maly has suggested that lactic acid is first formed by the lactic fermentation, and that it in turn decomposes the chloride of sodium, liberating chlorine, which will be at once seized by hydrogen to form hydrochloric acid. Ralfe has attributed the production of the acid to the passage of electric currents through the mucous coat causing a reaction between the carbonate of soda and the common salt of the blood—thus, $NaHCO_3 + NaCl = Na_2CO_3 + HCl$. None of these views is free from obvious objections. No suggested chemical reaction, bringing into play a new agent in the shape of a hypothetical acid, will explain the phenomenon. It is more likely to be due to molecular dissociation of chlorides, and possibly of water, brought about by the activity of the protoplasm of the cells specially devoted to this action, and the fact of immediate separation of the acid is favourable to this view. The base set free during the active formation of acid is eliminated from the blood by the kidneys, and accordingly we find that the acidity of the urine is, putting it generally, in inverse ratio to that of the stomach.

The granular matter in the interior of the principal cells appears to have no action on albuminous substances, but, if treated with sodium chloride or hydrochloric acid, pepsin is produced, and the albuminous matters are changed into peptones. It is thus evident that the granules do not consist of pepsin, but of a substance from which pepsin is derived. This substance is called *pepsinogen.* Thus, if we have removed from the mucous membrane of the stomach, by means of water or of glycerine, all the pepsin, we can obtain more pepsin by treating it afterwards with solutions of hydrochloric acid or of common salt. It has been supposed that the pepsin is united to a proteid in the glandular cell, and that it is liberated by the acid. Suppose that both pepsinogen and pepsin exist in a fluid, it has been ascertained that a 1 per cent. solution of carbonate of soda destroys more pepsin than pepsinogen, and that, on the other hand, a current of carbonic acid destroys more pepsinogen than pepsin. Both substances are decomposed or rendered inert at 54° C. to 57° C. (Langley and Edkins). The amount of pepsin in the juice varies as the digestive process goes on. It appears to fall at the beginning, to reach a minimum in the second hour, then to rise gradually to a maximum in the fourth or fifth hour, after which it returns to its usual proportion. Pepsin does not appear in the mucous membrane of the fœtal stomach until near the end of fœtal life. Hamersten has found it in the last week in the rabbit, and in the third week before birth in the dog. Beaunis states that in the fœtus of a dog, on the fifty-seventh day of intra-uterine life, he found that the mucus of the stomach neither contained acid nor could digest fibrin, but the mucus obtained just before birth had digestive powers.

Quantity secreted.—Great variations have been observed, from ·1 to 10 per cent. of the body weight. The pepsin in gastric juice varies from ·2 to 1·2 per cent. It is important, for experimental purposes, to recollect that it is readily given up to glycerine, so that we may obtain a digestive glycerine-extract by cutting the well washed mucous membrane in small pieces and immersing them in absolute alcohol for twenty-four hours. This is then poured off, and the pieces are allowed to macerate for several weeks in strong glycerine. The more elaborate method of Von Wittich of obtaining pepsin is to rub up the mucous membrane of the pig's stomach with powdered glass, and allow the mass to lie in strong glycerine for eight days. The fluid is then strained through a cloth, and mixed with alcohol. This precipitates the pepsin. Pepsin may also be obtained by Brücke's method of pouring on the mucous membrane, first a 5 per cent. solution of phosphoric acid, and afterwards a quantity of lime water. The phosphate of lime precipitated carries the pepsin with it. The precipitate is collected on a cloth, thoroughly washed with water, and then dissolved in a ·5 per cent. solution of hydrochloric acid. A solution of cholesterin, in 4 parts of alcohol and 1 of ether, is prepared, and this is added to the fluid containing the pepsin—a precipitate of cholesterin along with pepsin is thus obtained. This is washed with water slightly acidulated with acetic acid, then with water alone, and then with ether. The ether dissolves the cholesterin, and when the ether is drawn off, the watery fluid left contains pepsin. Krasilnikow has succeeded in dialyzing pure gastric juice. The pepsin remains on the dialyzer. It is then dried in vacuo and pulverized.

The following is an analysis of the gastric juice of man as contrasted with that of the dog and sheep, given by Hoppe-Seyler from the researches of C. Schmidt[1] :—

In 1000 Parts.	Man.	Dog.	Sheep.
WATER, - - - - - - -	994·40	973·0	986·14
Pepsin and Organic Matter, - -	3·19	17·1	4·05
Chloride of Sodium, - - - -	1·46	2·5	4·36
Chloride of Potassium, - - -	0·55	1·1	1·52
Chloride of Ammonium, - - -	...	0·5	0·47
Chloride of Calcium, - - - -	0·06	0·6	0·11
Free Acid, - - - - - - -	0·20	3·1	1·23
Phosphate of Lime $Ca_32(PO_4)$, - -	0·12	1·7	1·18
Phosphate of Magnesia, $Mg_32(PO_4)$, -		0·2	0·57
Phosphate of Iron, $FePO_4$, - -		0·1	0·33

The process of digestion, as already mentioned, may be carried on artificially. It goes on most efficiently at a temperature of from 35° to 40° C. Lowering the temperature delays the process until we reach 4° C., when it is entirely arrested. To show the action, take well washed fibrin, or boiled fibrin, or small pieces of hard boiled white of egg, and place several pieces in a number of small beakers. To one beaker add a little of the glycerine extract of pepsin, and it will be found that even after a period of several hours, at a temperature of 40° C., no solution has been effected. In another beaker place a little fibrin, along with a ·2 per cent. solution of hydrochloric acid, and in the course of half an hour the fibrin will become swollen and transparent, but it will not be dissolved. In this case, the fibrin has been changed to *syntonin*. In a third beaker place a few flakes of fibrin, along with a supply of a ·2 per cent. solution of hydrochloric acid and a few drops of glycerine extract of pepsin, and leave the beaker over a water bath, at a temperature of about 40° C. It will be found that in from one to two hours the fibrin will have entirely disappeared.

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[1] The third decimal figure has been omitted. See Hoppe-Seyler's *Physiologische Chemie*, p. 220.

Chemical Action of the Gastric Juice.—The gastric juice may also contain a milk-curdling ferment, to be afterwards mentioned, and occasionally a lactic acid ferment, which changes milk sugar into lactic acid. In the first stage of the process syntonin is formed, and this may be precipitated by careful neutralization with an alkali. At the same time, a portion of the proteid matter remains in solution in the neutralized fluid. This was first termed by Lehmann, in 1850, *pepton*, or *peptones*. These are bodies readily soluble and diffusible, and consequently in a condition permitting of ready absorption into the blood. Peptones are distinguished from albuminous substances by the following general characters :—

1. They are readily soluble in water.
2. They diffuse through organic membranes with great facility, and their endosmotic equivalent is small.
3. They are not coagulated by boiling, as happens with ordinary albumin.
4. They are not precipitated by mineral acids, nor by acetic acid and ferrocyanide of potassium, nor by the perchloride of iron, sulphate of copper, nor by the majority of metallic salts.
5. They are precipitated by tannic acid, corrosive sublimate, iodo-mercuric-iodide, phosphotungstic, and phospho-molybdic and picric acids.
6. They give *in the cold* a deep red or purplish red colour when added to an alkaline solution of hydrated cupric oxide, produced by adding caustic soda or caustic potash in excess to a solution of sulphate of copper. This is termed the *biuret reaction.*
7. They rotate the plane of polarized light to the left.
8. Kühne and Chittenden obtained a peptone which may be regarded as absolutely pure, and it had the following characters : Dried at 105° C., it is a dry light yellowish powder. It rapidly absorbs water from the air.

"It becomes sticky like pitch and melts to a tough mass, which does not become visibly thinner. What is truly surprising is the behaviour of the peptone towards water. A bit of the powder wet with a small drop of water hisses and steams like phosphoric anhydride when moistened, and when this—the powdered but not absolutely dry preparation which no longer hisses—is dissolved in water, a development of heat is to be noticed."[1]

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[1] Kühne and Chittenden on "Peptones," *Studies from Laboratory of Physiological Chemistry in Yale University*, 1885-6, p. 22.

In addition to true peptone, another albuminous body is formed, called *hemialbumose*, or propeptone. This substance is soluble in water, and it is precipitated from an aqueous solution by nitric acid. If, however, the precipitate is heated, it entirely dissolves, and is again precipitated in the cold. It may again be dissolved by excess of nitric acid. It gives the same reaction as true peptone with an alkaline solution of hydrated cupric oxide. Early in the process of digestion we find a large amount of hemialbumose and only a small amount of peptone, but as the process goes on, less and less hemialbumose and more and more peptone are found, until at the close there is only a little hemialbumose with a large quantity of peptone. The action is essentially a gradual hydration.

The researches of Kühne, Chittenden, Halliburton, and others, show that the conversion of proteids into true peptones is accompanied by the formation of a number of intermediate bodies, to which Halliburton's name of proteoses may conveniently be given. For example, if we digest albumin or fibrin, we may find, according to the stage at which we examine the products, (1) parapeptones, or syntonin, precipitated on neutralization with sodium carbonate; (2) proto-albumose, (3) dysalbumose, (4) hetero-albumose—all three precipitated by sodium chloride; and (5) deutero-albumose, still obtained from the fluid (after separation of the others) by adding acetic acid. All albumoses are precipitated by ammonium sulphate. These bodies, of which the last is nearest in chemical constitution to a peptone, may all be regarded as marking so many stages in the process. Kühne has indicated another important view of the matter, by stating that the proteid molecule may be split up into two groups—antipeptone bodies and hemipeptone bodies. The antipeptone molecule may be further decomposed by the ferment *tripsin*, in the pancreatic juice, into leucin and tyrosin, while the hemipeptone molecule, apparently more stable, is not further split up.

To obtain peptones from a fluid in which they have been formed, neutralize with barium carbonate, evaporate slowly, and filter. Add sulphuric acid to the filtrate. This precipitates the barium. Filter, and evaporate the filtrate to obtain the peptones.

The following quotation from Kühne and Chittenden[1] states how the presence of peptones may be ascertained:—

"In order to be certain of the presence of peptones in a digestive fluid, it must be made slightly acid with acetic acid, rubbed up with ammonium sulphate till saturated, and then filtered from the excess of salt and the albumose precipitate. If the filtrate is thereupon treated with a large excess of strong sodium hydroxide and then a few drops of a very dilute cupric sulphate be added, the appearance of the rosy-red colour of the biuret reaction will indicate the presence of peptones. If peptones are absent the fluid will be pure blue without a tinge of violet, since the solution can contain no other albuminous body."

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[1] Kühne and Chittenden, *op. cit.* p. 15.

The following conditions favour or retard the transformation of albumin into peptones: it is accelerated by a temperature of 40° C., and by movement, and, on the other hand, it is retarded by fall and rise of temperature, being arrested at 5° and 60° C. Alkalies rapidly destroy pepsin. Alcohol precipitates it, but the precipitate is redissolved by water in large excess. The salts of the heavy metals, concentrated solutions of alkaline salts, sulphurous and arsenious acids all arrest digestion. Small quantities of common salt favour it. Large draughts of cold water may retard it. The presence of an excess of peptones in the fluid also hinders the process, probably by the fluid becoming too concentrated.

Peptones agree in elementary composition with albuminous substances. Hoppe-Seyler first put forward the view that they are formed by a process of hydration, a molecule of water becoming united to a molecule of albumin. This view is confirmed by the fact that if we act upon peptone with a substance having the power of removing a molecule of water from it, such as anhydrous acetic acid, the peptone may be reconverted into precipitable albumin. Peptones may also be formed by the action of hydrochloric acid alone. Thus by the action of a ·4 per cent. solution of hydrochloric acid at a temperature of from 40° C. to 60° C. for several hours, they are produced. They are also formed by prolonged boiling of albuminous substances with water alone, and especially if boiled under pressure in a Papin's digester. In each of these cases the conversion of albumin into peptone is slow, and the special advantage of true pepsin digestion seems to be its rapidity. As to the action of the acid, it is important to note that while hydrochloric acid is the most effective agent, its place may be taken by solutions of ·1 to ·5 per cent. of phosphoric acid, of ·5 per cent. of acetic, or oxalic, or of succinic acid. Lactic acid may also be substituted.

Many theories have been advanced to explain or account for the apparently simultaneous action of the pepsin and the hydrochloric acid in digestion, and it cannot be said that any one is satisfactory. The most recent is that of Chandelon,[1] which suggests that the pepsin unites with syntonin to form a compound called syntonin-pepsin and oxygen. The syntonin-pepsin unites with water and hydrochloric acid to form peptone, zymogen (pepsinogen), and free hydrochloric acid. Lastly the zymogen or pepsinogen unites with the oxygen set free in the first change to reform pepsin. There is thus a cycle of changes, and the equations given by Chandelon show that the pepsin and hydrochloric acid are decomposed

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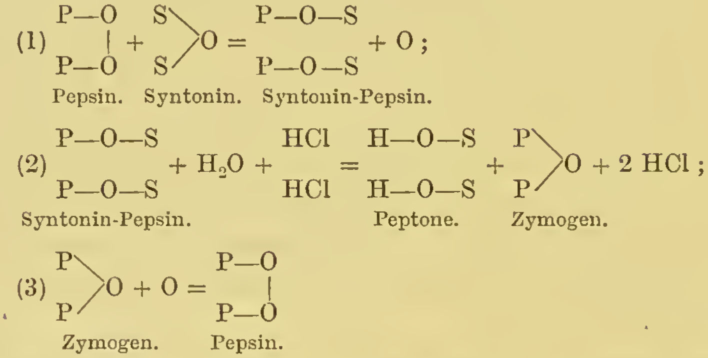
[1] Chandelon, *Bulletin de l'Académie Royale de Méd. de Belgique*, 1887, i. p. 289.

and re-formed in each cycle, and that thus a limited amount of these substances may carry on the digestive process. Thus—



3. **General Conditions of Digestion.**—The conditions which affect digestion in the stomach are the following :—

(*a*) The secretion of gastric juice is incessant during the whole period of digestion in the stomach, and the food is mixed with the most suitable proportions of acid and of pepsin, and in the most convenient state of dilution.

(*b*) The peptones are absorbed by the blood-vessels of the stomach along with other soluble matters and water as quickly as they are formed, or, they may pass with the rest of the food into the small intestine.

(*c*) The movements of the stomach also facilitate the action of the gastric juice by bringing successively all parts of the food into close connection with the juice secreted by the mucous membrane.

4. **Nervous Arrangements connected with the Secretion of Gastric Juice.**—When the stomach is empty and at rest its lining membrane is of a pale greyish colour and is covered with a small amount of alkaline fluid, probably mucus. When excited mechanically by food, or by a stimulating substance, such as a weak alkaline fluid, the mucous membrane becomes pink or even red in colour, drops of a clear fluid ooze from the surface, and fluid is copiously poured from it. The secretion may also be excited by emotions or feelings, as when we see or smell or even remember a savoury dish, a fact which indicates that it is connected with the central nervous system. Rutherford has shown that when the pneumo-gastrics are cut during digestion the mucous membrane of the stomach becomes pale, and that stimulation of the peripheral end produces no effect while stimulation of the central end causes the membrane again to become red. These facts show that impulses are transmitted from the stomach to the *medulla oblongata* along the vagus which

inhibit the action of a vaso-motor centre in that part of the nervous system. When this occurs, the nervous energy passing from it to the vessels of the stomach is weakened or removed, and consequently the vessels of the organ dilate. The motor tract by which influences pass to the vessels of the stomach so as to maintain them in a state of partial contraction is in the splanchnic nerves. The secretion may also be stimulated by the action of sapid substances on the sensory nerves of the mouth and tongue. Thus Richet observed in a case of gastric fistula (artificially produced, by Verneul, in a woman whose œsophagus had been occluded by a caustic alkali) that when sugar or lemon juice was placed on the tongue, gastric juice was secreted in the stomach. Any direct influence on gastric secretion, as in the case of the salivary glands, has not been discovered. In one case (a dog), Claude Bernard saw a flow of gastric juice after galvanization of the pneumo-gastric, but in another case there was no such effect. He also once observed that electrical irritation of the filaments going to the stomach from the semi-lunar ganglia arrested the secretion. Local centres no doubt exist in the stomach which have an influence both on the blood-vessels and on secretion. Even after division of both vagi below the œsophagus, if the animals (rabbits) survive, digestion has been found to go on in a normal way.

5. **Results of Digestion in the Stomach.**—By the combined influence of temperature, movement, and the action of the gastric juice, the food is reduced to a mass of matter having an acid odour and a colour and appearance varying according to the nature of the food.

This matter is called *chyme*, and it consists of various salts; of water; of saccharine matter, which has been obtained from starch by the action of the saliva; of starch which has escaped the action of saliva or has been set free by rupture of the walls of vegetable cells containing it; of fatty matter, either introduced as such in the food, or set free from animal cells; of albuminous substances of various kinds, either as peptones or in process of conversion into such; and of indigestible materials which are unsuitable for being acted upon by the digestive fluids. It is important to note that gastric digestion consists of two stages: first, a short stage in which the saliva swallowed with starch continues its diastatic action on that substance; and second, a prolonged stage of true peptonization, due to the action of the gastric juice. When the amount of acid in the juice reaches ·5 per cent., the diastatic action of saliva ceases. This amount may be reached in man in about half an hour after a meal.

The stomach always contains gas, either derived from the air swallowed from the mouth, or from the gases of the intestines. The oxygen of the air swallowed is absorbed by the vessels, and carbonic acid is exhaled, in a manner analogous to what occurs in the lungs. Thus the gas in the stomach is poor in oxygen and rich in carbonic acid. After a vegetable diet, Planer found that the gases from a human stomach contained the following volumes per cent. : carbonic acid, 33·83 ; hydrogen, 27·58 ; nitrogen, 38·22 ; and oxygen, ·37. Some of the hydrogen and carbonic acid was probably derived from butyric acid fermentation. He also found in the stomach of a dog 67 per cent. of nitrogen, 6 per cent. of oxygen, and 27 per cent. of carbonic acid. The acid of the gastric juice may hinder the butyric fermentation and thus the amount of hydrogen may be small in some cases.

1. ACTION ON PROXIMATE PRINCIPLES.

(*a*) *Fibrin* swells, and in a short time is dissolved so as to form a clear fluid, which is not affected by heat, being changed into peptone.

(*b*) *Fluid* or *Raw Albumin* assumes a milky appearance, then becomes coagulated, and is ultimately changed into peptone and albumose.

(*c*) *Solid or Coagulated Albumin* swells, assumes a flocculent appearance, slowly disintegrates, and in course of time is reduced to a soft pulp, which ultimately dissolves, with formation of peptones.

(*d*) *Casein* forms, after a considerable time, a turbid solution, which contains peptones. A substance containing phosphorus, similar to nuclein, is also said to be formed.

(*e*) *Glutin.*—Raw glutin disappears very quickly in the gastric juice, and it does not show the pulpy covering seen in semi-digested masses of other albuminous matters. When cooked, its digestion is the same as that of coagulated albumin.

(*f*) *Fat.*—A very small amount is decomposed into fatty acids and glycerine.

(*g*) *Syntonin* is quickly converted into a coherent jelly, which is transformed into peptone.

(*h*) *Legumin* is quickly digested in gastric juice, and this may occur with the action of acid alone, as legumin contains a substance analogous to pepsin.

(*i*) *Gelatin* is dissolved rapidly in the gastric juice without being previously converted into a pulpy mass, and the solution does not gelatinize on cooling, as a solution of ordinary gelatin would do.

(*k*) *Gastric Juice* has no action upon cellulose and starch, but it dissolves gum, cane sugar, and other soluble substances.

(*l*) *Salts* soluble in acidulated water, such as carbonates and phosphate of lime, are dissolved, whilst carbonates are transformed into chlorides with liberation of carbonic acid.

(*m*) *Milk Sugar* may be changed into lactic acid by the lactic ferment (*Bacterium lactis*), or it may be partly converted into grape sugar.

2. ACTION ON ALIMENTARY SUBSTANCES.

(*a*) *Milk* is rapidly coagulated in the gastric juice; the sugar and the salts dissolved in the fluid part are quickly absorbed ; the fat, in the form of butter, is liberated by rupture of the walls of the milk globules ; and the casein is converted by the gastric juice into peptone. Milk is not coagulated by the hydrochloric acid of the gastric juice, but by a special ferment. This is shown by the fact that the addition of carefully neutralized gastric juice to milk will soon cause coagulation. On the other hand, if the juice has been previously heated to 60° C., or to 100° C., no coagulation follows its addition to the milk. The inference is that a special ferment exists. This is called *rennet or milk curdling ferment.* The special peculiarity of this ferment is that it is readily destroyed by even weak alkaline solutions. It is said that 1 part of rennet can coagulate 800,000 of casein. Sometimes little masses of undigested casein escape into the duodenum, and these often enclose little drops of butter.

(*b*) *Muscle.*—The fibres are separated by the solution of the connective tissue; the transverse striæ become well marked, and the fibres show transverse cleavage. By these processes, the fibres are broken up into particles, which disappear. Muscle is more rapidly digested when cooked, probably because that operation assists in breaking down the fibres.

(*c*) *Connective Tissues.*—Such tissues as ligaments, tendons, membranes, and cartilages, especially if raw, are slowly dissolved. Cartilage may yield a chondrin-peptone and a copper-reducing substance. When cooked, they are acted upon in the same manner as gelatin. Corneous tissue, such as epidermis, nails, hair, wool, and nuclei are unaffected by the digestive fluid. Very prolonged digestion may dissolve elastic tissue, and an elastin-peptone may be formed. During digestion, fat is set free by the solution of the cell walls. Red blood corpuscles are dissolved by the gastric juice, the hæmoglobin becomes of a black brown hue, and decomposes into hæmatin and globulin. Globulin is changed into peptone. Mucin is unaffected. Bits of bone assume a corroded appearance, as if they were dotted over with little pits, in consequence of the acid having dissolved portions of the earthy salt. Bones may be completely digested in the stomach of a carnivorous animal.

d) *Vegetable Substances.*—In the raw condition, these are not easily digested by the human being, in consequence of their nutritive materials being usually enclosed in cellulose walls. Cellulose is not affected by the gastric juice. When cooked, the walls of cells are softened or ruptured so as to set free the sugar, starch, or glutin, contained in them, which are then acted upon in the manner already described. Some kinds of gum may be changed by the gastric juice into a saccharine substance capable of reducing salts of copper.

(*e*) *Salts.*—The gastric juice decomposes or dissolves certain salts, such as phosphate of lime and carbonates. The decomposition of carbonates leads to the evolution of carbonic acid. Thus the earthy salts in bone, phosphates, carbonates, and traces of fluoride of calcium, are dissolved out of the organic matter of bone. The latter is then digested into gelatin-peptone.

Rapidity of the Digestive Process.—Numerous experiments made with artificial digestive fluids have shown that digestion goes on much more slowly in such fluids than in the stomach. According to the experiments of Beaumont upon St. Martin's stomach, the rapidity of digestion varies according as the food is more minutely divided, whereby the extent of surface with which the gastric fluid can come in contact is increased. Liquid substances are for the most part at once absorbed by the vessels, and any solid matters suspended in them, as in soup, are concentrated into a thicker material before the gastric juice operates upon them. Solid matters are affected so rapidly during health, that a full meal, consisting of animal and vegetable substances, may be converted into chyme in about an hour, and the stomach left empty in about two hours and a half. Beaumont found that among the substances most quickly digested were rice and tripe, both of which were digested in one hour. Eggs, salmon, trout, apples, and venison were digested in one hour and a half; tapioca, barley, milk, liver, and fish in two hours; turkey, lamb, and pork in two hours and a half. Beef, mutton, and fowls required from three to three and a half hours, and these were more digestible than veal. These facts were different from what was anticipated, and show that prevailing notions as to the digestibility of different kinds of food are erroneous. It must be remembered, however, that easy digestibility does not imply high nutritive power. A substance may be nutritious, though so hard as not to be easily broken down; and many soft, easily digested materials may contain a comparatively small amount of nutriment.

In the dog, when fed on animal food, the digestive process begins as soon as food is introduced into the stomach. It reaches its maximum about the second hour, decreases from that time to the ninth hour, and is finished about the twelfth hour. As the diastatic action of the saliva of the dog is weak, starchy matters in its food are not changed into maltose and dextrin, and they pass from the stomach into the intestine unaltered.

General Conditions.—Excluding individual peculiarities, these may be briefly stated as follows:—(1) The quantity of food taken—the stomach should be moderately filled, but not distended; (2) the time which elapsed since the last meal—this should always be long enough for the food of one meal to have completely left the stomach before more is introduced; (3) the amount of exercise previous and subsequent to a meal—gentle exercise being favourable, and over-exertion injurious to digestion; (4) the state of mind—tranquility of temper being apparently essential to perfect digestion; (5) the bodily health; and (6) period of life—digestion being more active in the young than in the old.

The question as to *why the stomach does not digest its own walls* may be shortly discussed. The explanation does not lie in the fact that these tissues are in a state of life, because if the legs of a living frog or the ear of a living rabbit, still retaining their connection with the animal, are introduced into the stomach by a fistulous opening, they will be at least partially digested. This has been proved by various observers. The probable explanation is that the great vascularity of the stomach, more especially at the time when secretion is active, is the cause of its protection. The large supply of alkaline blood will neutralize the acid, which escapes, as we have seen, into the cavity of the stomach the moment it is formed. This view is supported by the fact that any cause stopping the flow of alkaline blood, such as ligature of the gastric arteries, or sudden death arresting the circulation while digestion is in progress, is often followed by a softening or partial digestion of the stomach. In cases of sudden death, such *post-mortem* digestion is often extensive, eating away a portion of all the coats of the organ, and even corroding neighbouring organs, such as the spleen, liver, and even the diaphragm. The chief difficulty in accepting this view is that it does not explain why the pancreatic juice, which is alkaline, and which has strong digestive powers, as regards proteids, does not digest the pancreas. Here clearly the alkaline condition of the blood will not explain the immunity of the organ from self digestion.

CHAP. XI.—SPECIAL MODES OF DIGESTION—RUMINATION.

The process of digestion is much modified in various animals, more especially in ruminants, and certain of these processes may here be shortly considered.

The stomach of the *pig* presents two portions, differing considerably both in appearance and structure. On the left side there is a cul-de-sac, which is really a dilated portion of the œsophagus, while the right portion constitutes the true stomach. The œsophageal portion has a thinner and drier mucous membrane. It is covered with papillæ, the epithelial layer consists of stratified pavement epithelium, and no glands are present. The right portion has a thick mucous membrane. It contains glands similar to those described as belonging to the fundus, showing principal cells and very large marginal cells, and near the pyloric end glands are found having only principal cells surrounding the lumen of the tube.

The stomach of the *horse* is remarkable for its small size in relation to the rest of the alimentary canal and to the large amount of food the animal consumes. Thus while the stomach of a large dog may have a capacity of 6 litres, that of a horse may not contain more than from 10 to 18 litres. The right half of the stomach-sac represents the true glandular stomach; the left, or œsophageal portion, is covered with a whitish shining mucous membrane, like that of the œsophagus, and has pavement epithelium. As in other animals, the first stage of digestion is the continuance of the diastatic action of the saliva, and it is said that two-thirds of the starch of the food may be changed into maltose and dextrin in the stomach. Then begins true gastric digestion which reaches its maximum in from 3 to 6 hours. The pyloric orifice is only loosely closed so that the movement of the stomach wall rapidly expels the contents into the duodenum. The stomach of the horse is so small that it cannot contain the total amount of a meal. Thus, as stated by Munk, suppose the horse receives 2·5 kilogrammes of oats (about 5 lbs. avoird.); this is mixed with 10 kilogrammes (about 20 lbs.) of saliva. This will more than completely fill the stomach, without the addition of water, and thus even during the meal, part of the food will be expelled into the duodenum.

The stomach of *ruminants*, such as the ox, sheep, goat, deer, chamois, elk, camel, dromedary, giraffe, etc., is remarkable for its complexity and also for the mechanism of rumination. It consists of four sacs—(*a*) the paunch or rumen, (*b*) the reticulum, (*c*) the psalterium or omasum, and (*d*) the abomasum or true stomach. The *paunch* is a sac of enormous capacity, in the ox capable of containing 100 litres, and in the sheep 4 to 6 litres. The mucous membrane is covered with pointed papillæ from 3 to 9 mm. in length, and the epithelial layer is of the stratified squamous variety. The paunch communicates with the lower end of the œsophagus and also with the *reticulum*. The paunch and reticulum are divided by a constriction and strong band of fibres from the psalterium and abomasum. This band lies in front between the reticulum and abomasum, then passes on the left of the œsophagus over the opening into the paunch, returning back on the dorsal aspect between the paunch and psalterium. Cleland has pointed out that the muscular fibres which lie on the edges of the constriction, forming the valve which separates the paunch and reticulum from the third stomach, are exactly homologous with the oblique fibres in the human subject, which are said to shut off the cardiac part of the stomach, leaving a direct communication between the œsophagus and pyloric end.[1] This sac has a capacity in the ox of 2 litres and in the sheep of ·2 litres. It shows, as its name indicates, a honeycomb-like appearance, or reticulum, each cell of which is polyhedral. The height of the walls of these cavities may be from 10 to 15 mm. Its muscular coat is stronger than that of the paunch, and consists mainly of striated muscle, the fibres of which are continuous with those of the œsophagus. The walls of the reticular spaces also contain muscular fibre. The wall of the reticulum can thus contract more powerfully and speedily than that of the paunch. Fine papillæ abound and the whole mucous membrane is covered with stratified squamous epithelium. The reticulum has three openings—a large one towards the paunch, a narrower one towards the

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[1] Cleland, *Anatomical Memoirs.*, p. 170.

psalterium, and a third which communicates with the œsophagus. At the opening into the psalterium, we find a sphincter surrounding an aperture narrowed by rugæ or folds, or by papillæ, so that matters entering into the psalterium from the reticulum pass through a kind of "perforated partition." The *psalterium* or *omasum* has a thin wall, and has two openings, one into the reticulum, already alluded to, and the other into the true stomach, or abomasum. The mucous membrane is thrown into the form of a number of leaves, projecting far into the lumen of the sac, and these are covered with small button-shaped papillæ, and by a layer of stratified pavement epithelium. This sac has in its wall involuntary muscular fibres forming strong longitudinal and circular layers. A layer of fibres also exists in the centre of each leaf or fold, in addition to a muscularis mucosæ. The structure of the *abomasum* or true stomach is like that already described as characterizing the stomach; it contains glands of the fundus and glands of the pylorus, and the mucous membrane is covered by cylindrical epithelium.

The lower end of the œsophagus opens into the paunch, but at the left side a deep groove runs along the inner wall of the reticulum, from the entrance of the œsophagus into the paunch to the entrance of the reticulum into the psalterium. This may be called an œsophageal canal or groove. To understand its true relations, we may regard the paunch and the reticulum as diverticula, or sacs developed from the *lower* wall of the œsophagus, and the psalterium as a diverticulum from the upper wall, supposing the animal to be on all fours in its normal position. We are now in a position to understand rumination. The food, coarsely masticated, forms firm and consistent masses which glide down the œsophagus into the paunch. Fluids pass partly into the paunch, but a certain amount, adhering to the œsophageal walls, passes along the œsophageal groove and may reach the psalterium direct. If the quantity be great, some of the fluid will pour over the lips of the groove and thus reach the reticulum. The more viscid the fluid is, the more tenaciously will it adhere to the œsophageal groove, and the more will reach the psalterium. On the other hand, limpid fluids will collect chiefly in the reticulum, and it is remarkable that in the llama and the dromedary the œsophageal groove has only one lip, while in the camel one lip is weaker than the other. The arrangements in those animals are thus specially suited for the conveyance of water into the reticulum.

The solid food is mixed with the saliva. Suppose an ox receives in a day 15 kilogs. (about 30 lbs.) of hay, it adds to this about 60 kilogs. (120 lbs.) of saliva, and it drinks from 15 to 25 litres of water. Thus about 100 kilogs. (200 lbs.) reach its paunch per day. The matter in the paunch is usually alkaline, sometimes neutral, or even faintly acid. It imbibes water, and the more solid matters sink into the deeper parts of the paunch, while fluid gathers above these and may even flow into the reticulum. Movements occur in the muscular walls of the paunch, so that the contents are moved about. In the paunch the matters of the food macerate, and become soft, and the diastatic action of the saliva on starch is carried on. At the same time certain substances are dissolved by the water, and a kind of watery extract is made. Favoured by the high temperature, about 40° C., the micro-organisms taken with the food, *torulæ*, *bacteria*, etc., set up fermentative and putrefactive processes. Thus the alcoholic fermentation, the butyric fermentation, the lactic fermentation, and putrefactive changes go on. Sugar is changed to lactic acid, giving an acid reaction to the fermenting mass, or the sugar may be converted into butyric acid, carbonic acid, and hydrogen, or there may be a putrefaction of proteids forming sulphuretted hydrogen and phenol. Light carburetted hydrogen (CH_4) may also be formed from a fermentation of cellulose. The fluid present may, as already mentioned, pour into the reticulum, (which is essentially a reservoir for fluid); when the wall of the reticulum contracts, it is thrown back into the paunch. Thus a thorough mixing of the food stuffs with water is accomplished. After a time, variable in duration from one hour to five or six hours, rumination begins. This act is similar to vomiting. The muscular walls of the paunch and of the reticulum contract on their contents, and the pressure is assisted by the contraction of the diaphragm and of the abdominal muscles. Small portions of matter are thus thrown into the mouth, the entrance into the posterior nares being shut off by the elevation of the soft palate, the approximation of the posterior pillars of the fauces, and the action of the uvula. The ejection of the ball of food to be ruminated is accomplished with great force, so that if the mouth is open the ball will be thrown out. Colin states that in the ox each mouthful ejected for rumination weighs from 100 to 120 grammes, and that it consists of solids and a considerable amount of fluid. It is now thoroughly masticated and mixed with a large amount of saliva. It is chewed usually for about 50 seconds, but for a longer time if the bolus is dry. The fluid expressed from it passes down the œsophagus. Munk gives the following interesting calculation :—

"If an ox receives 15 kilogs. of hay per diem and adds 60 kilogs. of saliva, 75 kilogs. reach the paunch. Suppose one-fifth of this—that is, 15 kilogs.—pass through the reticulum directly to the psalterium (rather a high estimated amount), four-fifths—that is, 60 kilogs.—remain in the paunch to be ruminated. Allowing each ball ejected from the paunch to the mouth for re-mastication to weigh 120 grammes, 500 bites will be required to re-masticate 60 kilogs. Each ball is ruminated for 50 seconds—that is, 500 × 50 = 420 minutes—and allowing for the interval of time between individual bites, at least 500 minutes, that is, more than 8 hours will be required for rumination. As rumination does not go on during sleep and work, and as from 2 to 3 hours will be used in the *first* mastication and swallowing of 15 kilogs. of hay, only a few hours remain in which an ox could do mechanical labour. Thus oxen, from their organization, are not suited for long continuous labour."[1]

After the ball has been well masticated, it re-descends the œsophagus, but as it is now finely comminuted and semi-fluid, it does not enter the paunch (a very small quantity may do so), but it glides along the œsophageal groove into the psalterium. The portions which may fall again into the paunch and reticulum will of course be again ejected into the mouth and re-chewed. The pultaceous and semi-fluid matters reach the psalterium, but as the openings between the reticulum and the psalterium and between the psalterium and the abomasum, or true stomach, lie near each other, the more fluid matters, adhering to the walls of the œsophageal groove, and guided by a shallow continuation of it running from the one opening to the other, pass directly into the abomasum or true stomach. The coarser particles or masses of food in the psalterium are submitted to a process of straining between the leaflets of that organ. The fluid is expressed, and by strong contractions of the muscular fibres in the leaves, thin cake-like masses of dry food stuff are formed. The fluid passes along the continuation of the œsophageal groove to the true stomach (abomasum), and the solid cake-like masses are ejected into this sac by strong contractions of the walls of the psalterium. In the abomasum, or true stomach, a true digestive process takes place, similar in all respects to that already described. It is said that the percentage of hydrochloric acid varies from ·05 to ·12, and that lactic acid assists in the process of petonization. Young ruminants, whilst suckling, have a small paunch, but this sac rapidly increases in capacity when the animal begins to take ordinary vegetable food.

CHAP. XII.—THE MOVEMENTS OF THE SMALL INTESTINE.

After the chyme has escaped from the stomach through the pyloric orifice, it is slowly propelled along the small intestine and mixed with three secretions, namely, the bile, the pancreatic juice, and the intestinal juice. As the chyme passes along the bowel, it loses water, soluble matter, and fats, as will be explained under absorption.

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[1] Munk, *op. cit.*, p. 337.

The movements of the small intestine consist of regular and successive contractions from above downwards by which the calibre of the tube is diminished, and also of contractions in the direction of the long axis of the tube which shorten the length of a small portion of it, and, when energetic, move a loop of intestine as a whole. The circular contractions are due to the actions of the circular fibres, whilst the others depend on shortening of bundles of the longitudinal fibres. When carefully watched, in an animal recently dead, it is easy to observe that both sets of fibres in a segment of the bowel may act at the same time so as to produce a peculiar twisting movement. Such movements are termed *peristaltic*, and by them the chyme is slowly propelled along the intestine. The rate of movement is about 10 mm. per second.

Nervous Arrangements of the Movements.—As already stated, there are *two nervous plexuses* in the coat of the intestine, the one (*Meissner's plexus*) found in the submucous coat of connective tissue, and the other (*Auerbach's plexus*) between the two muscular layers. The intestine is also supplied with filaments from the vagi and splanchnic nerves. As peristaltic movements occur readily on stimulation after a portion of the bowel has been severed from its nervous connections, it is evident that these movements are regulated by *ganglionic centres* in the wall of the bowel itself. Peristaltic movements may be excited in a portion of intestine either mechanically or by electricity; and it has been found that the amount of blood supplied to the bowel has also an influence upon them. Thus a state of emptiness or of great fulness of the vessels increases the movements, as when, by pressure on the aorta, a state of anæmia is caused, or when pressure on the great veins causes congestion of the veins of the bowel. In either case, there will be a diminution of oxygen and an increase of carbonic acid, and it is probable that the amount of the gaseous constituents of the blood is the exciting cause. The approach of death, by interfering with the circulation, and profuse hæmorrhage, by emptying the blood-vessels of the bowel, increase peristalsis. The increased supply of blood to the bowel during digestion acts as a normal stimulus in carrying on the movement. Excessive stimulation or prolonged congestion arrests peristalsis, and the bowel becomes paralysed. Inflammatory affections of the bowel, as in severe peritonitis, also cause paralysis, and in these circumstances, the muscular walls become distended by the gases in the bowel, a condition called *meteorism*. The movement, however, may be influenced by the action of the vagi or of the splanchnic nerves. Thus, stimulation of the vagus increases, whilst stimulation of the splanchnic arrests, the movements. The vagus may therefore be regarded as a motor nerve for reinforcing the activity of the ganglionic centres, and the splanchnic as an inhibitory nerve for restraining and controlling these centres. The inhibitory action of the splanchnic only continues when the circulation is normal and there is plenty of arterial blood in the vessels. If the blood becomes venous, stimulation of the splanchnic increases peristalsis. After death, stimulation of the splanchnic always produces peristalsis, like stimulation of the vagus. From this and other experiments, it has been suggested that the splanchnic contains not only motor fibres, but also inhibitory fibres, whose sensibility is lowered by venous blood. The splanchnic nerve, therefore, may be held to contain the following sets of fibres, distributed to the bowel: (1) inhibitory; (2) motor; (3) vaso-motor, to the blood-vessels, the walls of which contract when the nerve is stimulated; and (4) sensory. Intestinal movements may also be influenced by impressions coming from the higher nervous centres, as is seen in the constipated condition frequently met with in nervous affections. Strong emotional excitement may cause increased peristalsis, as indicated by the phrase "yearning of the bowels." This is due to the stimulus originating in the cerebrum acting on the vaso-motor centre through the *medulla oblongata*, and thus causing contraction of the vessels and anæmia.

Chap. XIII.—STRUCTURE OF THE LIVER.

This is the largest gland in the body, being from 250 to 300 mm. in the transverse direction, from 150 to 175 mm. from its posterior to its anterior border, and about 90 mm. in thickness in its thickest part towards the right and posterior part of the organ. It weighs from 1·42 to 1·7 kilogramme. It is estimated to be equal to about $\frac{1}{36}$th of the weight of the body, but in the fœtus, and in early life, its proportionate weight is greater (Quain). The excretory apparatus consists of the hepatic duct, the cystic duct, the gall-bladder, and the common bile duct. The hepatic duct, 50 mm. in length and 4 mm. in diameter, issues from the transverse fissure of the liver, and meets at its lower end with the cystic duct coming from the gall-bladder, the two then forming the common bile duct. The gall-bladder is a pear-shaped bag, 75 to 100 mm. in length, and from 37 to 40 mm. in breadth, and its capacity is about ·0355 litre. Its upper end or fundus, directed forwards, downwards, and to the right, projects beyond the anterior body of the liver, and from the other end issues the cystic duct;

about 40 mm. in length. The gall-bladder is absent in the horse, donkey, zebra, deer, camel, dromedary, elephant, rhinoceros, beaver, hamster, mouse, and whale. The common bile duct (*ductus communis choledochus*), about 75 mm. in length, and from 4 to 6 mm. in diameter, formed by the union of the hepatic and cystic ducts, reaches the descending portion of the duodenum, and after running obliquely for about 20 mm. in the walls of that portion of the bowel, opens into its cavity by a common orifice with the pancreatic duct, near the junction of the descending and inferior transverse portions of the duodenum, and about 75 to 100 mm. below the pylorus. The nature of the opening is such that none of the contents of the bowel can enter the duct. The organ is supplied with blood by the portal vein, and as this vein is formed by the union of the veins of the stomach, intestines, pancreas, and spleen, it is evident that the liver receives all the blood which has previously

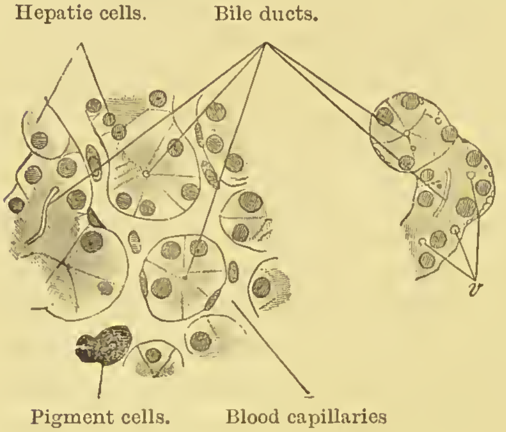

FIG. 51.—From a section of frog's liver. × 240 d. The gland cells surround the very narrow lumina, or bile ducts, or bile capillaries, and they have on the other side blood capillaries. The gland cells show different stages of secretion. *v.* vacuoles. (Method No. 31, Appendix.)

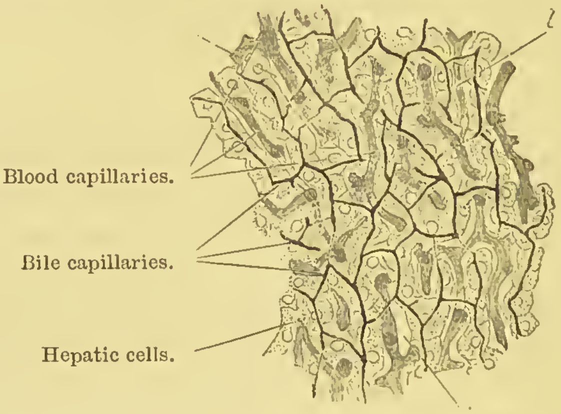

FIG. 52.—From a section of rabbit's liver in which the capillaries of the portal vein have been injected with red, and the bile capillaries or ducts with blue, injection. × 240 d. The hepatic cells have blood capillaries on both sides. (In some parts of the preparation, the red injection has contracted, so that gaps, *l*, occur between the hepatic cells and the blood capillaries.) The bile ducts do not touch the blood capillaries anywhere. They are always separated by half the breadth of a cell. The dark patches in the blood capillaries are optical transverse sections of capillaries passing vertically through the thickness of the section. (Method No. 32, Appendix.)

circulated in these organs. It is also supplied with arterial blood by the hepatic artery, a branch of the cœliac axis. The blood is conveyed from the liver to the inferior vena cava by the hepatic veins. We shall now consider its more minute structure.

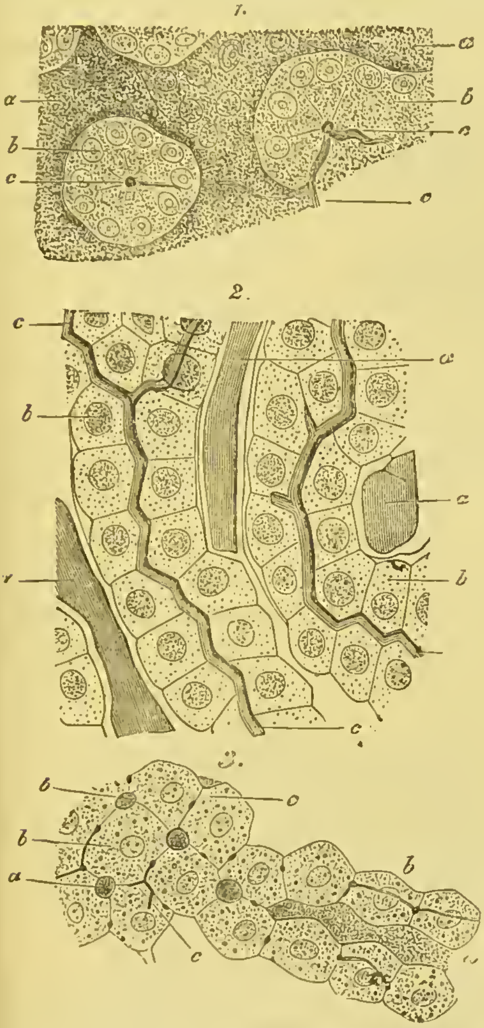

FIG. 53.—Three figures showing the relation o the hepatic cells to the bile capillaries and to the blood capillaries. 1. From the *snake*, according to Hering. Here we find the hepatic cells clustered round a fine bile duct, as in Fig. 51. 2. From the *salamander*, according to Eberth, showing a long bile duct between two rows of hepatic cells, and blood capillaries on the other side of the cells. 3. From the *rabbit*, showing that the bile capillaries, c, and the blood capillaries, *a*, never touch, but are always separated by the whole or the fraction of a hepatic cell.

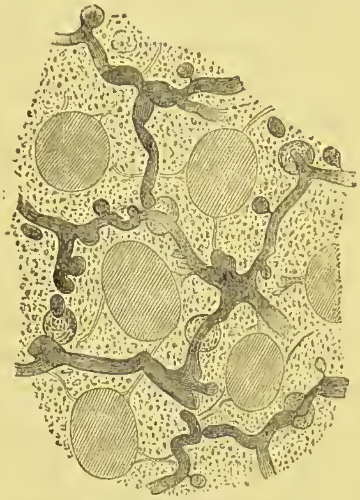

FIG. 54.—Bile capillaries in rabbit's liver, injected with Berlin blue solution. Observe the small intercellular passages give off shorter passages with blind ends, or vacuoles.

FIG. 55.—A preparation similar to that in Fig. 54, showing also fine threads passing from the bile capillaries into the hepatic cell. Vacuoles are also seen.

The liver is essentially a ramified tubular gland. It is found in this condition, however, during the whole of life only in amphibians and reptiles; in birds and mammals changes occur so early in development as entirely to conceal its tubular character. The special arrangement of the blood-vessels also confers on the liver peculiarities of structure. When we investigate the liver of the lower animals, or that of embryonic mammalia, we can establish the general principle of gland structure, namely, that one side of the gland cells is turned to the lumen of the gland and the other to the blood-vessels. The lumina of the glands, however, are very narrow, not broader than 1 to 2 μ, and they are termed *bile ducts*, or bile capillaries (Fig. 51, p. 106). Some have supposed that these have a distinct wall, not formed of endothelium. When we examine sections of the liver of adult mammals we do not find the same appearances. We find that each hepatic cell does not stand related to blood capillaries on one, but on many sides (Fig. 51). But the blood capillaries never come into close contact with the bile ducts or bile capillaries; a portion of a hepatic cell always intervenes. Thus the blood capillaries run along the edges of the hepatic cell, while the bile capillaries run along the middle of the side of the cell. This is the arrangement in the rabbit, but in man bile capillaries run along the edges also (Stöhr). The liver, therefore, differs from all other glands in having not one entire cell, but only a portion of a cell between the lumen of the gland and the blood capillaries, so that the blood capillaries are more intimately related to the secreting cell than in any other gland. This is well illustrated by Fig. 52, p. 106, and Fig. 53, p. 107.

By the method of injecting the bile ducts with a solution of Berlin blue, Kupffer has brought out several points of interest which are shown in Figs. 54, 55, and 56.

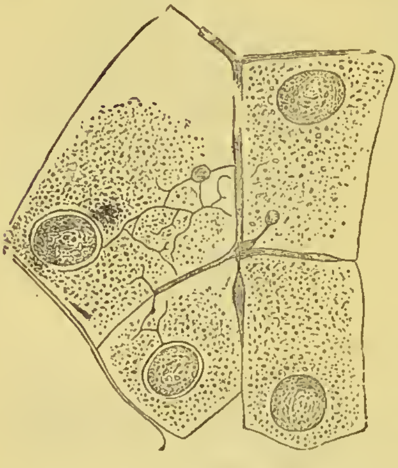

Fig. 56.—Frog's liver after the animal had a solution of sulpho-indigotate of soda injected into its blood. The colouring matter has been separated from the blood by the cells and thrown into the bile passages. Observe that the small branches in the cell ramify through the cell and anastomose.

Chrzonszczewsky was the first to employ the method of *natural injection*. An aqueous solution of sulpho-indigotate of soda is injected into the jugular vein. After 1½ hour, the animal is killed and the portal vein is injected with gelatin and carmine, or an injection of an aqueous solution of chloride of potassium may be introduced. The blue sulpho-indigotate is found in the network of bile capillaries. The appearance of the preparation thus obtained is shown in Fig. 57, but, as above explained, the bile capillaries have no ducts.

The Hepatic Cells and Blood-Vessels.—The hepatic cells, from 18 to 26 μ in diameter, are irregularly shaped cells, having angular borders

They have no cell wall, and the granular protoplasm of which they are composed contains one or several nuclei. In the protoplasm we also find pigment, and often small granules of fat, more especially in the cells of young and well-fed animals. The appearance of the cell varies according to its condition of functional activity (Figs. 58 and 59).

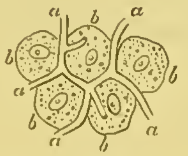

FIG. 57.—Portion of liver injected by natural method. *a*, bile capillaries; *b*, hepatic capillaries.

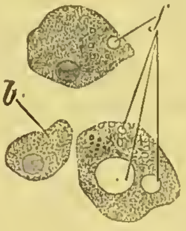

FIG. 58.—Human hepatic cells. ×560 d. Showing globules of fat in the cells. *b*, impression made by a minute capillary. (Method No. 33, Appendix.)

FIG. 59.—Human hepatic cells. × 560 d. 1, Cells during fasting; 2, cells during digestion. (Method No. 34, Appendix.)

During fasting the cells are small, dull in optical appearance, and their outline is indistinct. They become larger, clearer in the centre, and

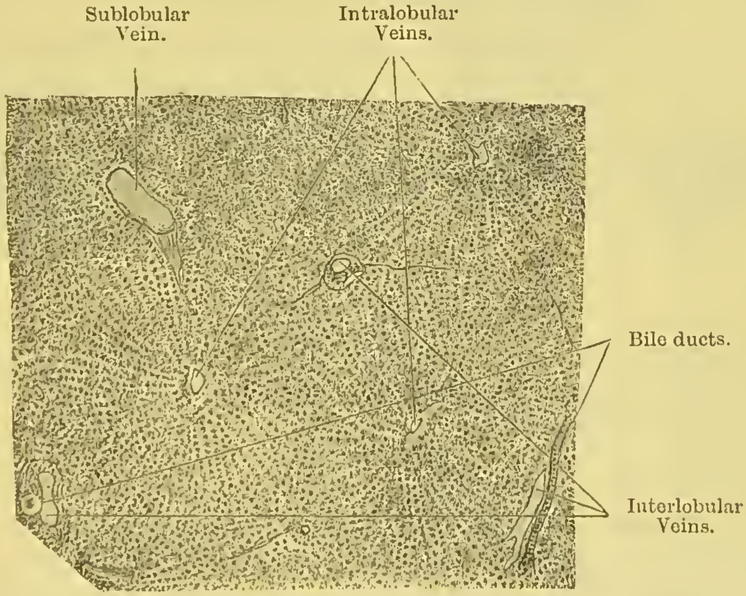

FIG. 60.—Section of human liver near the surface. × 40 d. Two entire lobules are seen and two-thirds of another in the upper right hand corner. The margins of the lobules are not sharply defined, and the existence of lobules is indicated chiefly by the section of the small vein in the centre. Observe the hepatic cells are arranged radially from the central vein. (Method No. 35, Appendix.)

they show a coarsely granular ring near the border during digestion Both conditions may be found in cells from the same liver. Much of the granular matter consists of glycogen. It is more abundant after a meal rich in carbohydrates. When no glycogen is present, a high power shows a reticulated structure in the protoplasm.

When we examine a thin section of the liver with a low power (25 diameters) we see irregularly polygonal areas more or less sharply differentiated by connective tissue. These are the *lobules* of the liver, and they consist of hepatic cells and blood-vessels. Usually slightly oval, or in transverse section polygonal, the length of a lobule is 2 mm., and its breadth 1 mm. Around the circumference of each lobule lie the ramifications of the portal vein, called the *interlobular* veins. Capillaries pass from these into the lobule, and they unite to form a central vein (Fig. 60). These capillaries have a diameter of from 10 to 14 μ, and they form numerous anastomoses with the vessels in adjoining lobules. The spaces in the capillary network are occupied by hepatic cells, and these are arranged in a radial manner round the vessel in the centre of the lobule. This central vessel is termed the *intralobular* vein. The intralobular veins are the radicles of the hepatic veins. Each intralobular vein opens into a *sublobular* vein, which runs on one side of the

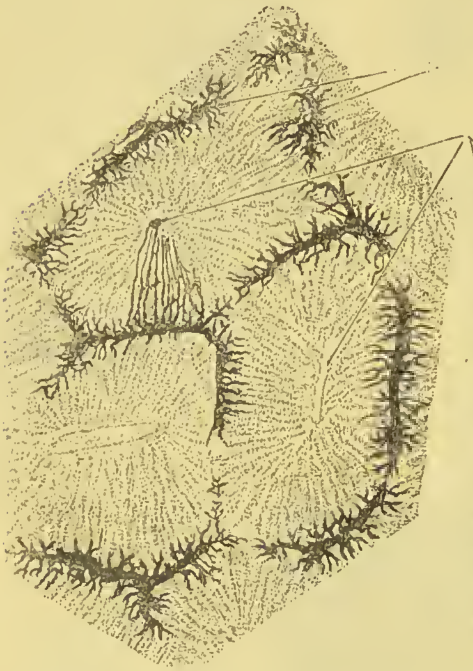

Fig. 61.—Section of rabbit's liver near the surface. Injected from the portal vein. × 40 d. Observe three lobules. The injection has filled the branches of the portal vein, called interlobular veins, and in the upper lobule it has entered the lobule and passed on to the central vein. (Method No. 36, Appendix.)

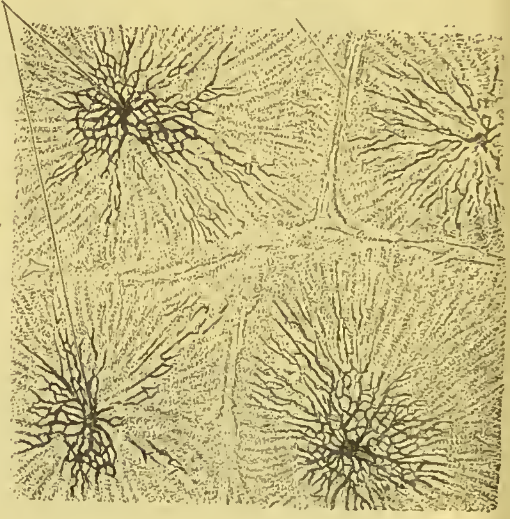

Fig. 62.—Section of cat's liver near the surface. Injected from the vena cava. × 40 d. Observe four lobules. The injection has filled the central vein and the capillaries leading into it, but it has not entered the portal capillaries, or interlobular veins. (Method No. 37, Appendix.)

lobule, and by the confluence of the sublobular veins the hepatic veins are formed. The branches of the *hepatic artery* run along with those of the portal vein, and they terminate in the interlobular tissue, where the branches of the portal vein, and of the hepatic veins, and the bile ducts, wind round these in a spiral manner. The small veins originating from the plexus formed by the hepatic artery open into interlobular veins of the portal system. The hepatic artery also supplies a network of fine capillaries found in the capsule of the liver. The course of the blood-vessels is therefore as follows: The portal vein enters the fissure of the liver, divides again and again into finer and finer branches which run between the lobules (interlobular veins). From these, small capillaries enter the lobules and terminate in the central veins (intralobular veins). Several of such veins form a sublobular vein, and these form the hepatic veins. The capillaries of the hepatic artery terminate outside the lobules (Figs. 61, 62, 63).

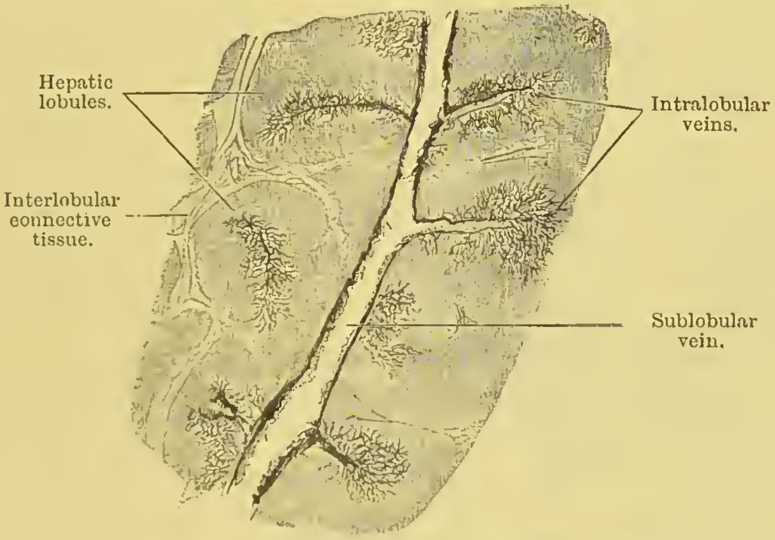

FIG. 63.—Portion of a vertical section of cat's liver. The injection was sent through the inferior vena cava. × 15 d. Observe the sublobular vein receiving several intralobular veins. The injection mass has fallen out of the larger vessels. (Method No. 38, Appendix.)

Unlike what we find in other glands, very few hepatic cells bound the lumen of the gland, not more than two being related to a single lumen or bile capillary, and the structure is complicated by the arrangement that bile capillaries do not lie on one but on several sides of a hepatic cell. These form a meshwork in which the hepatic cells are situated. The bile capillaries, or radicles of the hepatic ducts, are passages among the hepatic cells. Sometimes they are termed *intralobular bile passages.* At the margins of the lobules they pass into the interlobular bile ducts which have a distinct wall, composed of a structureless *membrana propria* and of flat epithelial cells. By the union of interlobular ducts the larger bile ducts are formed. The larger ducts have thick walls formed of connective tissue and elastic fibres, and they are lined by a single layer of cylindrical cells, each provided at the free border with a cuticular thickening, like those on the villi of the small intestine. Goblet cells may also be found. The hepatic, cystic, and common bile duct have a submucous coat and a *tunica propria.* The latter contains involuntary muscular fibres running both transversely and longitudinally. The *tunica propria* also contains short pear-shaped tubular glands lined with mucous epithelial cells. These are the glands of the bile ducts. The wall of the gall bladder shows the same structure, but the muscular coat is much thicker. Certain bile ducts end in cul-de-sacs outside the parenchyma of the liver, more especially along its left margin, near the portal fissure, and near the situation of the vena cava. They represent embryonic conditions of the liver substance.

The liver is covered with a capsule (*Glisson's capsule*) composed of connective tissue and elastic fibres. This is thickest at the portal fissure. It forms a sheath for the portal vessels and the ducts, and surrounding these, it penetrates into the substance of the liver. The connective tissue layers become thinner and thinner until they form an extremely thin layer surrounding each lobule, separating the lobules from each other. This may be called interlobular connective tissue. Delicate fibres of connective tissue also penetrate the substance of each lobule, forming intralobular connective tissue.

FIG. 64.—Section of human liver. × 240 d. *c*, blood capillaries, still showing at × blood corpuscles; *b*, intralobular connective tissue. The majority of the hepatic cells have fallen out of the capillary meshwork; on the right five cells remain *in situ.* Method No. 39, Appendix.)

The lymphatic vessels of the liver accompany the branches of the portal vein, surrounding these as a spiral network. They pass even into the lobules, in the form of minute channels surrounding the blood capillaries, and they communicate with similar spaces surrounding the intralobular and sublobular veins. There is also a narrow meshed network of lymphatics in the capsule of the liver which anastomoses freely with the deep seated lymphatics. Lymphoid follicles in small numbers occur in connection with the interlobular lymphatics.

The nerves of the liver arise from the cœliac plexus and from the vagi nerves, more especially the left vagus. They enter the liver in close relation with the branches of the hepatic artery. In the liver substance chiefly non-medullated fibres are met with, but a very few are medullated. Small groups of ganglion cells have also been observed. Pflüger has long held that certain nerve filaments end in hepatic cells. Maccallum has traced nerve filaments into connection with hepatic cells, both in man and in *Necturus.* He traces nerve filaments into a perivascular network and thence into a plexus among the cells of the lobule. From the fibrils of the intercellular network minute twigs are given off which terminate each in a delicate bead in the interior of the hepatic cell near the nucleus.[1]

Chap. XIV.—THE BILE.

The liver consists of a large number of lobules, each of which may be regarded as a liver in miniature. Each lobule receives a supply of blood from two sources, namely, (1) from the portal vein, and (2) from the hepatic artery. The first conveys blood to the lobule which has already passed through the capillaries of the stomach or intestines, and which is richly supplied with matters absorbed during its passage; whilst the second conveys arterial blood for the direct nourishment of the vessels, connective tissue, etc., of the lobule. From the blood of the portal vein, the hepatic cells in the lobule secrete various matters, some of which they pour into the origins of hepatic ducts, so as to form a fluid called *bile.* The blood is conveyed from the lobules by the radicles of the hepatic vein, which vessel pours it into the vena cava. This blood has lost certain materials which have been separated from it to form bile, and it has gained other materials which have been elaborated by the hepatic cells. The blood of the portal vein contains more albumin, hæmoglobin, fat, water, and salts than that of the hepatic vein, and it probably contains less cholesterin and lecithin. The portal vein also brings to the liver the form of sugar obtained by the digestion of carbohydrates, while the blood of the hepatic vein contains the sugar obtained from glycogen, and also glycogen itself. It will thus be seen that the functions of the hepatic cells are of a very complex character, inasmuch as they separate or form not only the elements of bile, but also are the seat of the changes which result in the formation of glycogen, sugar, diastatic ferment, urea, etc.

Fresh liver substance has a slightly alkaline reaction, but it becomes acid after death. It contains various proteid substances, but these have not yet been satisfactorily discriminated. The hepatic cells also yield from 1·2 to 1·6 per cent. of glycogen, a carbohydrate, the physiological relations of which will be afterwards considered. Fatty matters appear in the hepatic cells as minute refractive particles. They also yield traces of urea, uric acid, cholesterin, and jecorin, a peculiar body containing sulphur and phosphorus, and having the property of reducing cupric to cuprous oxide. The liver also yields to analysis inorganic matters in the form of potassium, sodium, calcium, magnesium, chlorine, and the mineral acids. It also contains iron sufficient often to give, in a liver hardened in alcohol, a blue colour with ferrocyanide of potassium and hydrochloric acid.

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[1] A. B. Macallum, B.A., University College, Toronto, *Quart. Journal of Micros. Science*, vol. xxvii. part 4. New ser. p. 452.

Metallic substances taken with the food, such as copper, mercury, lead, manganese, are readily found in the liver.

1. **Physical and Chemical Characters of the Bile.**—We have at present to consider the properties only of one of the products of the metabolism in the hepatic cells, namely, the bile, and especially its relations with the digestive and other processes occurring in the small intestine. The nature of the other products of metabolism, glycogen, urea, fat, etc., will be discussed in treating of nutritional changes. The bile may be considered both as a fluid concerned in the digestive process and as an excretion, that is to say, the bile takes part in physico-chemical operations in the bowel, and at least a portion of it is excreted as useless or injurious matter in the fæces.

For experimental purposes, bile may be obtained by the formation of an artificial fistula, an operation first performed by Schwann in 1844. This operation, which has been frequently performed on dogs, is difficult and dangerous. In the hands of competent observers, however, it has been the means of giving much information regarding the bile, which could not otherwise be obtained, as biliary fistulæ in the human being are rare.

The mode of establishing a *permanent* biliary fistula in the dog is as follows:—The animal having been anæsthetized, the abdomen is opened. A ligature is tied round the bile duct immediately after it receives the cystic duct; another ligature is applied round the duct near the intestine, and the duct between the two ligatures is divided. The fundus of the gall-bladder is brought to the wall of the abdomen, and secured there by stitches. The fundus is then opened, and a canula is inserted into the gall-bladder. A *temporary* fistula may be established by Rutherford's method, thus described:—"Through an opening in the *linea alba* a glass canula was inserted into the common bile duct, near to its junction with the duodenum, and tied therein. To the end of the canula projecting from the abdomen a short caoutchouc tube was attached, and to the free end of this a short glass tube drawn to a narrow aperture so that the bile might drop from it, as Röhrig had recommended. The gall-bladder was then compressed, in order to fill the whole tubing with bile, and the cystic duct was clamped to prevent its return to the gall-bladder, and to compel all the bile secreted by the liver to flow through the canula."[1] This is similar to the method of Colin by which, in 1850, he established temporary fistulæ in horses, oxen, sheep, and pigs.

Fresh bile is a yellowish-green or dark-green fluid in herbivora, and it is reddish-yellow or yellowish-brown in man, and in most carnivora. When allowed to stand in air, brownish-yellow bile becomes dark brown, and green bile more intensely green. It has a peculiar odour (especially

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[1] Rutherford on the "Physiological Actions of Drugs on the Secretion of Bile." *Trans. Roy. Soc. of Edinburgh*, vol. xxix. p. 138.

when heated) and a bitter taste. It contains no morphological elements except a few epithelial cells from the gall-bladder and a few mucous corpuscles. The specific gravity varies from 1026 to 1030; it gives a neutral reaction. After coming from the gall-bladder, it contains a large quantity of mucus, yielding mucin, readily thrown down by alcohol. A solution in concentrated sulphuric acid presents well-marked fluorescence: it is pink by transmitted, and green by reflected, light. Bile taken from the gall-bladder is darker in colour, and more inspissated, that is, thicker, than that taken from a fistula. Not only does the mucus of the gall-bladder add mucus to the bile, but a portion of the water of the bile is absorbed by the lymphatics in the wall of the gall-bladder. In 100 parts of bile taken from bile ducts there are about 5 of solid matters in the rabbit, 2 in the guinea-pig, and in man only from 1 to 1·5. After thickening in the gall-bladder, the amount of solid matter may rise to 10 or even 20 per cent. The solids consist of inorganic substances—cholesterin, colouring matters, soaps, neutral fats, and bile salts. Bile pigments and bile salts do not occur normally in any other part of the body. The bile also contains a considerable quantity (from 5 to 50 per cent. by volume) of carbonic acid and traces of oxygen and nitrogen.

The *mineral matters* contained in bile consist of chlorides of sodium and of potassium, phosphates of soda, lime, and magnesia, carbonate of soda, oxide of iron, and traces of silica. In many cases, also, traces have been found of manganese and copper.

The following analyses of bile show its percentage composition in different animals:—[1]

	I. Man.	II. Ox.	III. Pig.	IV. Dog.
Water,	86·3	90·4	88·8	85·2
Solids,	13·7	9·6	11·2	14·8
Bile Salts,	8·2	8·0	7·3	12·6
Lecithin, Cholesterin, Fats, Soaps,	2·5		2·2	1·3
Mucus and Pigment,	2·2	0·3	0·6	0·3
Inorganic Salts,	0·8	1·3	1·1	0·6

I., Frerichs; II., Berzelius; III., Gundlach and Strecker; IV., Munk.

In 100 parts by weight of human bile, Jacobsen[2] found ·1276 of chloride of potassium, 2·4508 of chloride of sodium, ·5984 of phosphate of soda, ·1672 of phosphate of lime, and ·4180 of carbonate of soda. The large amount of sodium salts is noteworthy. The amount of sulphur obtained from human bile varies. Jacobsen found from ·021 to ·925 per cent. in nine cases, and in one case as much as 2·67 per cent. Bischoff and Lossen found ·83 to 2·99 per cent.

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[1] Munk *op. cit.* p. 344.

[2] Jacobsen. Quoted by Hoppe-Seyler, *op. cit.* p. 299.

The *colouring matters* of bile are bilirubin and biliverdin, the general characters of which are described in Vol. I. p. 130. It is necessary here to allude to some of their special characteristics.

The chief pigment of the bile, *bilirubin*, $C_{16}H_{18}N_2O_3$, is insoluble in water, alcohol, or ether, and it is best obtained by the action of hot chloroform. From the chloroform solution it separates in the form of small, rhombic, orange-yellow prisms. It is identical with hæmatoidin, one of the derivatives of hæmoglobin (see Vol. I. p. 129). Bilirubin is held in solution in the bile by the sodium salts of the bile acids. The bile of herbivora also contains *biliverdin*, $C_{16}H_{18}N_2O_4$, another pigment derived from bilirubin by oxidation. It is a black-green powder. The *test* for the bile pigments is known as *Gmelin's* reaction. If we add to a little of the fluid supposed to contain the pigment spread out on the surface of a white plate a few drops of fuming nitric acid, a play of colours will be seen in a series of rings in the following order, green, blue, violet, red, and finally yellow. This test is delicate enough to detect bilirubin in a solution containing only 1 in 80,000 of water. The addition of bromine water to the solution of the pigment in chloroform produces the same play of colours. The reaction proposed by Brücke is to add to the fluid a solution of 1 part of pure nitric acid in 4 of water, and then to pour down the side of the test tube a little pure concentrated sulphuric acid. A play of colours appears at the junction of the fluids. This reaction is modified by E. Von Fleischl, who substitutes a concentrated solution of nitrate of soda for the nitric acid. If we add a little tincture of iodine to a fluid containing bile pigment, a green colour is produced. As to the spectroscopic examination of these pigments see Vol. I. p. 130, *et seq.*

The *bile salts* are glycocholate and taurocholate of soda. The glycocholate is found in small quantity in the bile of the human being and of omnivora, it is absent from the bile of carnivora, whilst it is very abundant in that of herbivora. It may be obtained as a precipitate from an aqueous solution of crystallized bile, by the addition of dilute sulphuric acid. Taurocholic acid contains sulphur; it is the only acid found in the bile of carnivora, and in human bile is in much greater abundance than the other acid.

If we make an alcoholic extract of bile and then add ether in excess, the bile salts separate out in a crystalline form. When the bile acids are boiled with acids, or with baryta water, or if they are boiled under pressure, both yield an acid, cholalic acid, which is non-nitrogenous (see Vol. I. pp. 106-7). This acid is united to taurin to form the one bile-acid, taurocholic acid, and to glycocin to form the other, glycocholic acid. The test of *Pettenkofer* is to add to the fluid containing the acids in solution a little of a strong solution of cane sugar, and then a few drops of strong sulphuric acid. The union of the acid with the water raises the temperature of the mixture to 60° or 70° C., and a beautiful purplish-violet or cherry-red colour is produced. (Vol. I. p. 108.) To avoid the blackening of the sugar by carbonization, the use of phosphoric acid has been suggested instead of sulphuric acid. Hay has pointed out that the bile acids or their soluble salts lower the surface tension of fluids. If a little sublimed sulphur be thrown on a fluid containing the bile salts, the particles of sulphur sink.

To obtain *glycocholic acid*, add to ox bile equal parts of hydrochloric acid and ether. Allow the mixture to stand, and after some days the acid will separate out in the form of fine shining needles. Neutral acetate of lead precipitates this acid from a mixture containing the two bile acids.

Cholalic acid, $C_{24}H_{40}O_5$, is obtained by boiling taurocholic acid with baryta water and it is one of the products of the putrefaction of bile. It exists in the form of four-sided prismatic crystals (see Fig. 40, p. 107, Vol. I.). Closely related to this substance is hyocholalic acid, $C_{25}H_{40}O_4$, obtained from pig's bile.

Glycocin, $C_2H_5NO_2$, or sugar of gelatin (so called because it can be produced by boiling gelatin with dilute sulphuric acid), appears in the form of rhombohedric or prismatic crystals, having a sweetish taste (Fig. 28, p. 91, Vol. I.). It does not occur in the free state.

Taurin, $C_2H_7NSO_3$, crystallizes as colourless six-sided prisms (Fig. 33, p. 96, Vol. I.). Besides existing in taurocholic acid, it is found in the muscles of various fishes and of the horse, and it exists in the kidneys and lungs of many mammals.

The bile also contains *cholesterin*, $C_{26}H_{44}O$, a substance held in solution by the bile salts. It forms the chief constituent of gall stones from which it may be readily prepared if we extract it from these with boiling ether, and then distil off the ether, dissolve the residue in alcohol, and allow the solution to cool. The crystalline mass is then heated with alcoholic potash. The crystals appear as rhombic plates, often having one obtuse angle wanting. (See Fig. 61, p. 147, Vol. I. ; the tests are there described.)

In the fresh condition, bile does not contain any of the derivatives of the bile-acids, but small quantities of other nitrogenous compounds, such as urea, lecithin, etc., may be found.

2. **Physiological Characters of the Bile.**—The quantity of bile secreted in twenty-four hours is much greater in herbivora than in carnivora.

In cases of fistula in an adult man, from 450 to 550 c.cm. of bile have been collected in twenty-four hours. This amounts to about 10 grms. of bile (containing ·5 grms. of solids) per kilog. of body weight. According to Bidder and Schmidt, the ratio per 1 kilog. of body weight is for the dog 20 grms., for the cat 18 grms., for the sheep 25 grms., for the rabbit 130 grms., and for the guinea pig 175 grms. By temporary biliary fistula, Colin obtained per hour from the horse 250 to 300 grms., ox from 100 to 120 grms., sheep from 10 to 18 grms., and pig from 75 to 160 grms. of bile. This observer also states that the liver of the horse secretes 6 kilogs., of the ox 2·64 kilogs., of the sheep ·34 kilogs. of bile in twenty-four hours. The smaller the animal, especially among herbivora, the greater the amount of bile secreted. Thus the liver of an adult guinea pig weighs about 40 grms. and it secretes in twenty-four hours about 175 grms. of bile, that is four times the weight of the liver. Since the bile of this animal contains about 1 per cent. of solids, and the liver substance about 25 per cent. of solids, almost one-fifth of the solids of the liver is resolved into bile in twenty-four hours (Munk). This indicates the active metabolism going on in the hepatic cells.

Variations during Digestion.—Bile is secreted continuously and under a certain pressure. The pressure under which the bile is secreted is very low. This is what may be expected when we consider the small diameter of the hepatic artery, and the fact that the portal vein originates in capillaries in the intestinal canal and spleen. Heidenhain found the pressure by which the bile is forced along the ducts to be about 15 mm. of mercury, or the one-fiftieth of an atmosphere. But even this small pressure is greater than that in the portal veins (double the amount in the dog, according to Heidenhain), and therefore the secretion of bile is not a mechanical filtration due to blood pressure. The bile is secreted by the hepatic cells. A small amount is secreted even during starvation. The amount is increased during the phases of digestion. In animals, such as the rabbit, in which the stomach is always more or less full, these variations are not so marked; but in man, and in the dog, the secretion increases shortly after the introduction of food, attains a maximum in the third, fourth, or fifth hour, then decreases, and rises again until the eighth or ninth hour, or perhaps as late as the fifteenth hour, when it reaches a second maximum, and then slowly declines. The total quantity of bile formed is also affected by the nature of the food. The quantity of bile secreted and the total amount of solids are increased by a meat diet. A diet composed exclusively of fat causes a great diminution. The amount is much greater in herbivora than in carnivora.

Influence of the Circulation on the Secretion of Bile.—The hepatic artery may be regarded as the nutrient vessel of the liver, and the portal vein supplies the blood concerned in the secretion of bile. The secretion is affected by changes in the amount of blood pressure in the capillaries of the organ. Thus, it is increased by injecting blood into the veins, and it may be diminished by bleeding or by compression of the aorta. If the flow of blood through the portal vein be obstructed, the secretion diminishes or may be suppressed, and death speedily occurs. Again, the amount will be affected by the readiness with which blood flows away by the hepatic vein. An obstruction to the hepatic circulation first increases the secretion, but afterwards diminishes it. It has been shown that if a branch of a portal vessel supplying a lobule be ligatured, a branch or branches of the hepatic artery supplying the same lobule will supply it with blood, and in these circumstances secretion of bile will continue, although the amount is very much reduced. As already pointed out, the bile is secreted by the hepatic cells, and even its watery constituents cannot be supposed to be produced by a mechanical filtration from the blood. The pressure in the portal vein is always less than that in the bile ducts. But, although pressure in the portal capillaries cannot account for the secretion, the *rapidity* of the flow of blood through these capillaries has an important influence. The activity of the hepatic cells depends on the amount of blood they receive in a unit of time. Suppose the pressure in the bile ducts to exceed fifteen mm. of mercury, the flow of bile ceases, but the bile is still secreted, and, as it cannot flow into the ducts, it passes by the lymphatics into the blood, and the pigment appears in the skin, retina (causing yellow vision), urine, etc., as is seen in jaundice. Ligature of the bile duct has been found to cause jaundice in pigeons after two hours, in rabbits after twenty-four hours, in dogs after forty-eight hours, and in man only after three days (Munk). In jaundice the stools become clay-coloured from the absence of stercobilin, and they have a very disagreeable odour, especially if fat has been taken in the food. There is usually also constipation, indicating diminished peristalsis, and the fæculent matters are hard, from the small amount of water present. The bile salts in the blood diminish the activity of the intracardiac nervous mechanism, only forty heart beats may occur per minute, and the movements of respiration may also be slowed. In such cases also, from the solution of blood corpuscles by the absorbed bile salts, more bile pigment may be formed in the blood, and hæmoglobin may appear in the urine along with a globulin derived from it. Ludwig and Schmulewitsch have succeeded in maintaining the secretion for some time after removal from the body, by passing a stream of warm defibrinated blood through the liver of a rabbit.

The question arises as to where the bile is actually formed. There can be no doubt it is formed by the hepatic cells. These cells, as already pointed out, page 108, are brought into remarkably close relations both to the blood capillaries and to the minute bile passages or bile capillaries. Imagine a minute polygonal cell having its surfaces flattened. In the centre of each flat surface is a groove, and, by coming into juxtaposition with a similar groove in an adjoining cell, a cylindrical channel is formed. This is a bile capillary, and it is clear there will be as many of these round a cell as there are sides to the cell. Then at the angles of the cells we find blood capillaries. The diameter of the bile capillaries is much less than that of the blood capillaries. These cells elaborate the bile salts and bile pigments. Neither in the blood nor in any organ or fluid of the body, except the liver and bile, do we find these substances. When found in the intestine, their origin is bile that has passed into it. Further, on extirpating the liver, neither bile acids nor bile pigments accumulate in the blood. There can therefore be no doubt that these substances are formed by the hepatic cells. Taurin, glycocin, and cholalic acid are formed separately, and by conjugation these form the bile acids.

As to the origin of bilirubin, various observations indicate that it is produced by the decomposition of hæmoglobin. When hæmoglobin is decomposed, as in a blood clot, one of the products is the crystalline pigment, hæmatoidin. This pigment is identical with bilirubin. We also know that the injection of solutions of hæmoglobin into the portal vein, or of substances which liberate hæmoglobin from the red blood corpuscles, is followed by an increase in the amount of bilirubin in the bile. Further, solutions of the bile salts have a similar effect, and there are strong grounds for believing that these salts have to do with the liberation of the hæmoglobin from the corpuscles, or, in other words, with the destruction of these bodies, and that the hæmoglobin, thus set free, is transformed into hæmatoidin, or bilirubin. This view is supported by the fact that a small amount of iron, as a phosphate, exists in the bile, and its presence can be accounted for by the decomposition of hæmoglobin, which contains this metal. The bilirubin undergoes a molecular change, involving the absorption of hydrogen and water, and becomes hydro-bilirubin, $C_{32}H_{38}N_4O_7$, a substance which appears in the fæces as stercobilin, and in the urine as urobilin.

The Expulsion of the Bile.—This is accomplished partly by the pressure in the smaller bile ducts, partly by the movements of respiration, and partly by the contraction of the involuntary muscular fibres in the larger bile ducts and in the gall bladder. The movements of respiration submit the liver and gall bladder to intermittent pressure, the inspiratory movements being the most effective. Inspiration also favours the flow of blood from the hepatic veins, and any increase of pressure on the abdominal viscera will press onwards towards the liver the blood in the portal system.

Influence of the Nervous System on the Secretion of Bile.—Nothing definite is known regarding the influence of the nerves distributed to the liver on biliary secretion. The vaso-motor filaments are undoubtedly partly in the vagi and partly in the splanchnics, so that section of the latter, or of the vagi in the neck, is followed by congestion of the organ. Section of the vagi below the diaphragm is said to produce no effect. Pflüger states that he has seen secretion of bile continue after section of all the hepatic nerves. He also says that galvanization of the liver arrested the secretion. The whole of this subject is in obscurity, and merits investigation.

3. Ultimate Destination of the Constituents of Bile.—When the bile reaches the small intestine, it exercises a comparatively feeble influence on the elements of chyme; but in the great intestine, at least a portion of it is decomposed, whilst the remainder is excreted unaltered in the fæces. The bile acids are split up into cholalic acid, glycocin, and taurin (taurocholic more easily than glycocholic); and the colouring matter, bilirubin, is transformed into hydrobilirubin or urobilin, which is reabsorbed to appear again as one of the pigments of the urine. A small portion of the bilirubin is also transformed into biliprasin, which does not give Gmelin's reaction. The greater part of these substances is reabsorbed, but there is much obscurity as to their ultimate destination. It has been suggested that the glycocin may be transformed into urea (Salkowski), and that cholalic acid is decomposed into water, dyslysin, and carbonic acid (see Vol. I. pp. 86, 91, and 108). Again, as taurin is decomposed by the action of alkalies, it has been supposed that the alkalies of the bile may split up, and thus give rise to the sulphates of the alkalies found in the urine (Vol. I. p. 96). A portion of the bile acids may unite with alkalies to form soaps, which are absorbed. Cholesterin and mucin are excreted in the fæces. These also contain traces of lecithin, probably derived from the bile. About $\frac{7}{8}$ths of the bile salts are reabsorbed. It adds to the complexity of the transformations of the bile when we recollect that all the matters thus reabsorbed by the portal capillaries are conveyed back again to the liver, so that this organ appears to produce certain compounds which are thrown into the alimentary canal, there decomposed, their constituents reabsorbed, and carried back again to the liver to form other compounds.

If the bile be prevented from entering the bowel, in consequence of the establishment of a permanent fistula, the animal soon becomes emaciated, but it may be kept alive for many months by giving it large quantities of food. The appetite is usually voracious. A dog will lose about 20 grammes per kilog. of body weight in twenty-four hours. In these circumstances, less fat is absorbed, from 40 to 50 per cent. of the fat appearing in the fæces. On the other hand, removal of the pancreas, or occlusion of its duct, does not affect to a great extent the amount of fat ingested, and thus it is evident the bile influences the absorption of fat.

4. **Action of the Bile on Elements of Chyme.**—The bile has no action upon albuminates, except to precipitate any soluble albumin by the action of the taurocholate of soda. The glycocholate of soda, or glycocholic acid, is also precipitated by the hydrochloric acid of the gastric juice, and it carries the pepsin along with it. The precipitate thus formed is yellowish, flocculent, and resinous, and it adheres to the villi on the lining membrane of the bowel. Thus, while bile arrests the process of digestion of albuminates by the gastric juice, it separates

peptones from albumin that has escaped the influence of the gastric juice, and it facilitates the further digestion of this albumin by the pancreatic juice. The peptones are absorbed, and the albumin adhering to the wall of the bowel is next attacked by the pancreatic fluid in an alkaline medium.

The bile has a feeble action upon carbohydrates, liquefying starch paste and changing it into sugar, or, at all events, into a substance that reduces cupric to cuprous salts.

Bile is one of the principal agents in the digestion of fats. It cannot decompose neutral fats into fatty acids and glycerine, but if fatty acids have been set free by the pancreatic fluid, it dissolves them and forms an emulsifying fluid. The fatty acids thus dissolved decompose the bile salts, and, by uniting with the alkaline bases of the bile salts, form soaps, setting taurocholic and glycocholic acids free. The soaps thus formed assist in emulsifying the fats in the intestine, and the bile acids then saponify any neutral fats in the intestine. As the bile is an alkaline fluid, it also assists in the absorption of fats by lubricating the mucous membrane of the bowel. If an animal membrane, such as a bit of bladder, or a paper filter, be moistened with bile, fluid fat will pass through under much less pressure than if the bladder or filter paper are moistened with water. A normal dog will absorb about 90 per cent. of the fat supplied in its food, but a dog having a permanent biliary fistula, by which none of its bile is allowed to flow into the bowel, has been found to take up only about 40 per cent. of fat, the remaining 60 per cent. appearing in the fæces. The stools in such a dog become clay-coloured, very hard, and they have a putrescent odour. It may also act as a stimulant to the movements of the bowel, increasing peristalsis. A constipated condition exists when the bile is not poured in sufficient quantity into the alimentary canal, partly from diminished peristalsis, and partly because the fæces are dry and hard. A large increase in the flow of bile has usually a purgative effect, as in bilious diarrhœa. The bile itself is readily putrescible. The power the bile apparently possesses of diminishing putrescence of the fæces is due chiefly to the fact that, by increasing peristalsis, it hastens the passage of putrescible matters through the bowel. If such matters remained for a considerable time in the intestine, even in the presence of bile, putrefaction would take place.

CHAP. XV.—THE PANCREAS AND THE PANCREATIC JUICE.

A. STRUCTURE OF THE PANCREAS.

The pancreas is a long narrow gland which lies across the posterior wall of the abdomen, behind the stomach and opposite the first lumbar vertebra. The broader end, termed the head, is embraced by the curvature of the duodenum, and the narrow end or tail is in contact with the spleen. It measures in an adult in length 175 mm., and its average breadth is 37 to 40 mm. It weighs from 60 to 90 grms. The duct of the pancreas, named the *duct of Wirsung*, runs along the whole length of the gland (see Fig. 65), and it opens into the duodenum at a point from 75 to 100 mm. below the pylorus, along with the common bile duct. It is about 3 mm. in breadth. Along with the chief duct we often find a number of smaller passages opening into the intestine from neighbouring acini. In carnivora and the horse there is a smaller duct termed the *duct of Santorini*. The pancreatic duct of the rabbit is single, and opens into the bowel 30 mm. below the point of entrance of the bile duct.

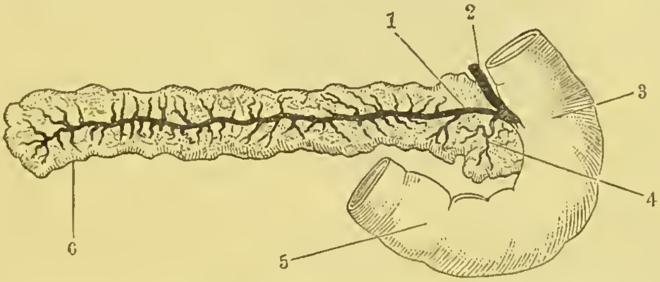

FIG. 65.—View of duodenum and pancreas, *seen from behind*. Quarter natural size. 1. Duct of Wirsung injected; 2, common bile duct; 3, descending part of duodenum; 4, branch of the duct passing into the head of the gland; 5, horizontal part of duodenum. (Krause.)

The duct is lined by cylindrical epithelium, and the wall consists of firm connective tissue. Small branches spring from it, and these terminate in the acini of the gland. The striated epithelial cells found in the salivary glands are absent. In the intercalary parts of the ductlets, before reaching the acini, the cylindrical cells become more and more flattened. The acini contain short cylindrical or conical cells, containing bright refractive granules in the part of the cell next the lumen, thus differing from all other gland cells. The appearance of the cell is modified by its state of functional activity. At the beginning of digestion, the granules gradually disappear, and the clear part occupies the greater portion of the cell. After prolonged rest the granular part of the cell is equal in bulk to the clear part.

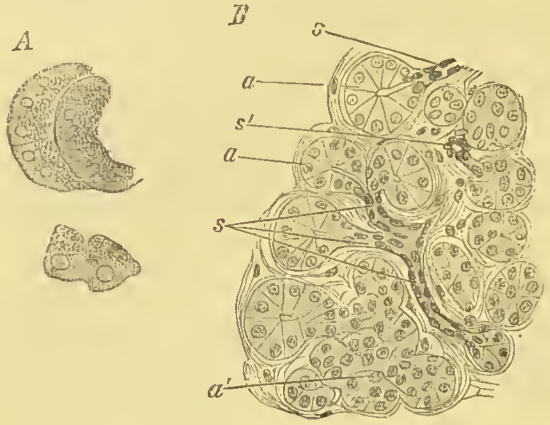

FIG. 66.—*A*, Gland cells of pancreas of cat. × 560 d. Above we see groups of cells, and below two isolated cells. *B*, Transverse section of pancreas of an infant. × 240 d. *s*, intercalary portions of ducts showing flattened epithelium; *s*¹, transverse section of intercalary duct; *a*, *a*, transverse sections of acini; *a*¹, oblique section of acini. (Method No. 40, Appendix.)

Saviotti has found delicate passages between the individual cells after forcing a coloured injection mass backwards along the pancreatic duct. In some places, between the acini, small masses of epithelial-like cells are found, surrounded by capillaries. Their nature is unknown.

The pancreas is supplied with blood-vessels from the splenic, and from the superior and inferior pancreatico-duodenal branches of the hepatic and superior mesenteric arteries, and the blood is carried away from the organ by the splenic and superior mesenteric veins. A rich plexus of capillaries surrounds each acinus. The gland is supplied with nerves by the solar plexus. Non-medullated nerve fibres may be traced into the organ, and small groups of ganglionic cells are found here and there. The mode of termination of the nerve filaments is unknown. The pancreas is also supplied with lymphatics.

B. THE PANCREATIC JUICE.

1. Physical and Chemical Characters of the Pancreatic Juice.—We may obtain the pancreatic juice from the dog or ox by introducing a tube into the duct and drawing off the fluid or by means of a permanent fistulous opening.

The following is the method devised by Claude Bernard, as applicable to the dog. The anæsthetized animal is laid on the left side, and a longitudinal incision, 70 mm. in length is made towards the right side of the mesial line. Expose the duodenum and pancreas, isolate the duct, which will be recognized by its bluish-white colour, open the duct with scissors, and insert and tie in a canula of proper diameter. Bring the canula through the abdominal wound, and carefully stitch the latter by sutures. In a few days the wound will heal.

When obtained pure from the dog, the juice is a colourless, viscous fluid, which may form a thin coagulum when heated. It contains from 6 to 10 per cent. of solids. It is strongly alkaline. The juice contains: (1) *serum albumin* coagulable by heat, and also other albumins that have not been accurately discriminated; (2) *several ferments* to be afterwards considered; (3) *nitrogenous bases*, such as leucin, guanin, tyrosin, xanthin, etc., in small quantity; (4) minute quantities of *soaps*; (5) *salts* (about 1 per cent.), such as chloride of sodium, alkaline and earthy phosphates, and alkaline carbonates. The pancreatic juice of herbivora is more watery and contains only from 1 to 3·5 per cent. of solids, but after a fistula has existed for some days in a dog, the quality of the secretion becomes more like that of a herbivorous animal, that is to say, it becomes more watery, less viscid, and then contains only from 1 to 2 per cent. of solids. In one case Herter collected a small quantity of human pancreatic juice from the duct of Wirsung. It was a clear, colourless, odourless, limpid, strongly alkaline fluid, yielding 2·4 per cent. of solids, of which 1·8 per cent. were organic substances. Sometimes concretions, similar to salivary concretions, have been found in Wirsung's duct. They consist of a basis of organic matter along with ⅔rd parts of phosphate of lime and ⅓rd part of carbonate of lime. The following is an analysis of 1,000 parts of pancreatic juice of the dog obtained by C. Schmidt:—

	From a permanent fistula.[1]	Collected on first opening the duct.
Water,	979·0	900·8
Solids,	20·1	99·2
Organic matter,	12·4	90·4
Salts,	7·5	8·8
The ash from 1,000 parts of juice yielded:		
Soda,	3·32	0·58
Chloride of sodium,	2·50	7·35
Chloride of potassium,	0·93	0·02
Phosphates of alkaline earths and iron,	0·08	0·53
Phosphate of soda,	0·01	...
Lime and magnesia,	0·01	0·32

Hoppe-Seyler found in the pancreatic fluid of a horse the following percentage amounts: albumin, ·022; ferments soluble in water after action of alcohol, ·86; soluble salts (much phosphate of soda), ·82; insoluble salts, ·038, and water, 98·2.[2]

2. Physiological Characters of the Pancreatic Juice.—*Quantity.*—From the dog, about 2·5 grammes per kilogramme of the weight of the body have been collected in twenty-four hours. During very active secretion, and only for a short time, 1 to 2·5 grammes per hour have been collected from the dog. Colin obtained from the horse (on an average of four hours) 175 grammes per hour, from a cow, 200 to 270 grammes per hour, while a pig only gave 12 to 15 grammes per hour.

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[1] Mean of analyses. Quoted by Maly in Hermann's *Handbuch*, vol. V. p. 189.
[2] Hoppe-Seyler. *Physiologische Chemie*, p. 95.

From these data, and taking into account the weight of the pancreas in man, it has been roughly calculated that about 150 grammes may be secreted by a human being in twenty-four hours.

Variations during Digestion.—The secretion of pancreatic juice is intermittent in carnivora and continuous in herbivora. In dogs it begins immediately after the introduction of food into the stomach, attains a maximum about the close of the third hour, afterwards diminishes to the fifth or seventh hour, it may increase while the chyme is in the intestine up to the ninth or eleventh hour, and it slowly diminishes between the eighteenth and twenty-fourth hour. It is secreted, however, in small quantities during the intervals of digestion. Judging from what has been seen in animals having a fistulous opening, at the commencement of digestion it is viscous and very coagulable, and towards its close it becomes more limpid, is not coagulable, and has a much lower specific gravity. By such observations, also, it has been ascertained that a large amount of nutritious food increases not only the quantity, but improves the quality of the secretion, and that any circumstances affecting the general health of the animal have a contrary effect.

The pancreas in the dog is of a pale grey colour while the animal is fasting; when food reaches the stomach it soon assumes a pink red colour. The vessels are full of blood, the capillaries are dilated, and they, and even the veins, pulsate. The blood in the veins is of a venous colour. During this period the gland cells increase in size, assume a conical form, show a clear zone, readily stained by carmine, next the *membrana propria*, and a dark granular zone next the lumen. As secretion goes on, the inner zone diminishes while the outer zone increases in size, that is the granular zone is used up and the clear zone increases. Towards the close of secretion the granular inner zone increases so as almost to fill the cell and the clear zone is very small and shrunken.

Pancreatic juice is secreted under considerable pressure. Heidenhain states that in the rabbit it amounts to 17 mm. of mercury.

3. **Action of Pancreatic Juice on Elements of Chyme.**—The pancreatic juice has an influence upon carbo-hydrates, fats, and albuminous substances: (1) By the action of an amylolytic ferment, it transforms starch into sugar in a manner identical with the action of saliva, but much more rapidly. It acts not only on starch paste and boiled starch, but also on raw starch, and the action is not much influenced by the presence of bile or of gastric juice. It is asserted that the juice of the newly born child does not possess this property. (2) It has a double action upon fats: (*a*) forming an emulsion, in which the fatty particles

are very finely divided; and (*b*) it decomposes the neutral fats into fatty acids and glycerine, and the fatty acids thus set free unite with the alkalies of the pancreatic juice to form soaps. If we add to a little fresh butter, having a neutral reaction, a few drops of alkaline pancreatic juice, keep it for some time, say about fifteen or twenty minutes, at a temperature of 35° C., and then add to the mixture a solution of blue litmus, the colour of the mixture soon becomes red, showing development of acid. The redness deepens in tint showing that the action continues in an acid medium. The acid is set free by the decomposition of the fat into fatty acids and glycerine. The formation of an emulsion requires careful study. Suppose we shake up a little olive oil with water, the oil globules at first are uniformly diffused in the water, but they soon separate and float to the surface. The rapid separation of the oil globules is interfered with if we mix with the fluid any colloid matter, such as a strong solution of gum arabic or white of egg. If we shake up oil with these, the globules remain separate for a considerable time, but by and by they rise to the surface. The light reflected strongly from the surface of innumerable little globules gives the mixture a white appearance. This is well seen in milk and in some of the milky juices of plants. Finally, a more permanent emulsion is formed if we shake up oil with a solution of caustic soda or caustic potash, or of carbonate of potash, especially if a small amount of free fatty acid be present, as when the oil is slightly rancid. If, for example, a rancid fat or oil is brought into contact with a small quantity of a ·25 to a ·5 per cent. solution of caustic soda, a fine emulsion will be at once formed, even without shaking the mixture. In this case, the free fatty acid combines with the alkali to form a soap, and the soap forms a thin layer round each drop of oil, thus producing a true emulsion. Pancreatic fluid has the power of emulsifying to a remarkable degree, and this power depends (1) on its viscosity from the presence in it of albumin, (2) on the alkaline carbonates it contains, and (3) on the soaps formed by its chemical action on fats, the fatty acids liberated uniting with the alkali of the pancreatic fluid itself or with the alkali of the bile. The bile also emulsionizes fats, although not so thoroughly as is done by the pancreatic juice. The presence of bile appears to favour the emulsifying action of the pancreatic juice, as the addition of bile increases the amount of fats decomposed, but the exact way in which it thus acts is not known.

(3) The action of the juice on albuminous matter is more complicated, and may be divided into three successive stages, namely: (*a*) albuminates are converted into peptones; (*b*) these peptones are partially converted into leucin and tyrosin; and (*c*) from the leucin and tyrosin

thus formed, peculiar substances are produced, having a strongly fæcal odour, amongst which indol has been found. The proteolytic ferment which acts on albuminous bodies is termed *tripsin.* Tripsin shows its peculiar power in an alkaline fluid, and it apparently loosens the albuminous molecule to such a degree that it decomposes into many simpler bodies. Thus a glycerine-extract of pancreas, with the addition of a small quantity of a 1 per cent. solution of carbonate of soda quickly digests fibrin. Tripsin does not exist in the pancreatic cells but it is produced by the decomposition of a body called *tripsinogen.* The proof of this is that a glycerine-extract of pancreas, freshly prepared, may have no influence on fibrin, but if it is exposed to the air for twenty-four hours, and diluted with water, it may then show active properties. The peptones, or as they might be termed, *triptones*, formed by pancreatic digestion, differ in some respects from peptones produced by the gastric juice. They are soluble in water, and they give the biuret reaction (deep red or purplish red) with caustic soda and a weak solution of sulphate of copper. The molecule is still further decomposed, leading to the formation of amido-acids, such as leucin, $C_6H_{13}NO_2$, or amido-caproic acid, tyrosin, $C_9H_{11}NO_3$, or oxy-phenyl-amido-propionic acid, aspartic acid, or amido-succinic acid and glutamic acid (an amido-compound related to tartaric acid). Then appear badly smelling substances, belonging to the aromatic compounds, such as phenol, indol, skatol, the two latter giving the odour of fæces. Indol may also be produced by decomposition of proteids, by the action of alkalies at a high temperature, and by the action of super-heated steam. Putrefactive germs also find a suitable medium for development in an alkaline fluid in which the pancreatic digestion of proteids goes on, and no doubt they assist in the further decomposition of the digestive products. Thus it has been supposed that they also may form amido-acids, aromatic bodies, etc. The chief agent in carrying on these processes of decomposition is undoubtedly tripsin, as Kühne demonstrated that if we prevent putrefactive changes by adding to an extract of pancreas a ·33 per cent. of salicylic acid or a ·5 per cent. of acetic acid, peptones and amido-acids are still formed.

These observations of Kühne have recently been corroborated and much extended by Harris and Tooth[1] using antiseptic solutions of 1 to 2 per cent. of mercuric chloride, ·24, ·5, and 1 per cent. of carbolic acid, 1·25 per cent. of thymol, 1 per cent. of sulphate of quinine, and solutions of salicylate of soda and iodine, and carefully following the methods of bacteriology. They arrive at the conclusion that

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[1] Harris and Tooth, "Micro-organisms and Pancreative Digestion." *Jl. of Physiology*, vol. ix. No. 4.

the pancreatic ferment is able to convert proteids into peptone without the aid of micro-organisms. On the other hand, they never obtained an appreciable amount of leucin and tyrosin unless micro-organisms were also present. The formation of indol has been often attributed to micro-organisms. These observers find that no indol may be present although there are swarms of micro-organisms, while organisms are always found in a fluid which yields indol. It is not unlikely, therefore, that the production of indol may be due to a specific organism.

As to the nature of leucin and tyrosin, see Vol. I. pp. 91-93, and indol and skatol, see Vol. I. pp. 109-111. Aspartic acid, $C_4H_7NO_4$, or $CO_2H.CH_2.CH(NH_2).CO_2H$, that is amido-succinic acid, appears as silky, shining, rhombic crystals, soluble with difficulty in cold water and alcohol, but readily soluble in boiling water.

Chap. XVI.—THE INTESTINAL JUICE AND INTESTINAL DIGESTION.

The juice called *succus entericus*, secreted by the glands of Brunner and the crypts of Lieberkühn, is very difficult to obtain in a pure condition.

It has however been obtained by making an intestinal fistula. The abdomen is opened and a loop of bowel, from 300 to 500 mm. in length, is cut across at the two extremities. The lower end of the bowel situated above the portion thus cut across is brought into connection by sutures with the upper end of the lower portion, so that the canal of the intestine is continued onwards. The portion of bowel thus detached from the upper and lower parts of the bowel, but still connected to the wall of the abdominal cavity by the portion of mesentery belonging to it, is carefully emptied of its contents, and the lower end is sewed up by sutures, so that the loop of bowel now becomes a cul-de-sac. The edges of the upper end are connected by sutures with the edges of the wound in the abdominal wall. This is a fistula after the method of Thiry. If both ends are left free, and if both are sutured to the abdominal wound, a fistula after the method of Vella is formed. In both cases, a fluid is secreted which can be collected in sufficient amount for analysis and experiment.

Intestinal juice is a transparent, viscid, slightly yellowish fluid, strongly alkaline, and coagulable by heat and by acids, and having a specific gravity of 1011. It contains from 1·25 to 2·5 per cent. of solid matter, which consists of organic matter, chiefly albumin and mucin and salts, of which the chief are carbonate of soda and chloride of sodium. It contains a ferment which transforms cane sugar into inverted sugar. The variations during the digestive process are unknown.

From the difficulty of obtaining the juice in a pure condition, and free from admixture with the other digestive fluids, it has been found almost impossible to ascertain its specific actions. The only chemical action clearly demonstrated is that it converts starch into maltose and dextrin. It also, by the mucin it contains, lubricates the mucous membrane, and thus facilitates the gliding of the intestinal contents onwards.

General Characters of Intestinal Digestion.—When the chyme passes through the pylorus into the small intestine, the action of any gastric juice mixed with it is soon arrested. The acid chyme excites the efflux of bile, pancreatic juice, and intestinal juice. As these juices are alkaline, they gradually neutralize the acidity of the chyme, so that that fluid towards the end of the duodenum becomes first neutral and then alkaline, and remains so till it leaves the small intestine. The alkalinity is most marked in the layers next the wall of the bowel, and the innermost layers, even as low as the middle of the small intestine, may still be faintly acid. In carnivora, the chyme may be acid in a great length of the small intestine, but in the dog, fed on a mixed diet, the acidity disappears at a distance of 10 or 12 inches from the pylorus (Munk). In the small intestine, all the elements of food, albuminates, starches, fats, and sugars, are transformed so as to be assimilable. As already pointed out, glycocholate of soda is precipitated, along with pepsin, by the hydrochloric acid of the gastric juice. At the same time the taurocholate of soda throws down the non-peptonized albuminous matters, such as coagulable albumin, and syntonin, while the hemialbumose and the peptones remain in solution. The precipitate thus formed is thick, resinous, and viscid. In the upper part of the intestine, the chyme is coloured slightly yellow by the bile, but it becomes of a paler colour towards the lower end of the bowel. As it passes downwards, it gradually becomes more alkaline, from the action of the alkaline bile, alkaline pancreatic juice, and alkaline intestinal juice, and contains a smaller quantity of alimentary matters not digested, and traces of leucin and tyrosin. So soon as the chyme has become alkaline, triptic digestion begins. The resinous precipitate formed by the bile dissolves, but the pepsin, although redissolved, cannot act as it is now in an alkaline and not in an acid medium. Any starch in the chyme is quickly changed into maltose, the fats are decomposed or emulsionized, and albumins are split into leucin, tyrosin, etc.

It is important to observe that, as these changes are going on, the chyme is slowly propelled along the bowel by the peristaltic movements of the muscular coats. At the same time soluble matters are absorbed, as in the stomach, by the blood-vessels and by the intestinal villi. Thus the amount of chyme is gradually diminishing, and the character of the chyme is also changing. So quickly are matters thus removed that in some animals, the dog for example, the intestine is rarely found full of chyme, although the animal may have had, shortly before the observation, a full meal of flesh. Even between the sixth and ninth hour after a full meal, when the pancreas is in a state of great activity, only a little bilious looking mucus may be found in the intestine of a dog. It would thus appear that, in the dog, only so much matter is ejected from the stomach at intervals as can be *rapidly* digested and absorbed in the intestine, and that there is a regulative mechanism at work (Munk). The small intestine of herbivora, and even of omnivora, often contains large quantities of chyme. Even in the lower part of the small intestine, fermentive and putrefactive processes are actively going on. These are carried on to a still greater extent in the great intestine.

CHAP. XVII.—CHANGES IN THE GREAT INTESTINE.

When the alkaline chyme, poor in alimentary matters in consequence of absorption, reaches the great intestine, it has certain of the characters of fæces, and these become more marked towards the termination of the great intestine. This part of the alimentary canal receives only the secretion from numerous tubular glands, similar to those in the small intestine.

1. Movements of the Great Intestine.

The movements of the great, differ from those of the small, intestine by occurring more slowly. In consequence of the slowness, the passage of material occupies a much longer time than in the small intestine, although the latter is at least three times the length of the great intestine. Thus the time occupied in the small intestine is from two to three hours, whilst from twelve to twenty-four hours are required for transmission through the great intestine. This arises from the matters remaining for a lengthened period in the cæcum, where they become more solid in consistence from the absorption of water. They are also delayed by the sharp ridges projecting into the interior of the bowel, which divide the elongated cavity into a series of loculi or compartments. Finally, the matters accumulate in the rectum, where they are retained by the action of the sphincters.

Nervous Arrangements of the Movements.—Nothing definite is known regarding this point, except that irritation of the vagus excites the movements, whilst irritation of the splanchnic is followed by no effect. It is probable that the latter nerves exercise an inhibitory influence over the ganglia in the wall of the bowel.

2. Physical and Chemical Changes in Great Intestine.

The matters in the great intestine are frequently alkaline near the intestinal wall and acid in the centre, more especially after food rich in starchy matters. In the horse, the contents of the cæcum are alkaline, so that any acids formed by the fermentation of carbohydrates are neutralized by the alkalies of the bile, pancreatic juice, and intestinal juice. On the other hand, the contents of the rabbit's cæcum are usually acid. In man, alimentary matters do not undergo any further digestion in the great intestine, and the fæces are gradually formed from the refuse materials of food, biliary products, and various substances excreted from the wall of the bowel. In herbivorous animals, however, a kind of secondary digestion occurs in the greatly enlarged cæcum met with in these animals. Ruminants possessing a complicated series of pouches, in which the food is subjected to fermentive and putrefactive changes before it reaches the true stomach, have a comparatively small cæcum; but in other herbivora, in which the stomach is simple, so that the vegetable food passes into the small intestine, we find a very large cæcum. This latter condition is illustrated in the horse, which has a cæcum 1 metre in length, and having a capacity of 30 litres, almost double that of the stomach. The masses of partially digested food in this animal may remain in the cæcum for twenty-four hours. As the peristaltic movements of the great intestine are very slow, the contents of the cæcum become closely packed. Fermentive and putrefactive changes go on actively in the conditions of moisture from the presence of a considerable amount of water and of a temperature of about 40° C. Putrefaction of the albuminous matters gives rise to amido-acids, ammonia, carbonic acid, and sulphuretted hydrogen, and also to the aromatic bodies, phenol, cresol, indol, skatol, phenyl-acetic acid, etc. Putrefaction may also give rise to succinic acid and palmitic acid.

The following are the chief reactions of several of these bodies :—

1. Phenol (carbolic acid), C_6H_6O, the hydroxyl of benzol, C_6H_5HO, crystallizes in white needles or long prisms, is soluble in water to the extent of 6 per cent., and is readily soluble in alcohol. It yields with salts of iron a violet colour, which is destroyed by acids. It yields with bromine water a white precipitate of monobromphenol and dibromphenol, and if more bromine water is added, a yellow colour is produced by the formation of tribromphenol, $C_6H_2Br_3OH$. The bromine water reaction will detect 1 of phenol in 50,000 parts of water.

2. Cresol, C_7H_8O, a methyl substitution product of phenol, $C_6H_4(CH_3)OH$, appears as colourless prisms, having a smell like that of phenol. It is soluble in water with difficulty, and it strikes a blue colour with iron salts.

3. Indol, C_8H_7N, is slightly soluble in water, and is readily soluble in alcohol and ether. Its solution in water gives a blood-red colour with fuming nitric acid, and when concentrated, a red precipitate of nitro-indol is thrown down.

4. Skatol, C_9H_9N, is a white crystalline substance, having a peculiar and most disagreeable fæcal smell. It is very slightly soluble in water, and the aqueous solution gives with diluted fuming nitric acid a milky colour.

Starchy matters are also subjected to putrefactive and fermentive processes. Thus are formed lactic acid, $C_3H_6O_3$ (that is fermentation or ethylidene lactic acid, $CH_3.CH.OH.COOH$, Vol. I. p. 165), and various fatty acids, such as formic acid, CH_2O_2, acetic acid, $C_2H_4O_2$, propionic acid, $C_3H_6O_2$, butyric acid, $C_4H_8O_2$, etc. Some of these in turn may decompose. Thus formic acid may be resolved into carbonic acid and hydrogen, and acetic acid into carburetted hydrogen and carbonic acid. The higher acids are not decomposed.

The fats also are decomposed into glycerine and fatty acids. The glycerine is further changed into carbonic acid and water, and the fatty acids, if not absorbed into the blood, unite with the bases of earthy salts, such as lime and magnesia, to form peculiar soaps found in the fæces.

A portion of the bile reaches the great intestine, and is there transformed into taurin, glycocin, cholalic acid, choloidic acid, and dyslysin, all of which, along with bile acids and bile pigments, are found in the fæces.

Characters of the Fæces.—These have a peculiar odour, which is characteristic not only of the animal, but even of the individual, and varies from time to time. This odour depends upon the products obtained by the decomposition of peptones. Fæces may be acid, alkaline, or neutral. The acid reaction is due to the fermentation of carbohydrates, as it is greatest after a diet rich in these substances. Alkalinity is due to the decomposition of albuminous matter. Fæces vary in colour, according to the kind of food and the amount of biliary matter present. Thus, with a rich animal diet, the fæces are dark coloured; with a vegetable diet, light, or slightly green; and a mixed regimen produces a brownish-yellow colour. They become clay-coloured, and very offensive during jaundice, a condition in which little or no bile passes into the alimentary canal. Fæces may be black in the dog, fed on meat, greyish-green in oxen, and yellow or brown in the horse. The pigments present are stercobilin (related to urobilin) and biliprasin.

The microscopical examination of fæces shows the presence of elastic tissue, fragments of muscular tissue, cholesterin, fat globules, starch grains, spiral vessels, epithelial cells, vegetable cells and fibres in various states of disintegration, and crystals of triple phosphate, etc. We may also find salivary matters, bile pigment, cholalic acid, dyslysin, fats, undissolved fatty acids, soaps, volatile fatty acids, nuclein, undigested albuminous matter, phenol, indol, and skatol. With a meat diet, human fæces may contain about 50 per cent. of water, and with a mixed diet about 75 per cent. The fæces of the ox contain about 85 per cent., those of the horse 75 per cent., and the hard fæces of sheep, goats, rabbits, etc., only 55 per cent. In the case of man 25 per cent. consist of solid matter, of which from 3 to 4 per cent. are composed of various salts, the chief being the triple phosphate of ammonia and magnesia. Saline matters occur in human fæces to the extent of 1 per cent., in that of the horse and ox 2·5 to 3 per cent., in that of the sheep 6 per cent., and in that of the pig 8 per cent. The salts in the excrement of the horse, ox, and sheep consist of $\frac{2}{3}$rds of silica (derived from epidermis of plants and from sand taken with food), along with the triple phosphate; only traces of chloride of sodium and of carbonates and sulphates of the alkalies are present. Large concretions or *enteroliths* are not uncommon in the horse, sometimes reaching a weight of 20 lbs. avoird. They are more rare in man and in herbivora. Surrounding a nucleus formed of the stone of a fruit, or a bit of undigested bone, we find layers of triple phosphate and calcium phosphate. Thus the enterolith of a horse has yielded in percentages, 15 of water, 5 of calcium phosphate, and 80 of triple phosphate.

Planer found in the small intestine of the dog 40 per cent. of carbonic acid, 45 per cent. of nitrogen (from atmospheric air swallowed), and 14 per cent. of hydrogen, arising from butyric fermentation. When the animal was fed with peasemeal the amount of hydrogen increased. In the large intestine, the chief gas is carbonic acid, from 66 to 98 per cent., with a little hydrogen and sulphuretted hydrogen. The gas of the large intestine of man contains carburetted hydrogen, CH_4, to the extent of 13 per cent., after a meal rich in leguminous matter. The large intestine of the horse has yielded 50 per cent. of carburetted hydrogen, 42 per cent. of nitrogen, and only 8 per cent. of carbonic acid. The large and small intestines of oxen have been found to contain carburetted hydrogen, carbonic acid, a little hydrogen, and from 20 to 30 per cent. of nitrogen. In the tympanitic condition following feeding on damp green food, the gases are chiefly carburetted hydrogen and carbonic acid. Some of these gases, in certain conditions, may be absorbed into the blood, and then be separated by the lungs.

The weight of the fæces passed in twenty-four hours by a man living on a mixed diet varies from 100 to 200 grammes, and it may even be so high in some individuals as 450 grammes. The amount is increased by a vegetable diet absolutely and also in proportion to the amount of food consumed, because vegetable food contains more matter that is indigestible, or can only be digested with difficulty, and the amount reaches a minimum with an animal diet. The excrements of herbivorous animals are, *cæteris paribus*, always greater in amount than those of carnivorous animals.

Movements of Defæcation.—Pressure of the fæces on the mucous membrane of the lower part of the rectum excites a desire, which is followed by evacuation. When this pressure does not pass a certain limit, the tenacity of the sphincter, to a certain extent under the control of the will, resists evacuation. When the desire reaches a certain intensity, there ensues a series of reflex intermittent contractions of the rectum, and of the sigmoid flexure of the colon, which tend to expel fæcal matters. These contractions overcome the resistance of the internal sphincter, but the external sphincter, by an effort of will, may be still firmly closed. If the desire be now yielded to, the matters are voided by the combined action of the rectum, and of the abdominal muscles, which latter are assisted in their efforts by fixation of the diaphragm. These muscles compress the abdominal cavity, and thus assist in expulsion. The *levator ani*, which forms the floor of the pelvis (Fig. 67), contracts, and, as it were, draws the rectum, and more especially its lower part, over the fæces, as they are expelled downwards. The movements are under the control of a special reflex centre, situated in the lumbar region of the spinal cord. It would appear, also, that this centre is under the control of still higher centres, as paralysis of the sphincters, and involuntary evacuations, occur when the higher centres are affected, as in coma.

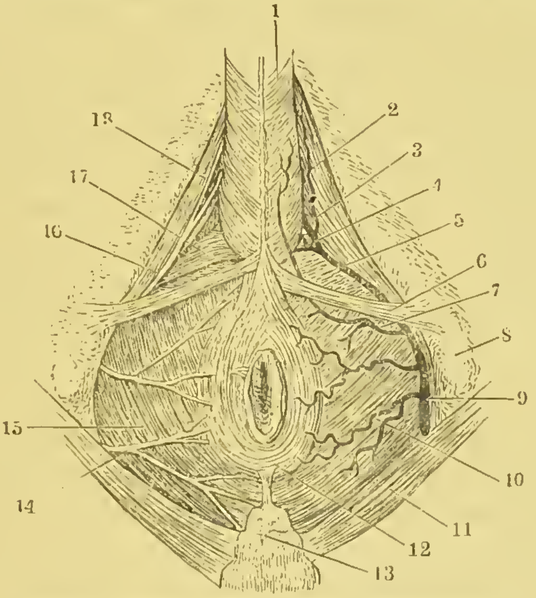

Fig. 67.—Male Perinæum, *seen from below*, showing the arteries and nerves. Half natural size. 1. Bulbus cavernosus, showing muscular fibres; 5. deep layer of fascia; 6. superficial transverse muscle; 8. tuber ischii; 9. internal pudendal artery; 11. glutæus maximus. 12. external sphincter ani; 13. tip of os coccyx; 14. branches of nerves of perinæum; 15. levator ani; 17. deep transverse muscles; 18. ischio-cavernosus muscle (Krause).

SECTION II.

ABSORPTION.

Chap I.—GENERAL CONDITIONS OF ABSORPTION.

We have studied the changes by which nutritious matters are rendered soluble in water, so as to form a fluid holding various substances in solution, and we have next to consider the mechanism by which these matters are absorbed into the blood. Another aspect of the problem is to regard the blood—a fluid holding matters in solution—as existing on one side of an organic membrane, while on the opposite side we have another fluid, in which, also, many substances are dissolved. To what extent do the substances in each of the fluids intermingle, and what are the laws regulating the movement of substances from one fluid to the other? Suppose two fluids, capable of mixing without any chemical action taking place, are brought into contact by gently pouring one fluid over the other, diffusion between the fluids will go on until a uniform mixture has been effected. Diffusion will take place in these circumstances even supposing a lighter fluid is poured over a heavier one, that is to say, some of the heavier fluid will pass upwards into the lighter fluid, even against the influence of gravity. This phenomenon is similar to the diffusion of gases, only the time required for liquid diffusion is very much greater than for gaseous diffusion. Thus many weeks will elapse before a layer of a solution of sulphate of copper will mix with an underlying layer of a solution of common salt, and the time will be much longer when a layer of a solution of albumin is laid over a layer of water. A rise of temperature quickens liquid diffusion.

If the fluids are separated by a porous partition, as of earthenware, they will pass into the pores of the partitions, forming an immense number of little columns of fluid, and diffusion will occur in these in the same manner as in the layers above described. This process is designated *imbibition without increase of volume*, or *capillary imbibition*, and it is to be distinguished from the change, with increase of bulk, that takes place when such a substance as gelatin is soaked in water. In the latter case, the water is absorbed into the molecular interstices of the substance. Albumin, starch, the connective tissues, and almost all tissues behave in this way, and the process is called *imbibition with increase of volume.*

Dry tendons take up almost double, cartilages more than double, connective tissue treble, and cornea more than quadruple their own weight. Dry animal membranes do not swell so much in salt solutions as in water, and less in proportion as the salt solution is concentrated. When a solution of salt is imbibed, more water than salt enters into the substance, so that saline solutions become more concentrated if we immerse distensible substances in them. The water is attracted by the walls of the pores, while mixtures of water and salt are found in the centre of the pores. Thus each pore or canal contains two fluid layers—one next the periphery consisting almost wholly of water, and the central one consisting of a solution of salt of the same degree of concentration as the surrounding fluid. The imbibed fluid is therefore less concentrated than the surrounding one (Munk).

We have next to consider the case of two fluids separated by a membrane, but subject to the same pressure. Suppose a strong solution of common salt thus separated from distilled water. Diffusion takes place, a stream of water passing in one direction, and a stream of salt solution in the other, the first being greater than the second, so that the volume of the salt solution increases. This action, which may be termed *diffusion through membrane,* will go on until we find on both sides of the membrane a solution of salt of the same degree of concentration (see Vol. I. p. 348).

Colloids pass through membranes only to a very small extent, and they have a large endosmotic equivalent, that is to say, they draw a large amount of water towards them. It has been supposed that so called colloid bodies are not in a state of free solution, but in something like fine suspension. When a mixture of a crystalloid and colloid is submitted to diffusion, the crystalloid diffuses only a little slower and the colloid much slower than if each existed alone in the fluid, so that salt will diffuse almost completely out of a solution of albumin, especially if the distilled water into which the salt is allowed to diffuse is frequently changed. Thus, as first shown by Thomas Graham, colloids may be separated from crystalloids.

When fluids pass through animal membranes under pressure, the process is termed *filtration.* Large-pored membranes, such as filter paper, allow not only fluids but even morphological elements to pass through. Thus the corpuscles of blood and the globules of milk pass readily through such membranes. Animal membranes, on the other hand, usually arrest morphological elements. When a fluid holding various crystalloids in solution is filtered, the degree of concentration of the filtrate is the same as that of the fluid poured on the filter; but if solutions of colloids, such as albumin or gum, are forced under pressure through animal membranes, the filtrate contains less of the colloid than the original fluid. The difference varies with the degree of concentration of the original fluid, the amount of pressure, and the nature of the membrane, especially the width of its pores. If a fluid containing both colloids and crystalloids is filtered under pressure, then the filtrate is richer in colloidal matter than it would be, *cæteris paribus,* if the colloid alone existed in the fluid.

If we suppose a fluid forced by pressure through a porous canal, of extremely narrow diameter, the water, as already pointed out, will form a peripheral layer, while the central layer will contain the substances in solution. The flow of this central current will depend on the viscosity of the fluid, or in other words, on its internal friction. Thus fluids rich in colloids, by reason of their great viscosity, will pass through more slowly than fluids rich in crystalloids, and we may also suppose that if the colloids are not in a state of true solution, their larger molecules will be mechanically kept back in passing through narrow canals. This will explain why a filtrate contains less colloidal matter than the original fluid.

Chap. II.—ABSORPTION FROM THE INTESTINAL CANAL.

By the chemical processes of digestion, matters insoluble in water are rendered soluble in that fluid, and certain matters, such as fats and oils, that are insoluble in water under any conditions, are so altered as to be emulsified, or divided into minute particles. These matters are taken up from the intestinal canal by capillary blood-vessels and by a special set of absorbents which belong to the lymphatic system, to be afterwards described. The question as to whether the lymphatic vessels are the only absorbents, or whether the capillaries take part in the process was finally settled by Magendie. He showed that if the thoracic duct of an animal is ligatured and if a soluble poison is then introduced into the intestine, the animal will die as quickly as a normal animal. He also showed that if a portion of intestine into which a soluble poison has been introduced is left in connection with the body only by the blood-vessels, the animal will soon die.

1. **Absorption by the Capillaries.**—The mucous membrane of the stomach and intestines is richly supplied with capillary blood-vessels placed immediately beneath the epithelial layer. In injected preparations, the capillary plexus is so distinctive in character as to

identify the mucous membrane to which it belongs. Thus, in injections of the stomach, the capillaries form meshes of irregular shape; in the small intestine, the vessels exist as a network, from which arise loops, passing into the villi, whilst in the great intestine, the meshwork is so regular as to present the appearance of a honeycomb. These vessels during life are filled with blood of a certain specific gravity, moving slowly onwards and exerting a certain pressure on their inner surface. On the other side, and separated by the walls of the vessels, by connective tissue, and by an epithelial layer, we find the chyme containing substances in solution. It is evident that, under these circumstances, the conditions are favourable for the passage of a certain amount of material directly into the blood. The whole of the matters thus absorbed—peptones, sugar, water, and salts—passes to the liver. The mucous and submucous layers also contain many lymphatics.

We must now consider these phenomena more in detail. Bearing in mind the physical principles laid down in the last chapter, it is evident that there must be an interchange of matter between the blood in the capillaries and the lymph in the lymphatic vessels on the one hand, and the fluid contents of the stomach and intestines on the other. This interchange takes place according to the laws of hydro-diffusion. Water, saline matters, and sugar in solution pass out of the intestinal canal into the blood and lymph, when the fluid in the canal is richer in these substances than the blood and lymph. The greater the difference between the contents of the canal and of the vessels, the more rapidly will diffusion take place. The physical process is one of diffusion, and not of filtration under pressure caused by the peristaltic movements of the intestinal wall, as some have erroneously supposed.

The rapidity of diffusion is increased by the fact that the fluids (the blood, the lymph, and the intestinal fluid contents) are in motion, so that new layers of fluid are brought constantly into juxtaposition. Thus the same degree of concentration on each side of the membrane is not likely to occur. The movement of the blood and lymph, on the one side, and the movement of the fluid contents of the intestine, on the other, caused by peristalsis, present conditions most favourable for diffusion. This process, however, accounts only for the absorption of water, salts, and sugar. Albumin and fat cannot be thus absorbed. When an albuminous fluid is separated from another fluid by an organic membrane, only a trace will pass through, and even this trace only when there is much albumin on one side and almost none on the other. But the blood in the capillaries contains from 7 to 8 per cent., and the fluid in the lymph from 3 to 4 per cent., of albumin.

Albumin must therefore, as we have seen in the study of digestion, be converted into peptones, which are soluble in water and which readily diffuse. But absorption of peptones, etc., can hardly be considered as occurring in the same way as diffusion, through a dead organic membrane. The tissue between the fluid contents of the stomach and intestine and the blood in the capillaries is living tissue, and the membrane is clothed with living cells. As will be afterwards seen, the vital activity of these cells must be taken into account, and it is highly probable they have a power of selective cellular absorption, by which certain matters may be taken up and others rejected.

Absorption occurs to a slight extent in the mouth. In the stomach, the process is much more rapid; it attains its maximum in the small intestine, and it occurs also in the great intestine.

2. **Absorption by the Villi.**—The mucous membrane of the small intestine is clothed with small conical bodies termed the *villi*. Placed closely together on the mucous membrane, their number is enormous, reaching, in the human being, according to Krause, to four millions. They are larger in carnivora than in herbivora. The structure of a villus has already been described, p. 76, and it will be sufficient to notice here certain points of special importance with reference to their mode of absorption. The substance of each villus consists largely of fine adenoid or retiform tissue, similar to that seen in lymphatic glands, and the reticulum contains numerous lymph corpuscles. Running down the centre of the villus to within a short distance of its base, we find a large space communicating freely with minute spaces in the surrounding retiform tissue. This space has no distinct wall, but it is lined by a layer of endothelial cells, and it may be regarded as a large lymphatic space. Near the base of the villus, the space acquires a distinct wall, and even valves, and becomes a lymphatic vessel or *lacteal*. Between the lacteal and the *membrana propria*, on which we find the epithelium, smooth muscular fibres exist, some running longitudinally, and others surrounding the lacteal in the form of circular bands. The villus also contains a network of blood capillaries, supplied by a small artery, and from which the blood is carried away by one, two, or three minute veins. It has been supposed, from the arrangement of the vessels, that when the villus is richly supplied with blood, as is the case during absorption, it is rendered tense and firm, like a minute erectile organ. Covering the villus, we find a single layer of columnar epithelial cells, narrower at the attached end, and showing at the broader free end a finely striated border. Each cell contains one or two nuclei, the protoplasm is finely granular, and very fine fibrils spring from the attached

end, which are continuous with the retiform tissue in the substance of the villus (see Figs. 41 and 42, p. 76; Fig. 44, p. 77; Fig. 45, p. 78; and Fig. 47, p. 80).

During absorption (after a meal containing fat), fine highly refractive molecules of fat are found either in the substance of the epithelial cells, or between the cells, or between the attached ends of the cells and the lymphatic spaces in the centre of the villus, or in the retiform tissue, or in the lymphatic spaces themselves, or, finally, in the lacteal towards the base of the villus. The fatty particles make their way from the intestinal canal into the lacteal. Many explanations have been offered of this process. Some have supposed that they are in a manner squeezed through the epithelial cells by the peristalsis of the intestine, but a more likely theory is that these cells, acting like minute protoplasmic organisms, take up fatty particles and pass them along by the fine protoplasmic filaments at their attached end. These filaments may be regarded as pseudopodia, and this view is supported by the observation that amœboid movements have been seen to occur in these processes. If the fatty particles have reached these processes, we can then understand that rhythmic contractions of the smooth muscular fibres in the villus will not only empty the villus of blood but will press onwards the fatty particles into the large lymphatic space in the centre, from it into the lacteal at the base, and from the lacteals in adjacent villi into the lymphatics in the submucosa. Suppose next that the muscular fibres relax, the blood will rush into the vessels, distend the villus, and remove pressure from the lymphatic spaces. These cannot be filled by the fluid passing backwards from the lacteals, because it is prevented from doing so by the valves near the base of the villus, and consequently any fatty particles in the epithelial cells, or in their processes, will be, as it were, aspirated into the lacteal. The process of emptying will then again be repeated, and thus the epithelial cells are relieved of their burden of fatty particles by a series of consecutive suction-like actions. The objection to this view as a complete explanation is, that it does not take into account the existence of the adenoid tissue in the villus. Another theory is that this tissue plays an important part in the absorption of the fatty particles. Some have supposed that the lymph corpuscles in the retiform tissue send out fine processes between the epithelial cells, and that these suck up or absorb fatty particles and then draw them into the cell. It can be shown that lymph corpuscles take up finely divided particles of semi-solid fat, or even particles of fatty acids having a high melting point. The obvious objection to attributing all the absorptive power to the lymph corpuscles is that it does not take cognizance of the specially constituted epithelial cells, and accordingly the view suggested by Schäfer, that the processes connected with the attached end of the epithelial cells are continuous with the processes of the lymph cells, and these again with the lymph tissue forming the lymphatic space, is more reasonable. If this be so, one can imagine the epithelial cells absorbing the fatty particles in the first instance and passing these on to the lymph cells, and these again may carry them on to the lymphatic space. The difficulty still remains of accounting for the progression of the fatty particles in one direction, and here the mechanical action of the muscular fibres may come into play, the fatty particles being aspirated onwards, after they have been absorbed by the joint action of the epithelial cells and of the lymph corpuscles.

The villi, however, are not solely concerned in the absorption of fat. Both by their blood-vessels and by their lacteals, peptones, and some of the products of pancreatic digestion, are also absorbed. This absorption is also connected with the functional activity of the epithelium of the mucous surface. Peptones introduced directly into the blood are rapidly eliminated by the kidneys, so that it would seem that they are first taken up by the epithelium cells, passed on by these to the lymph corpuscles that exist in great numbers below the layer of epithelium during active absorption, and probably modified, in a molecular sense, during this transition. This process may be called *cellular absorption*. The process also occurs to some extent in the great intestine, as shown by the well-known effects of administering nutritive enemata. It has been shown by Voit and others that not only peptone, sugar, saline matters, and water are absorbed from the rectum, but that even soluble albumin, especially when given along with a solution of common salt, is readily taken into the vessels of the whole of the great intestine.

The power of absorption of various matters in the intestinal canal can only be exercised within certain limits. Thus, in the case of fat, the limit is quickly reached, beyond which no fat is absorbed. Voit found that a large dog can absorb daily only a maximum amount of 300 grms. of fat, and Bidder and Schmidt state that only ·5 grm. of fat is taken up by dogs per kilogramme of body weight. The same is true in the case of the human being. If more than a moderate amount is taken in the food, the excess is voided in the fæces. In like manner, the ingestion of excessive quantities of sugar causes diarrhœa, probably by inducing a transudation of fluid from the vessels, or by the increased peristalsis arising from the irritant action of the lactic or butyric fermentations. A diet containing excess of starchy matters may likewise cause diarrhœa, and the fæces will be highly acid. An excess of albuminous matter is more easily tolerated.

Chap. III.—THE CHYLE.

During digestion, more especially if the food contains a considerable amount of fatty matter, the lymphatic vessels in the villi and in the mesentery, the latter commonly called *lacteals*, are filled with a milky fluid, the *chyle*. When the food contains no fat, the fluid in the lacteals is a clear, transparent, slightly yellowish fluid, which cannot be distinguished from ordinary lymph. The lacteals of the mesentery unite to form larger and larger vessels, and these pass to lymphatic glands in the mesentery, commonly called the mesenteric glands. The efferent vessels of these glands unite to form a single large lymphatic trunk, which presents a wide dilatation, the so-called *receptaculum chyli*, before it ends in the thoracic duct. The latter duct also receives lymph from the pelvic organs, and from the lower extremities by large lymphatic vessels coming from these parts. The thoracic duct passes through the diaphragm, and traversing the thoracic cavity reaches the root of the neck, where it joins the venous system on the left side at the junction of the left internal jugular with the left subclavian vein. The wall of the duct consists of various layers, an inner epithelial layer consisting of a single layer of flattened, oblong, or lanceolate, nucleated cells, and resting on a layer of longitudinal elastic fibres, a middle coat of smooth muscular fibres mostly arranged in a circular manner, but a few running longitudinally, and mixed with elastic fibres and with layers of white fibrous tissue, and an external coat of white fibrous tissue.

The chyle, obtained from the *receptaculum chyli* after a meal rich in fat, is a faintly alkaline, milky, or opalescent fluid; having a specific gravity of from 1018 to 1027. When examined under the microscope, it is found to consist of a fluid, in which are numerous molecules, highly refractive particles of fat or oil, and cells, of irregularly globular form containing minute granules, and similar to the colourless corpuscles of the blood. These are *lymph corpuscles*. Prior to the passage of the chyle through the mesenteric glands, it abounds in molecules and fatty particles, but afterwards these are less numerous, and the cells make their appearance.

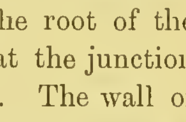

Fig. 68.—Drop of chyle. On the left, corpuscles lying amongst molecular matter; on the right, corpuscles altered by the addition of acetic acid.

When chyle is removed from the *receptaculum chyli*, or from the thoracic duct, it forms a coagulum of feeble consistence, surrounded by a milky serum. When taken from the thoracic duct, shortly before it joins the venous system the chyle has a slightly pink appearance, due probably to admixture with red blood corpuscles, and the clot is firmer.

The following analyses show the percentage composition of chyle taken from different animals :—

	Man.	Dog.	Horse.	Ass.
Water,	90·5	91·2	92·8	90·2
Solids,	9·5	8·8	7·2	9·8
Fibrin,	0·1	0·1	0·1	0·4
Albuminous Matters,	7·0	2·7	4·0	3·5
Fat,	1·0	4·9	1·5	3·6
Extractive Matters,	1·4	0·3	0·8	1·6
Salts,		0·8	0·8	0·7

Chyle contains from 7 to 10 per cent. of solids, that is about 3·5 per cent. more than lymph, owing to the amount of fat found in it. Hoppe-Seyler has found 6·5 per cent. of fat in the chyle of a dog, and Zawilski as much as 8 per cent. ; the chyle of horses and of oxen contains only from ·5 to 1·5 per cent (Munk).

The quantity of chyle formed daily cannot be estimated with accuracy. The amount of milky chyle depends on the amount of fat taken in the food. Even when no fat is absorbed, water, salts, sugar, and soluble proteids are absorbed into the lymphatic spaces in the villi, and they thus reach the lacteals; but it is likely that these soluble matters quickly diffuse out of lymphatic spaces and lacteals into the blood-vessels lying in close connection with them, and that it is only when a considerable amount of fat is absorbed that they (water, salts, etc.) mix with the true chyle.

Along with chyle, the lymphatics of the mesentery and of the walls of the intestinal canal, carry away the true intestinal lymph, which, like lymph in other tissues, is the surplus of fluid that has transuded from the capillary blood-vessels, less the matters selected from this fluid for the nourishment of the tissues.

CHAP. IV.—ABSORPTION BY OTHER ORGANS.

(*a*) *Absorption by the Skin.*—The skin may absorb in certain conditions matter either in the form of a gas, a liquid, or a semi-solid substance. The absorption of gases and of volatile matters by the skin has been long known. Thus, an animal may be poisoned by plunging its body in an atmosphere of sulphuretted hydrogen, after every precaution has been taken to prevent the entrance of the gas into the respiratory passages. Much controversy has taken place as to the possibility of absorption of liquids by the skin. The layer of sebaceous or oily matter which covers its surface, and the thick stratum of more or less modified epithelial cells forming the epidermis, appear almost to render absorption impossible. The pressure in the interior of the ducts of the glands of the skin acting outwards also tends to prevent the entrance of fluids. On the other hand, experiment has shown that a small quantity of water and soluble substances may pass into the blood through the skin during immersion in baths, and that even oily matters may be absorbed with the aid of friction. It is well known, also, that the repeated external application of mercurial ointment to the skin may be followed by the physiological effects of that substance. In these cases, absorption occurs by the matters penetrating the ducts of the sebaceous and sudoriparous glands, and coming into contact with the capillary vessels surrounding these ducts. Diffusion will then take place. It is not easy to settle the question whether or not absorption of saline matters occurs when the body is immersed in a bath of water holding these in solution. In the first place, absorption may occur by any mucous surfaces thus bathed, such as urethra, rectum, etc. Even supposing precautions have been adopted to eliminate this source of error, it is still possible that the saline matter may be breathed as vapour. Thus, after a bath containing iodide of potassium in solution, the salt may be discovered in the urine, but if a layer of oil be poured over the surface of the water, no iodide of potassium will be found in the urine. On the other hand, alcohol, ether, oil of turpentine, etc., may be introduced into the blood by cutaneous absorption. Finally, if the epidermis is abraded or denuded, so as to expose the capillaries of the *cutis vera*, absorption of poisons readily occurs, as may happen in the *post-mortem* room.

(*b*) *Pulmonary Absorption.* — Gases and volatile substances are rapidly absorbed through the lining membrane of the air cells of the lungs. Although fluids and soluble substances are absorbed more slowly, it is remarkable that a large portion may quickly be taken up. Thus, the entrance of water into the air-passages of an animal, up to a certain limit, is not followed by asphyxia. It is difficult to account for the presence of particles of carbon or of silica in the bronchial glands, and tissues of the lungs, of persons employed in certain occupations, unless we suppose that these may be taken up by the epithelial cells lining the air cavities.

(*c*) *Absorption by Serous Membranes.*—In the course of inflammatory affections, serous fluids frequently accumulate in the shut sacs of the body such as the pleura or the peritoneum, and these fluids may, after a time, become absorbed. Histological research carried on by numerous observers, and in particular by Von Recklinghausen and Klein, has shown that in serous membranes, lined by a single layer of endothelial cells, numerous openings, termed *stomata*, occur, which communicate with the lymphatic system. Von Recklinghausen showed that if we inject the abdominal cavity of a rabbit with a coloured fluid, the injection passes underneath the pleural covering of the diaphragm, that is to say, it finds its way into the lymphatics of the diaphragm through stomata on the peritoneal surface. This fact may be demonstrated by another experiment. The central tendon of the diaphragm of a rabbit is cut out and pinned over a cork ring, so that the peritoneal surface is uppermost. If a drop of milk is now placed on the upper surface, and viewed under the microscope, the milk globules may be seen rushing round in certain places as if in a whirlpool and disappearing in the centre of the vortex. These vortices indicate the position of the stomata. The cells forming the margin of a stoma can alter their form so as to close or open the aperture. These openings no doubt facilitate the distribution of fluid between the peritoneal cavity and the lymphatics of the diaphragm. When the pressure in the abdominal cavity is greater than that in the thoracic cavity, fluid will pass upwards. Thus each inspiration by increasing pressure in the abdominal cavity and diminishing it in the thoracic cavity will tend to suck up fluid from the abdominal cavity. Stomata also are found on the pleural surface of the diaphragm. The great serous sacs are in a sense part of the lymphatic system.

The fluid found in the serous cavities resembles lymph. It has an alkaline reaction. It contains from 4 to 6·5 per cent. of solid matter when collected from any of the large cavities. The fluid in the ventricles of the brain, central canal of the cord, and arachnoid and sub-arachnoid cavities (usually termed *cerebro-spinal fluid*) contains only 1 per cent. of solid matter.

(*d*) *Absorption in Connective Tissue.*—When a soluble substance is introduced into the cellular tissue underneath the skin, it is rapidly absorbed, a fact which has been taken advantage of in the method of the subcutaneous injection of remedies.

Chap. V.—THE LYMPHATICS.

As has been already pointed out, the tissues are nourished by fluid matter which exudes through the walls of the capillaries. A portion of this fluid matter is taken up by, and incorporated with, the living protoplasm of the tissues; and the remainder, which may be regarded as being in excess, is removed. It is also to be remembered that one of the conditions of the activity of living tissue is chemical decomposition of the protoplasm of the tissue; the living matter dies, undergoes molecular changes, and the waste products thus formed pass again into the fluid state, so that they may be removed.

In recent times, the researches of histologists have thrown light on the origin of the lymphatics in the tissues. It has been shown that lymphatics abound in all the tissues and organs which receive blood, except the corneous tissues and cartilages, and in many cases a lymphatic vessel may completely or partially surround an artery or a vein. This arrangement is found in the central nervous system, in the salivary glands, and in the testicle. Such lymphatic spaces surrounding vessels are called *perivascular canals.* Lymphatics originate in *lacunæ,* or spaces between the fibres of the connective tissues, and these are lined by flattened endothelial cells. These spaces are drained by lymphatic vessels, the arrangement presenting an analogy to the vascular system of insects and crustacea. Masses of protoplasm—the connective tissue corpuscles—abound in many tissues, occupying some of the interstitial spaces. The spaces communicate freely with each other, the passages joining them being tubular in form, constituting small pores or canals. These lymphatic spaces and channels may be injected with a coloured fluid forced into the tissue by a hypodermic syringe. Such an experiment may be performed by passing the needle-like nozzle of the syringe into the fascia covering muscle or into the testicle of a recently-killed animal. Thus there appears to be, more or less, throughout every tissue, what may be termed a drainage system for the purpose of carrying off waste products and excess of pabulum. The fluid thus drained off is the *lymph.* But the lymph does not pass directly into the blood. It is conveyed in the first instance to *lymphatic glands,* small bodies placed in the course of the lymphatics, as shown in Fig. 70.

FIG. 69.—*a, b, c, d,* Various forms of connective tissue corpuscles.

We shall now consider more in detail the histological structure of the lymphatics and the lymphatic glands, and thus clear the way for the discussion of the nature, mode of origin, and destination of lymph.

1. **The Lymphatics.**—These were first discovered by Caspar Aselli in 1622. The wall of the lymphatic vessels, from ·2 to ·8 mm. in thickness, consists of three layers. The inner layer, or *intima,*

consists of endothelial cells and delicate networks of elastic fibres running longitudinally. The middle layer, or *media*, is composed of smooth muscular fibres passing transversely, along with a few elastic fibres. The external layer, or *adventitia*, is formed of connective tissue bundles, mostly running longitudinally, and interspersed with elastic fibres and a few involuntary or smooth muscular fibres. The larger lymphatics are provided with small semilunar valves, opening towards the heart, and immediately above the valve we find a dilatation. Hence injected lymphatics show a varicose appearance, owing to the little swellings being close together. The smaller lymphatics, and especially the lymph capillaries, are composed entirely of fine endothelial cells. The lymph capillaries form networks, and they show dilatations, more especially at the points of division. Some have held that the lymph capillaries are closed on all sides, but the more generally accepted view is, that they originate in fissure-like spaces, and that they are open towards the periphery. Between the tissue elements we may find, not only fissures containing fluid, but delicate and extremely minute canals of irregular form, freely uniting together. If we suppose the lymph capillaries to be complete tubes, according to the first theory, it is evident that the fluid which has oozed out of the blood capillaries into the tissues, in so far as it is not used up by these tissues, must penetrate by osmosis into the lymph capillaries; but, according to the second view, such a fluid would be drained out of the tissues by the open lymph capillaries which freely communicate with the spaces and canals among the tissue elements.

FIG. 70.—Superficial and deep set of lymphatics and of lymphatic glands in the right axilla. Quarter natural size. 1. Deep lymphatics of the upper arm; 2. axillary vein; 3. section of the tendon of the pectoralis minor muscle inserted into the coracoid process; 4. subclavian muscle; II. and III. second and third ribs; 5. lymphatic network in the skin round the nipple of the breast, showing its communications with the lymphatics in the axilla. The nodules represent the lymphatic glands. (Krause).

2. **The Lymphatic Glands, or Lymphatic Bodies.**—These are small, round, or oval bodies, often resembling a bean in shape, placed in the path of the lymphatics. They vary much in size. Usually on one side we find a depression, termed the *hilum*, from which the lymphatic vessels issue, but these vessels may enter at any part of the lymphatic gland. The gland is covered by a sheath of connective tissue, from which partitions or *trabeculæ* pass inwards, so as to divide the cortical part of the gland into a number of compartments. Both the sheath and the partitions frequently contain involuntary muscular fibre. The following is a simple conception of the structure of a gland. At certain places from two to six lymphatic vessels break up into smaller ones, these anastomose so as to form a dense plexus or reticulum, and from this plexus lymphatics emerge and unite to form the same number of large lymphatics, as at first. The vessels that thus subdivide are called *vasa afferentia*, and those formed by the anastomoses of smaller ones *vasa efferentia*. In the meshes thus formed we find small spherical or oval masses of adenoid tissue. The spherical or oval masses are found around the periphery of the gland and elongated rounded bands or strands of the same kind of tissue exist in the centre; these masses are supported by the trabeculæ of connective tissue penetrating from the external capsule. The trabeculæ do not touch the masses of adenoid tissue, but they are separated from them by lymph sinuses or spaces, traversed by fine bands of connective tissue. From the trabeculæ delicate processes of connective tissue pass into the interior of the lymphatic vessels or channels, and also into the interior of the cortical and medullary masses

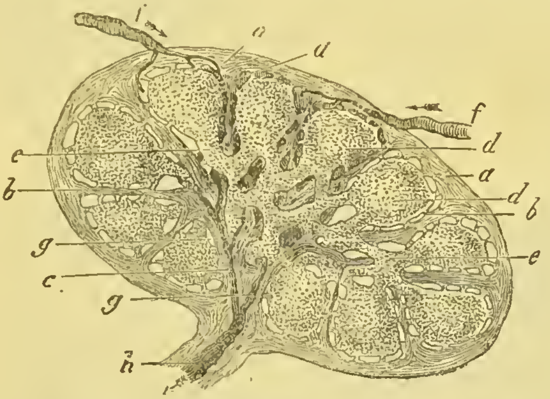

FIG. 71.—Section of a lymphatic gland; *a*, *a*, strong fibrous capsule sending partitions into the gland; *b*, partitions between the follicles or pouches of the *cortical* or outer portion; *c*, partitions of the *medullary* or central portion; *d*, *e*, masses of protoplasmic matter in the pouches of the gland; *f*, *f*, lymph vessels which bring lymph *to* the gland; *g*, confluence of those leading to the efferent vessel, *h*, which carries the lymph away *from* the gland.

of adenoid tissue, affording a support for the numerous leucocytes found in all these localities. Thus the gland consists of a *cortical substance* and of a *medullary substance.* The cortical contains the round masses of adenoid tissue (sometimes called *secondary nodules*), these are continuous with the oval masses found in the medullary portion, and both the round masses and the oval masses are surrounded by the lymph channels, termed *lymph sinuses.* These latter are pervaded by reticular connective tissue springing from the trabeculæ. The nodules, both round and oval, are composed of adenoid tissue (see Vol. I. p. 327) in the meshes of which we find numerous leucocytes. In many of the masses of

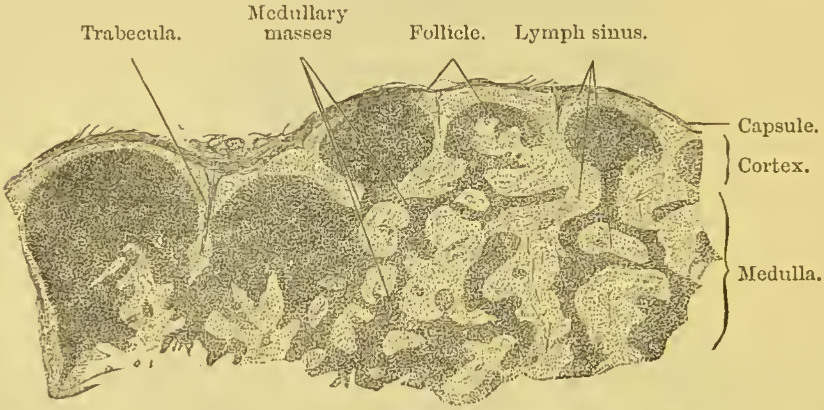

FIG. 72.—Vertical section through the lymphatic gland of a kitten nine days old. × 30 d. (Method, No. 41, Appendix.)

adenoid tissue we find in the centre a darker portion, crowded with cells showing karyokinetic division. This is termed a *germ centre.* In the bands of adenoid tissue found in the medullary part cell division also goes on, but not to so great an extent as in the round masses of the cortex. The germ centres in particular are the seat of the formation of leucocytes. These pass into the lymph sinuses and thence into the *vasa efferentia.* The lymph sinuses are lined by a single layer of flat endothelial cells, a similar layer covers the surface of the round masses in the cortex, the strands in the medulla, and the surface of the trabeculæ, and flat endothelial cells are even found in the bands of reticular connective tissue passing from the trabeculæ. The structure of a lymphatic gland is complicated because (1) the round masses in the cortex often coalesce; (2) the strands in the medulla may combine to form a coarse network; (3) the trabeculæ may also form a network; (4) the strands in the medulla and the trabeculæ may coalesce; and (5) the lymph sinuses are often so crowded with leucocytes as to obscure the details of structure. This appearance has given rise to the terms pulp or parenchyma being applied to the soft substance in a lymphatic gland.

The lymphatic glands are richly supplied with blood-vessels, either entering the hilum or distributed over the surface. Those on the surface ramify on the capsule, and penetrate the gland by running along the centres of the trabeculæ. The large vessel entering the hilum divides into branches, surrounded by connective tissue, and these also run along the trabeculæ. From these, minute branches spring which run through the lymph sinuses, and are ultimately distributed to the round masses in the cortex and to the strands in the medulla, ending in a very fine meshed capillary network. The veins pass out of the gland at the hilum. Nerves also penetrate lymphatic glands, and medullated and non-medullated fibres have been traced, but their mode of ending is unknown.

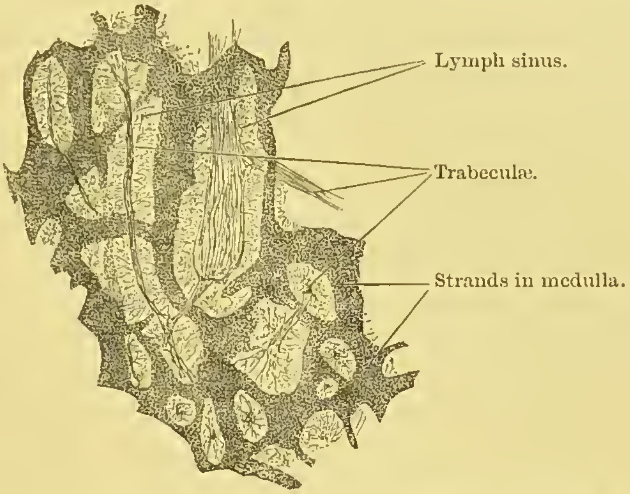

FIG. 73.—From a vertical section of a lymphatic gland of an ox. × 50 d. In the upper half, the trabeculæ and strands are cut lengthways, and in the lower half they are cut transversely. Observe in the lymph sinus the delicate fibres of the reticular connective tissue. Leucocytes exist in the meshes. (Method No. 42, Appendix.)

It is important to observe that adenoid tissue containing leucocytes is not limited to lymphatic glands, but is found in many mucous membranes, sometimes diffused in a stratum and sometimes in sharply defined masses. We also find small nodules or follicles in mucous membranes, containing germ centres, and resembling the round masses in the cortex of a lymphatic gland. Such structures are seen in the solitary and the agminated glands of Peyer in the intestinal canal (see p. 78). These vary much in number in different species of animals, and even in individuals of the same species, and they differ from ordinary lymphatic glands chiefly in the less intimate connection that exists between them and lymphatic vessels. The leucocytes originating in them probably do not enter the lymphatic system directly, but wander through the epithelial covering to the surface of the mucous membrane. Amphibia have no lymphatic glands, but, as may be seen in the frog, there are large lymphatic spaces below the skin, between it and the underlying muscles. These spaces are traversed by very delicate bands of connective tissue.

3. The Formation of Lymph.—The blood is brought to the tissues by the arterioles which divide into capillaries, and these anasto-

mose to form a network. The walls of the capillaries are extremely thin, and they are porous in a physical sense, so that, as the blood flowing in them is under a considerable pressure (probably about half that existing in the aorta), a plasma transudes through their walls and bathes the surrounding tissues. As this is essentially filtration under pressure, the plasma will be as rich in saline matters and water as blood plasma, but considerably poorer in albumin. This parenchymatous fluid contains nutritious matters for the upbuilding of the tissue elements, and it also contains oxygen set free from the hæmoglobin of the red blood corpuscles. It is thus both a nutritive and a respiratory fluid. The blood on the one hand loses water, salts, and albumin, and on the other the tissues are bathed by a fluid containing these substances. Each living tissue element appropriates the substances it needs, but there is always an excess of the transudative fluid. This excess is drained out of the tissues, and as it still contains nutritive matter, useful in the economy of the body, it is not thrown away as useless, but is collected by the lymphatic vessels and carried back to the blood.

Sometimes a larger quantity of fluid transudes into the tissues than can be used up by these or carried off by the lymphatics, and it then collects in the tissues, causing puffy swelling or *œdema*, or it may accumulate in the peritoneal or pleural cavities, or in one or other of the serous sacs. The same effect is produced when an obstruction is presented to the free flow of lymph, as is seen in venous congestion. Again, paralysed limbs may become swollen from the accumulation of lymph, because there are no active muscular movements to drive it onwards.

The lymphatics of the lower extremities, the pelvic organs, and the abdominal organs, join the thoracic duct, which also receives the lymph of the left side of the thorax and left lung, the left upper extremity, and the left side of the head and neck, so that most of the lymph is poured into the venous system, along with the chyle, at the junction of the left subclavian vein with the left internal jugular. The remaining portion of the lymph, collected from the right side of the thorax and right lung, the right upper extremity, and the right side of the head and neck, is collected by the right lymphatic duct, which opens into the venous system at the junction of the right subclavian vein with the right internal jugular vein.

We have now to endeavour to picture what happens in a lymphatic gland. The lymph is poured into the lymph sinuses of the gland by the *vasa afferentia*, and it may then percolate through the substance of the gland and issue from it by the *vasa efferentia ;* or if we suppose that the muscular fibres in the capsule and in the trabeculæ come into action, the lymph will be pressed through the delicate reticulations of adenoid tissue crowded with lymph corpuscles, and it no doubt washes these out of the gland, as we find that the lymph stream issuing from a gland is always rich in these corpuscles. The structure of the gland shows that the flow of lymph through it must be very slow, and the gland has been compared to a fine filter which will catch particles suspended in the lymph. Thus, when the skin of the arm is tattooed with cinnabar many particles of the pigment may be found in the adenoid tissue of the axillary glands long after the operation. In like manner, animal poisons, more especially those associated with the presence of organisms, are caught in the substance of the lymphatic glands, causing these to swell, as shown in the formation of a bubo, after specific infection of the genital organs, or the swelling of the glands of the axilla following a *post-mortem* or dissection wound. The number of corpuscles is much greater in the lymph after it has passed through a gland, and we find that lymph collected from regions where there are few glands, as the lower extremities, is always poorer in albumin and richer in water than the lymph of the great lymphatic channels in the trunk. The amount of fibrin is also increased by passage through a gland, so that the tendency to coagulation is more marked, a fact to be accounted for by the observations of Schmidt and others, showing that fibrinoplastic substance, and the fibrin ferment (both factors in the formation of fibrin), exist in the lymph corpuscles and in the white blood corpuscles.

Physical and Chemical Characters of Lymph.—As already indicated, the chemical composition of lymph resembles that of the blood plasma, except that it is poorer in albumin. When obtained pure from the thoracic duct of a fasting animal, it is a colourless, faint yellow, or faint pink, or slightly opalescent fluid, alkaline, and having a specific gravity of 1017 to 1025. It contains numerous lymph corpuscles, and sometimes a few coloured blood corpuscles. The *lymph-corpuscles* are smaller than colourless blood corpuscles; they are globular in form, and consist of a large nucleus (often containing nucleoli) surrounded by a narrow border of finely granular protoplasm. Unlike the chyle, only a small quantity of molecular matter is found in it. It sometimes forms a soft coagulum, separating ultimately into a clot and a fluid. The clot is readily formed if a little defibrinated blood is added, as fibrinoplastic substance is thus supplied. Lymph contains only about ·1 per cent of fibrin. As the lymph is not only the excess of transudate from the vessels, but also contains various substances in solution derived from the katabolic changes occurring in the tissues, we would expect to find its composition vary when collected from different parts of the body, and to discover in it traces of many chemical substances. We therefore may find in the fluid a varying percentage of albuminous matters (serum albumin and globulin, or fibrinogen), a small quantity of leucin, urea, etc., fats, fatty acids, lecithin, volatile fatty acids (especially butyric acid), cholesterin, sugar, urea, and various salts, such as the phosphates of potash and soda, chloride of sodium (about ·8 of the total salts), sulphates, and traces of iron. Lymph contains only a trace of oxygen, but as much as 50 per cent. by volume of carbonic acid. In chemical composition, it shows a close approximation to chyle, except that in the latter albumin and fats are in greater quantity, as may be seen by the following table showing the percentage composition of lymph and chyle (see also p. 144) :—

100 parts contain	Lymph of Man.	Lymph of Horse.	Lymph of Donkey.	Lymph of Cow.	Chyle of Man.
Water,	95·0	95·8	96·5	96·4	90·5
Solids,	5·0	4·2	3·5	3·6	9·5
Fibrin,	0·1	0·1	0·1	0·1	0·1
Albumin,	4·1	2·9	2·7	2·8	7·0
Fat,	Trace	Trace	Trace	Trace	1·0
Extractive Matter,	0·3	0·1	0·1	0·1	1·4
Salts,	0·5	1·1	0·6	0·6	

Quantity of Lymph.—It has been estimated that an amount of lymph is formed in twenty-four hours equal to from ·10 to ·14 of the weight of the body. Colin obtained from a horse from 8 to 21 kilogs. in twelve hours; from oxen in twenty-four hours, 21 to 95 kilogs.; from sheep, 3 to 4·5 kilogs.; from dogs, ·5 to 2·5 kilogs. In all cases the animals had not received food for several hours before death. It was ascertained that animals soon die after the loss of a considerable quantity of lymph.

Movements of the Chyle and Lymph.—Both the chyle and lymph move from the radicles of the vessels towards their trunks. This is proved by the fact that if a poisonous substance in solution is injected into the cellular tissue below the skin, its physiological effects are soon apparent, that is to say, it must have passed into the lymphatic spaces in the tissues and been drained from these into the blood-vessels. If lymphatic vessels are cut, a slow continuous flow of lymph is observed. The movement is slow, as compared with that of the blood—4 mm. per second in a lymphatic vessel in the neck (Weiss). Numerous researches indicate that the efficient cause of this movement in the higher animals is the pressure of the blood in the arteries. The existence of a *vis a* *tergo* was first demonstrated by Ludwig. He connected a manometer containing a strong solution of sodium carbonate (specific gravity, 1008) with a canula introduced into a large lymphatic in the neck of a dog. He found that the pressure varied considerably, that some of the variations were synchronous with the respiratory movements, and that muscular action, as when the animal struggled, caused a rise of pressure. The pressure was equal to that of a column of carbonate of soda solution of from 8 to 10 mm. in height. By a similar method, Weiss found the pressure in the lymphatic of a horse to be from 10 to 20 mm. Thus, increase of pressure is followed by an increased discharge from severed lymphatics, and, no doubt, this pressure operates at the radicles of the vessels. As fluids always flow from positions of high pressure to positions of low pressure, it follows that the pressure at the radicles of the lymphatic vessels must be greater than the pressure in the lymphatic trunks, and the pressure must be smallest where the lymphatic trunks join the venous system. The pressure at the radicles of the lymphatics must be derived from the pressure of the blood in the smallest blood-vessels. Assuming that the pressure in the capillaries is about one half of that in the aorta, it is evident that this pressure, as already pointed out, causes the transudation of fluid into the lymphatic spaces in the tissues, and although a part of this pressure is used up in overcoming capillary resistance, a sufficient amount remains to drive the lymph into the lymphatic vessels, and to force it onwards through these and through the lymphatic glands. Ludwig has shown that increase of blood pressure increases, while a fall of blood pressure diminishes, the flow of lymph, as one would expect from the considerations just presented. Thus, by compressing the vein of such an organ as the testicle, the blood pressure rises and the flow of lymph increases. But there are other accessory agents in forcing the lymph onwards. Thus we have the presence of valves opening towards the heart so that compression, by muscular action, must force the lymph and chyle onwards. When the muscles of a limb contract, the lymphatics are subjected to pressure, and as the valves prevent the lymph from flowing backwards it must flow onwards. In this way all rhythmic movements of limbs, as in running, drive the lymph onwards. Ludwig and Schweigger-Seidel have shown a remarkable mechanism affecting the circulation of the lymph in tendons, fasciæ, and in the diaphragm. These organs have two lymphatic plexuses, one deep seated and the other superficial. The lymphatics belonging to the latter open into lymphatic vessels furnished with valves. Each movement dilates the deep lying vessels, so that they suck up lymph while, at the same time, the superficial vessels are compressed, and their contents are forced into the neighbouring vessels supplied with valves. The movements of the diaphragm in this way remove any superfluous lymph that might accumulate in the pleural and peritoneal cavities. The movements of respiration affect the rate of flow of lymph—inspiration accelerating the movement in the thoracic duct, whilst expiration diminishes it. During inspiration the capacity of the chest is increased, and its contents are subjected to a negative pressure, that is, to a pressure less than atmospheric pressure. The peripheral lymphatics, however, are subjected to full atmospheric pressure, and thus the lymph is driven towards the direction of the negative pressure, or, in other words, it is sucked from the peripheral vessels into the lymphatics in the thorax. The subclavian veins also, being near the heart, are mostly in the condition of only a very low or even a negative pressure, and this is increased by each inspiratory movement, and thus the lymph (or chyle) is sucked into the veins.

Rhythmical contractions of the lymphatics of the mesentery have been observed, and it is well known that special contractile sacs, sometimes called *lymph-hearts*, are met with in many animals, such as the frog.

These were first discovered in amphibians by J. Müller in 1832. A lymph-heart is a small dilatation having striated muscles in its walls. Amphibians possess four such dilatations, two anterior and two posterior. In the frog it is easy to find a lymph-heart on each side of the coccyx, between the ilio-coccygeal muscle and the muscles running from the pelvis to the back of the leg, namely, the *glutæi* and *pyramidales* muscles. The two anterior hearts lie above the transverse processes of the third dorsal vertebra. These cavities pulsate about once in the second. The lymph-hearts may be one inch in length in the turtle, and they pulsate in this animal only once in eighteen seconds. They may be paralysed with woorara, when they cease pulsating, and the lymph then collects in the great lymph spaces below the skin. Their pulsations are in no way related in time to that of the true blood heart.

SECTION III.

THE BLOOD.

CHAP. I.—THE BLOOD GLANDS.

As has been already explained, the blood receives fresh supplies of material from the alimentary canal and from the lymphatic system. From the first, it receives matters either directly by the blood-vessels (which carry these in the first instance to the liver through the portal circulation), or indirectly by the chyle, and from the second it receives lymph. Oxygen is introduced by the process of respiration. Finally, the blood receives morphological elements from certain organs found in various parts of the body and usually, although somewhat erroneously, termed blood glands. The following organs are grouped under this designation:—(1) *lymphatic glands*; (2) *the solitary and the agminated glands of Peyer*; (3) *the thymus gland*; (4) *the spleen*; (5) *the thyroid body*; (6) *the supra-renal capsules.* It is very doubtful if the last two are true blood glands, and it has been satisfactorily shown that the pituitary gland and the pineal gland do not belong to this category. On the other hand, *adenoid tissue*, wherever found (as in the tonsils) and below the alimentary mucous membrane in many parts, and the *marrow of bone* must be considered as blood-forming tissues. The structure of the lymphatic glands and of Peyer's glands has already been considered p. 149 and p. 78, and we shall now give a brief account of the structure of the remaining organs.

1. **The Thymus Gland.**—This organ attains its greatest size at the end of the second year of life. It is then an elongated body situated in front of the trachea in the neck as high as the lower border of the thyroid (covered by the sterno-hyoid and sterno-thyroid muscles), and in the superior mediastinal space, in front of the great vessels and pericardium, and behind the sternum as far down as the fourth rib-cartilage. It consists of from four to eleven large lobules in each lateral half of the gland. These have a sheath of connective tissue containing elastic fibres. From the sheath covering each lobule, partitions run into its substance dividing it into numerous small secondary lobules, each about one millimetre in breadth. Each minute

lobule consists of adenoid tissue, more dense towards the circumference than in the centre, as shown in Fig. 74. The gland is richly supplied with blood, and its substance contains a dense network of capillaries. Lymphatics are also numerous, the larger ones entering by the cortex, sub-dividing and running into the medullary portion. In the retiform tissue there are numerous lymph cells. When the thymus has undergone a considerable amount of atrophy, we find in it numerous small concentrically striated corpuscles, from 15 to 180 μ in diameter. These are known as the *corpuscles of Hassall.* Each consists of an envelope of epithelial cells enclosing two or more giant cells. Some have supposed these to be masses of modified epithelium, and others that they are portions of atrophied blood-vessels. Watney has pointed out that they are probably structures of physiological importance, inasmuch as they are most abundant when the gland is in a state of great functional activity. In the thymus of the dog, Watney has found cysts lined with ciliated epithelium. As the gland atrophies, its connective tissue increases, encroaches on the lobules, and these undergo a kind of fatty degeneration. Nerve fibres derived from the vagi and sympathetic nerves reach the thymus, but their mode of termination is unknown.

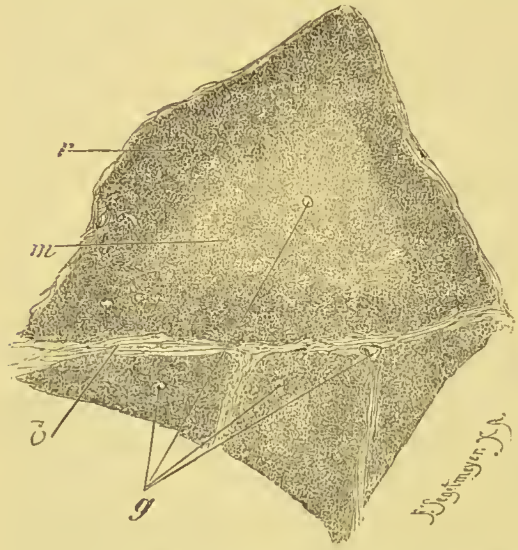

FIG. 74.—Section of thymus of a rabbit 7 days old, showing a small lobule. × 50 d. *r*, cortical portion; *m*, medullary portion. Portions of other three lobules have been cut tangentially, thus showing only the cortical part in each. *b*, connective tissue; *g*, blood vessels. (Method No. 43, Appendix.)

2. **The Spleen.**—This organ is placed in the back of the left hypochondrium, between the cardiac end of the stomach and the diaphragm. The largest of the blood glands, the spleen, measures about 125 mm. in length, 100 to 120 mm. in breadth, and 25 to 48 mm. in thickness. It is covered by a strong capsule of connective tissue, on the surface of which is a layer of peritoneum. Elastic fibres in the form of networks are intermingled with the connective tissue fibres, and involuntary (smooth) muscular fibres are found in the capsule of the spleen of the cat, dog, pig, etc., but not in that of man. From the capsule, broad septa or rounded cords, termed *trabeculæ,* pass into the substance of the organ and from these more slender bars or fibres, forming a network, in the meshes of which we find the spleen pulp.

These trabeculæ also contain plain muscular fibres. At the hilum of the spleen, directed towards the cardiac end of the stomach, the capsule furnishes sheaths for the large blood-vessels and lymphatics. These connective tissue sheaths enter the spleen with the vessels, and they are infiltrated with leucocytes. The latter may either form a continuous layer along the border of the artery, as is seen in the spleen of the guinea pig, or they may be limited to certain spots. In the latter case, the masses of leucocytes form spherical bodies, varying in diameter from ·2 to ·7 mm., called the *corpuscles of Malpighi.* These are well seen in the spleen of man, the cat, the ox, etc. The corpuscles are found attached to the small arteries, so that the artery either passes through the middle of the corpuscle or through one side of it. This arrangement is shown diagrammatically in Fig. 76. The Malpighian corpuscles exactly resemble in structure the small round bodies in the cortical part of a lymphatic gland, and they sometimes contain germ centres. The *pulp of the spleen* consists of a network of fine fibres (adenoid tissue) having in its meshes numerous lymph corpuscles,

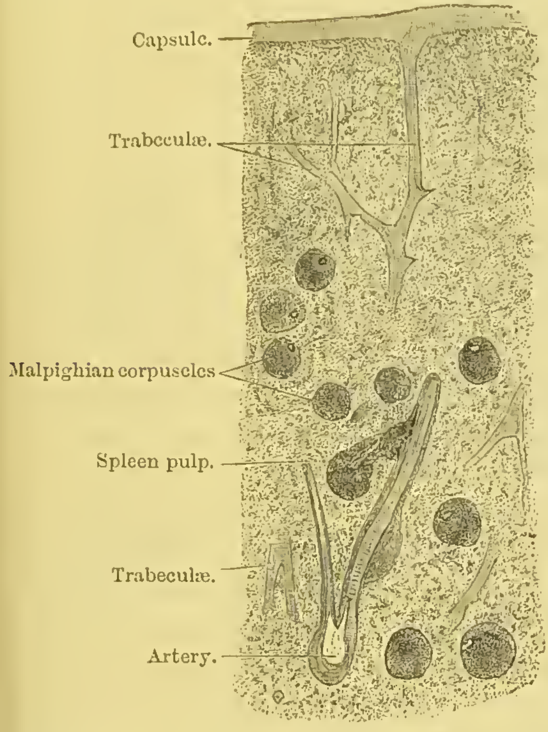

Fig. 75.—Transverse section of human spleen. × 10 d. The Malpighian corpuscles are well shown, each having an artery passing through it at one side. Along the right branch of the artery, there is a continuous layer of leucocytes. (Method No. 44, Appendix.)

Fig. 76.—Portion of splenic artery, *a*, *b*, *b*, having Malpighian bodies; *c*, *c*, *c*, attached to branches.

Fig. 77.—Elements of the human spleen. ×560d. 1. Colourless cells (leucocytes); 2. endothelial cells; 3. coloured blood corpuscles; 4. cells containing granules—the upper one enclosing a coloured blood corpuscle, *b*. (Method, No. 45, Appendix.)

and other cellular elements. We find not only leucocytes and ordinary lymph corpuscles (characterized by a large nucleus, surrounded by a small amount of protoplasm), but also corpuscles containing bodies like red blood corpuscles, and, finally, free red blood corpuscles, Fig. 77. The arteries of the spleen divide into branches, which ramify on the trabeculæ and the bands of adenoid tissue in the pulp, and send still more minute branches to the Malphighian corpuscles. The veins collect the blood from a number of very wide capillaries, sometimes termed capillary veins, which are situated between the trabeculæ and the bands of adenoid tissue in the pulp. The larger veins run close to the arteries. The exact relation of the arteries to the veins has not been satisfactorily determined, but it is known that the arteries end in long wide capillaries, which do not anastomose in the usual way to form a network. From these arterial capillaries the venous capillaries above alluded to originate. According to this view, the blood of the spleen is contained in vessels throughout, but other observers hold that the arterial capillaries carry the blood into spaces, termed the *intermediary lacunæ*, having no proper wall, and with which the veins communicate by sieve-like apertures. This will account for the well-known difficulty in injecting the spleen, the injection being usually found in masses apparently outside the vessels. In the lower animals, lymphatics are abundant on the upper surface of the spleen, but in man this superficial plexus is feebly developed. The deep-seated lymphatics are comparatively scanty, and their relation to the other histological elements of the spleen has not been elucidated. Nerve fibres have been traced into the spleen. They are probably distributed to the blood-vessels.

FIG. 78.—Reticular or adenoid, tissue of human spleen. ×560d. On the left, the cellular elements have been brushed away. (Method, No. 46, Appendix.)

FIG. 79.—Three kinds of nuclear division seen in a portion of the spleen of a dog. ×560d. The chromatic filaments cannot be seen with this magnifying power. (Method, No. 47, Appendix.)

3. **The Thyroid Body.**—This organ, which is commonly classed among the blood glands, forms a rounded projection upon the trachea and larynx. It consists of two lobes united by an isthmus, and each lobe stretches from the inferior cornu of the thyroid cartilage, which it covers, to the fifth or sixth ring of the trachea. The isthmus is usually stretched across the second, third, and fourth rings of the trachea. Each lateral lobe is about 50 mm. in length, 30 mm. in breadth, and

18 mm. in thickness, and the isthmus is nearly 12 mm. in breadth and 10 mm. in depth. At an early period in embryonic life, the thyroid body has a duct, the *ductus thyroglossus*, which opens into the *foramen caecum* of the tongue. The duct is soon obliterated. Each lobe of the thyroid body shows completely closed pouches or acini, bound together by connective tissue. These shut sacs vary in diameter from 40 to 120 μ. They are lined by a single layer of cubical epithelium cells resting on a *membrana propria*, and they are filled either with a fluid or with a peculiar yellow glairy matter, termed the *colloid substance.* We may also find leucocytes or lymph-like corpuscles and red blood corpuscles, partially disintegrated and decolorized. The colloid matter sometimes exists in large amount, distending the shut sacs, and causing the enlargement of the gland known as *goître* (Fig. 81).

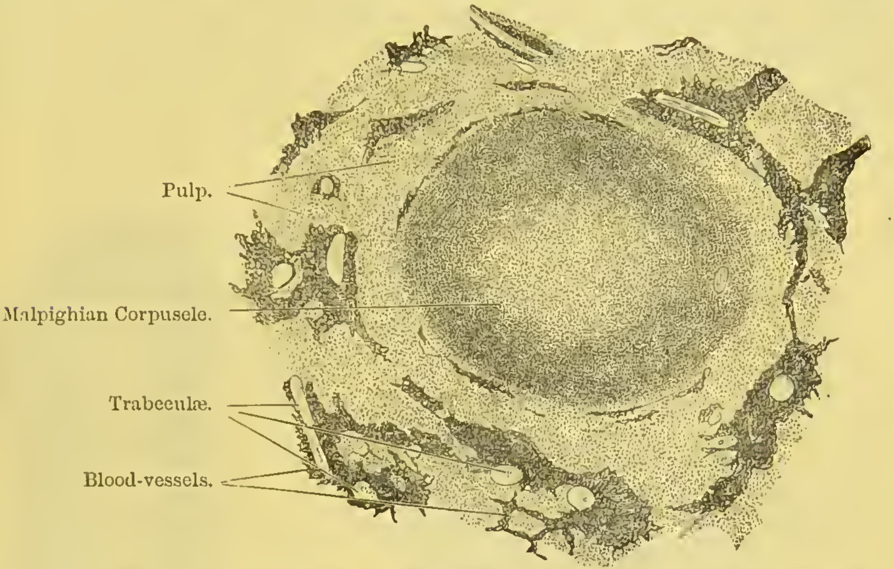

FIG. 80.—From a transverse section of the spleen of a cat. × 50 d. The transverse section of the artery related to the Malpighian corpuscle is seen on the right. The dark vessels are chiefly capillary veins lying between the bands of adenoid tissue in the pulp and the trabeculæ. (Method No. 48, Appendix.)

The numerous blood-vessels, derived from the inferior and superior thyroids on each side, are remarkable for their large size. They end in a dense capillary plexus surrounding the acini. The veins, also large, form plexuses on the surface, whence originate the superior, middle, and inferior thyroid veins, which carry the blood to the internal jugular and innominate veins. The lymphatics are numerous, commencing in a network between the acini. Nerves pass to the thyroid body from the middle and inferior cervical ganglia of the sympathetic and they probably are distributed to vessels, but their mode of termination is unknown.

4. **The Supra-renal Bodies** are situated immediately above the kidneys, one over each kidney. Each measures about 30 mm. in length, 30 mm. in breadth, and 6 mm. in thickness. A supra-renal body

possesses a capsule of connective tissue, which sends processes into the interior of the organ, dividing its parenchyma into distinct portions. The parenchyma shows a cortical and a medullary portion. The cortical portion shows cells of a roundish form and composed of a coarsely granular protoplasm, in which is embedded a clear nucleus, and often refractive fatty globules. In the outermost zone of the cortical substance (Fig. 83, 1) these cells are arranged in rounded masses, in the middle zone, 2, they exist in cylindrical columns, and in the innermost zone, 3, they are irregularly distributed in a network of connective tissue fibres. The cells of the inner zone are often pigmented. The cortex may thus be divided into (1) *zona glomerulosa*, (2) *zona fasciculata*, and (3) *zona reticularis*. The medulla, sometimes clearer and at other times darker than the cortex, contains numerous finely granular cells having a clear nucleus. These are arranged to form elongated bands which unite so as to constitute a network (Fig. 83, 4).

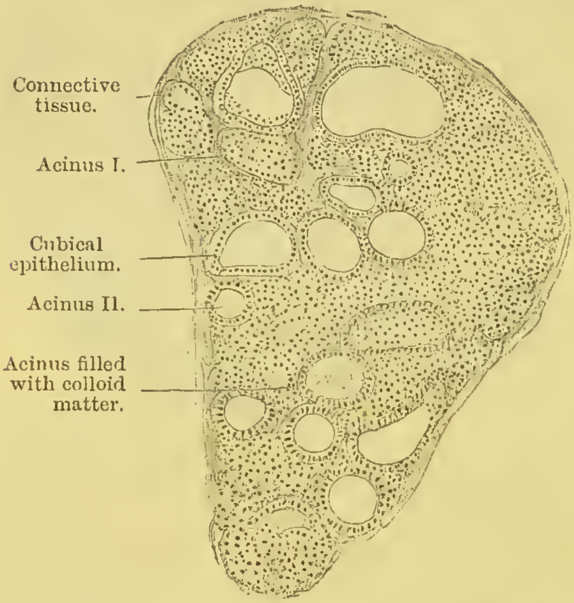

FIG. 81.—Section through the thyroid gland of an adult man. × 80 d. Acinus 1. shows surface view of epithelium. Acinus II. shows side view of epithelium. (Method No. 49, Appendix.)

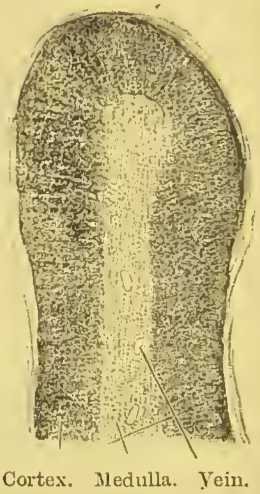

FIG. 82.—Portion of a section of the supra-renal capsule of a child. × 15 d. (Method No. 50, Appendix.)

The *arteries* of the supra-renal body ramify and subdivide on the cortex until they become of fine diameter, and these delicate branches then pass into the substance of the organ and form a long-meshed capillary network in the cortical portion. In the medullary part, the network shows round meshes, from which the veins originate. The *veins* are accompanied by longitudinal bands of smooth muscular fibres. In the medullary substance the veins unite to form a chief supra-renal vein. In man, about 33 *nerves* enter the cortex of the supra-renal body and pass on to the medullary part, where they form a dense plexus. These nerve branches, derived chiefly from the cœliac plexus, consist of non-medullated fibres, and numerous ganglionic cells exist in the course of the fibres and also in the medullary substance (Fig. 83, 6).

5. **The Red Marrow of Bone** must also be considered as a blood forming structure (see Vol. I. p. 334). It contains (1) a small amount of fibrillar connective tissue; (2) fat cells; (3) leucocytes; and (4) myeloplaxes or giant cells. The latter are large cells of very irregular shape, consisting of protoplasm and of one or more nuclei. The shape of the nucleus may be round, irregular, ribbon-like, or annular, or it may show a network (Fig. 75, p. 210, Vol. I.). Out of the giant cells containing one nucleus, cells containing many nuclei may be developed by the fission of the single nucleus (Fig. 84, 3, *r*), or sometimes accompanied by fission of part of the protoplasm. If both nucleus and protoplasm divide, cells with one nucleus are formed. We also find in red marrow cells having part of their protoplasm (almost like a nucleus) coloured yellow, and resembling red blood corpuscles. These are *hæmatoblasts*, or the mother cells of the red blood corpuscles.

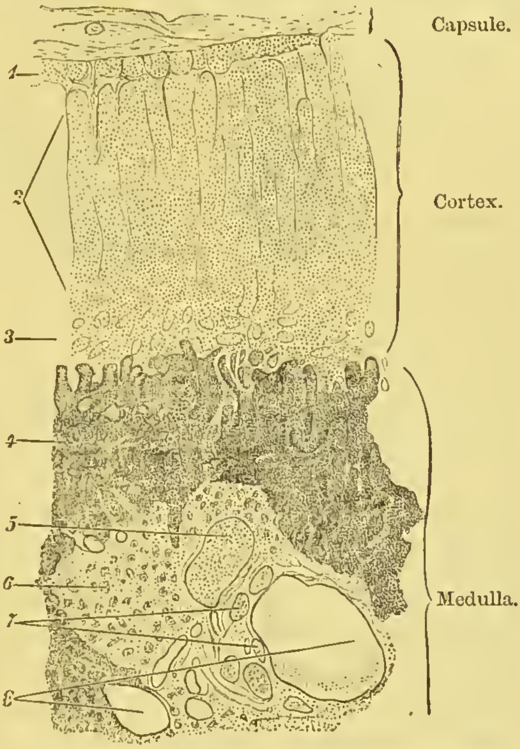

Fig. 83.—Section of a supra-renal capsule of a man. × 50 d. 1, zona glomerulosa; 2, zona fasciculata; 3, zona reticularis; 4, cellular masses in medulla; 5, section of a nerve; 6, ganglion cells; 7, sections of bundles of plain muscular fibre; 8, sections of veins. (Method No. 51, Appendix.)

Chap. II.—THE FUNCTIONS OF THE BLOOD GLANDS.

In perusing the preceding chapter, it must have been noticed that these organs resemble each other in structure, consisting of pouches or shut sacs, rich in protoplasm and adenoid tissue, and containing many lymph corpuscles. They have no ducts, and are very vascular. No difference can be distinguished between the contents of these organs and those of the lymphatic glands; and other facts connected with their morbid states—more especially the production of *leucocythæmia* or *leukæmia*—serve to convince us that they are concerned in sanguification, and hence their modern name of blood-glands. Leukæmia is characterized by anæmia, debility, the existence of an excessive number of colourless corpuscles in the blood, and a hypertrophied condition of one or more of the blood glands. The disease was identified and described almost simultaneously by Hughes Bennett and Virchow, but the latter was the first to state its true pathology. There can be no doubt that the opinion of Hewson, applied by Virchow to the explanation of this disease, namely, that these glands have to do with the formation of blood, exercised a most important influence on our present theories as to the formation of blood. The whole system of lymphatic glands may be said to secrete or form certain elements of the blood.

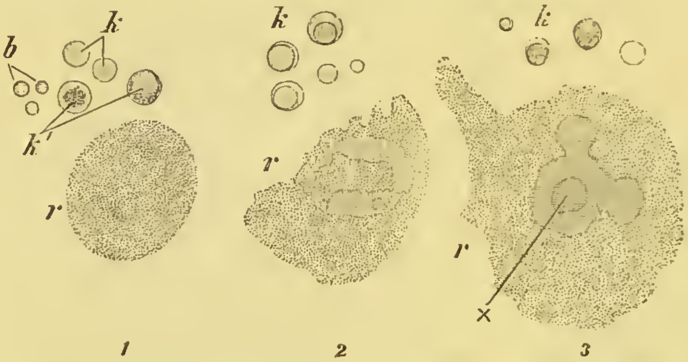

Fig. 84.—Elements of bone marrow from vertebra of a calf. × 560 d, 1, in a solution of common salt; 2, coloured with picrocarmine; 3, after addition of acidulated glycerine. *k*, marrow cells; k^1, two marrow cells containing pigment; *b*, coloured corpuscle (without nucleus); *r*, giant cells. The figure on the right shows two nuclei in process of fission, and one on the surface ×. (Method No. 52, Appendix, Vol. I.)

With the view of preparing for the study of the functions of the blood glands, we shall first consider the structure of the formed elements or corpuscles of the blood.

A. The Blood Corpuscles.

The morphological elements of the blood consist of (1) the red or coloured corpuscles, (2) the colourless corpuscles, (3) the blood plates, and (4) the granules.

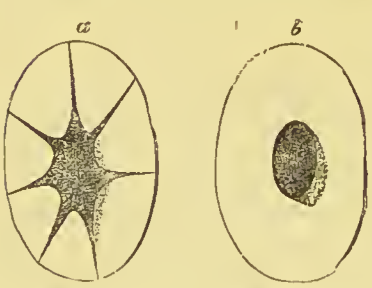

Fig. 85.—Effect of water on red blood corpuscle of newt or frog.

1. **The Red or Coloured Corpuscles.**—These have already been described in Vol. I. p. 299, and they are shown in Fig. 146, p. 300. The corpuscles were first seen in the blood of the frog by Swammerdam in 1658, by Malpighi in the hedgehog in 1661, and by Leeuwenhoek in man in 1673. The mean diameter of the red blood corpuscle of man is 7 μ ·7, but the dia-

meter varies to a considerable extent. Thus Malassez has found that about 3 per cent. measure 6 μ to 7 μ, 7 per cent. 4 μ, 13 per cent. 7 μ ·25, 18 per cent. 7 μ ·50, 24 per cent. 7 μ ·75, 18 per cent. 8 μ, 9 per cent. 8 μ ·25, 5 per cent. 8 μ ·35, and 3 per cent. from 8 μ ·75 to 9 μ ·65. The average thickness is 1 μ ·19. In man, and in all mammals, with the exception of the *camelidæ*, the form is that of a bi-concave non-nucleated disc. In the *camelidæ* they are oval and bi-convex. In birds, reptiles, and fishes, the corpuscles are oval, bi-convex, and nucleated (see Figs. 86 and 87).

The red corpuscles in a drop of blood placed on a slide usually adhere by their flat surfaces, forming rouleaux, like piles of coins. These rouleaux cross so as to form a network, in the meshes of which, here and there, a colourless corpuscle may be readily identified by its want of colour, larger size, somewhat irregular form, and granular aspect. Each corpuscle consists of a framework of pale, transparent protoplasm, termed the *stroma*, impregnated with the pigment, hæmoglobin. One reaction is of special interest as throwing light on their structure. If a drop of a 2 per cent. solution of boracic acid be added to a drop of frog's blood, the red matter (enclosing the nucleus) will shrink off the periphery of the corpuscle, or it may separate from the corpuscle. Brücke, who first observed this reaction, termed the stroma the *œcoid*, in which the red living matter, the *zooid*, lived, like the protoplasm of a sponge on its framework of silicious or calcareous particles. A somewhat similar appearance may be produced by the cautious addition of water (Fig. 85). The place of the nucleus is occupied by a colourless sphere, *b*, while in other cases numerous processes radiate from the sphere to the periphery, *a*. Hayem applies the term *hæmatoblast* to minute coloured corpuscles from ·0015 to ·003 mm. in diameter, sometimes seen in great numbers in the blood (216,000 to 346,000 per cub. mm.). Gibson has called these *coloured microcytes.* They probably represent disintegrating coloured corpuscles. The term hæmatoblast has unfortunately been applied to various kinds of corpuscles. Thus it has been given to the following structures:—(1) the globulins of Donné or the elementary corpuscles of Zimmermann; (2) the white corpuscles formed of hyaline protoplasm of Hayem; (3) granulations in white corpuscles called eosinophiles of Hayem; (4) nucleated cells having buds of Bizzozero, Salvioli and Foa; (5) myeloplaxes of Robin and Heitzmann; (6) vasoformative cells of Ranvier and Wissotsky; and (7) nucleated red corpuscles of Neumann.[1]

No corpuscle similar to the coloured corpuscle is found in the blood of invertebrates, where, however, bodies not unlike the colourless corpuscle are met with.

2. **The Colourless Corpuscles or Leucocytes.**—These have already been referred to at p. 299 of Vol. I., and they are represented in Figs. 86 *d* and 88. They are colourless, irregularly spherical, and larger than the coloured corpuscle. One of their most remarkable properties is

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[1] Malassez. *Travaux du lab. d'histologie du Collège de France*, 1882, p. 4.

that of amœboid movement, first discovered by Wharton Jones in 1846, in the skate, and by Davine in 1850, in man. When carefully watched on a hot stage (with an arrangement as shown in Fig. 90), they may be observed slowly assuming such forms as are depicted in Fig. 88. These movements occur more readily at the temperature of the body. By such changes of form also they may absorb into their substance small particles of fat, pigment, or foreign bodies, or they may wander from place to place, and even pass through the walls of blood-vessels, as shown in Fig. 89. This process is termed *diapedesis*. Hence they are often termed *migratory* or *wandering cells*. Colourless corpuscles are found in connective tissues, bone, marrow, adenoid tissue, lymph, and chyle. In the blood, especially of amphibians, like the newt or frog, three varieties of these corpuscles may be found :—(1) a large finely granular

Fig. 86.—Blood corpuscles. *a*, two coloured corpuscles showing shadowed appearance in the centre, indicating bi-concave form; *b*, corpuscle seen edgeways; *c*, slightly oval corpuscle; *d*, colourless corpuscle; *e*, coloured corpuscles in rouleaux. For method of examining blood corpuscles, and an account of their behaviour to various reagents, see Appendix, Method No. 53.

Fig. 87.—Blood corpuscles of various animals, magnified in the same scale. *a*, proteus; *b*, salamander; *c*, frog; *d*, frog's corpuscle, after addition of acetic acid, showing nucleus; *e*, bird; *f*, camel; *g*, fish; *h*, crab or other invertebrate animal.

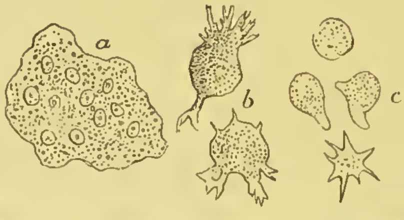

Fig. 88.—*a*, mass of nucleated protoplasm from marrow of bone; *b*, lymph-cells, from inflamed eye, showing amœboid processes; *c*, various forms of colourless cells of the blood.

Fig. 89.—Blood-vessel in mesentery of frog during inflammation, showing migration of colourless cells of the blood. *a*, cells passing through membranous wall of vessel; *b*, cells which have passed through; *c*, coloured cells in stream of blood.

body of irregular form, showing occasionally processes or pseudopodia, and a tripartite nucleus with vacuoles; (2) a medium sized coarsely granular form, showing very active amœboid movement; and (3) small corpuscles like those in human blood. Even in human blood, corpuscles of various sizes may be detected, more especially about one or two hours after a meal. When examined with very high powers, after the action of chloride of gold, an intra-cellular and intra-nuclear network may be observed.

3. **The Blood Plates.**—This somewhat inappropriate name has been applied by Bizzozero to small, colourless, round or oval discs of a diameter varying from a third to a fourth of that of the coloured corpuscle (about 3 μ) (see Fig. 146, 9, p. 300, Vol. I.). They are sometimes present in considerable numbers in the blood, even to the extent of 18,000 to 250,000 in a cubic millimetre, and not unfrequently they form little irregular masses by adhering together. Such masses may be found on threads placed in a drop of fresh blood. Blood plates are readily shown by mixing a drop of blood with a 6 per cent. solution of osmic acid, or by mixing the blood, freshly drawn with a few drops of a ·75 per cent. solution of common salt tinted with methyl-violet. Gibson terms these bodies *colourless microcytes.*

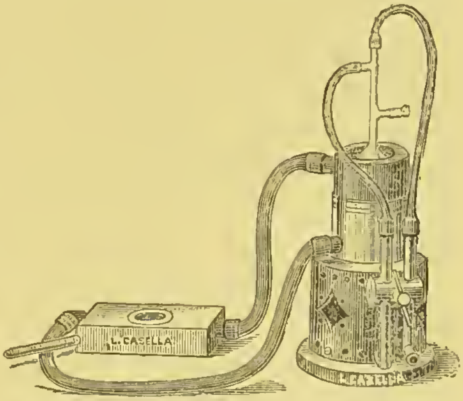

FIG. 90.—Schäfer's hot stage. The stage is seen on the left. It is a box, having a well in the centre. Through the box a stream of hot water circulates, and this stream also passes through a double-walled circular vessel seen on the right. In the centre of the circular vessel is a thermal regulator, with a very large bulb. A small gas flame is placed below the circular vessel, and the stream of gas is regulated so as to produce the required temperature. Placing the hot stage under the microscope, the height of the gas apparatus and circular vessel can be so adjusted that the hot water will flow up by one tube into the stage box, and back to the circular vessel surrounding the thermometer by the other.

4. **The Elementary Granules** are minute, round, refractive particles. Some are of a fatty nature, and probably derived from the chyle, while others are small bits of protoplasm produced by the disintegration of leucocytes, or detached from the protoplasmic germ centres in lymphatic glands. The latter may be regarded as minute blood plates.

In addition to these four kinds of corpuscles, Norris believes that he has succeeded in demonstrating the existence in the blood of numerous corpuscles, of a bi-concave form, which cannot be seen by the microscope, not because of their minuteness, "but owing to the fact that they have the same refractive index and colour as the *liquor sanguinis* in which they are submerged." By various methods, (such as altering the refractive index of the *liquor sanguinis,*) conducted with great ingenuity and technical skill, and with the aid of photography, he believes that he has made these corpuscles visible, and he has prepared photographs in which such colourless forms may be seen. After a careful examination of numerous photographs submitted to my inspection by Norris, I am satisfied that the pale corpuscles cannot be accounted for by supposing that they are simply decolorized red corpuscles, or that they have assumed the appearances in the photographs by reason of the processes to which they have been subjected. Some of the appearances are, in my opinion, illusory, especially those in which a single pale round body (or space) is seen among a number of corrugated corpuscles, and I think Norris attaches undue importance to these appearances, but on the other hand his method brings into view not a few very pale corpuscles of the form of red blood corpuscles. They are neither red blood corpuscles decolorized, nor are they the blood plates of Bizzozero (often seen by the earlier observers but passed over as unimportant), nor are they leucocytes. I think, therefore, that Norris has demonstrated a corpuscle not usually seen, which is probably *a transitional corpuscle*, that is one which, in the evolution of the ordinary red blood corpuscle, has not yet received its full complement of hæmoglobin. Norris designates these as "lymph discs"; he holds that these become the "invisible discs of the blood," and that they subsequently became visible by the acquisition of colour.[1]

Lastly, we sometimes find in the blood *nucleated coloured corpuscles*, similar to those met with in embryonic life. These are usually somewhat oval in shape, and they enclose a body having the form and a little of the colour of a coloured blood corpuscle. They are sometimes termed the *corpuscles of Neumann.* Such are also found in the spleen and in the marrow of bone.

B. THE ORIGIN OF THE BLOOD CORPUSCLES.

The lymph and chyle supply new morphological elements to the blood, the lymph corpuscles. These originate chiefly in the adenoid tissue of the lymphatic glands, and they are washed out into the larger lymphatics by the flow of lymph. In like manner the lymph corpuscles in the adenoid tissue of the villi are washed out by the flow of chyle. There is thus a constant influx into the blood of corpuscles, the lymph corpuscles, which are identical with the colourless corpuscles of the blood. These would accumulate in great numbers in this fluid if they were not utilized in the formation of other substances. We find in the

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[1] Dr. Richard Norris on the Physiology and Pathology of the Blood, 1882.

blood, however, not only colourless but coloured corpuscles, and it has long been held that a genetic relationship exists between them. This relationship has not yet been thoroughly explained, but there can be no doubt that certain of the colourless are the parents of the coloured corpuscles. The coloured corpuscles exist in immense numbers in the blood, and one can scarcely conceive them to be permanent structures. Little is known however of any alterations they may be assumed to undergo in the circulating blood, or of any exchanges occurring between them and the blood plasma. The chief evidence in favour of the view that coloured corpuscles undergo disintegration somewhere in the body is the fact that all animal pigments are derivatives of hæmoglobin, the pigment of the red blood corpuscles. Thus the pigments of the bile are undoubtedly derivatives of the blood pigment, and as the blood pigment does not exist in the fluid plasma of the blood but in the red blood corpuscles, it follows that it must escape from these corpuscles before it is decomposed into derivative pigments. Decomposition of red blood corpuscles must therefore take place. The chief localities in which such a decomposition occurs are the liver and spleen. As we have already seen, bilirubin, the chief bile pigment, is identical with hæmatoidin, a pigment free from iron, which is found in the remains of extravasations of blood in the brain and in many other localities. But hæmoglobin contains iron, and the iron thus set free probably appears in the form of phosphate of iron, a salt constantly found in the bile, and the presence of which cannot be explained on any other assumption than that the iron has been derived from the hæmoglobin of the blood. Another locality in which red blood corpuscles perish is the spleen. In the spleen-pulp large protoplasmic masses are found enclosing red blood corpuscles, sometimes perfectly formed, at others pale and shrivelled, and at others fragments of corpuscles, appearing as red or yellow pigmented granules. These large giant cells, having the power of amœboid movement, surround effete coloured blood corpuscles and decompose them. In the spleen of man, the horse, and ox, peculiar yellowish granules have been found. These consist mostly of oxide of iron. The dry spleen may yield as much as five per cent. of its weight of iron, and we cannot account for this except on the supposition that red blood corpuscles (or, at all events, hæmoglobin) are decomposed in that organ.

If there is a decomposition of red blood corpuscles, there must also be a process of rapid formation of these bodies. In normal blood, the number of red blood corpuscles per cubic millimetre does not undergo great variation. We also know that after venesection, by which the number of red blood corpuscles may be much reduced, they are replenished with such rapidity, that the blood may again contain the normal number per cubic millimetre in the course of a few days or weeks. The source from which the coloured corpuscles are thus replenished is the abundant supply of colourless corpuscles. A colourless corpuscle changes into a nucleated coloured corpuscle, in the case of fishes, amphibians, reptiles, and birds, and produces a non-nucleated coloured corpuscle, in the case of mammals. Many steps of this process have been traced by Von Kölliker, Von Recklinghausen, and others, but nothing is known as to the chemical changes involved, and, more especially, nothing is known of the origin of hæmoglobin, except that in all probability it is formed in the spleen.

The colourless cells, which are the parents of the red corpuscles, are the *hæmatoblasts* found in the spleen, and especially in bone marrow. They are pale, granular, contractile bodies, like ordinary leucocytes. The nucleus becomes a larger corpuscle, and then the cell is a corpuscle of Neumann. Later on the nucleus is expelled from the corpuscle, and the remaining part of the cell is charged with hæmoglobin and becomes a red corpuscle. Another view is that Neumann's cells give off little buds, which acquire hæmoglobin and become red corpuscles. Malassez has given the name of *globuligenic cells* to the cells of Neumann, and his view is that the red corpuscles are merely buds given off from these cells, but they are not buds in the same sense as the buds of a yeast cell, that is to say, the bud can never become like the parent organism. The bud is merely a detached portion of the cell, differentiated for the special purpose of acquiring hæmoglobin and of becoming a red corpuscle. The nucleated red corpuscle of birds, reptiles, amphibians, and fishes is one of Neumann's corpuscles arrested at this stage and charged throughout with hæmoglobin, but in the mammalia, by this peculiar process of budding, the matter of the cell, exclusive of the nucleus, is, as it were, divided into many parts, thus increasing the respiratory surface. A mammalian red corpuscle, therefore, is not a modified nucleus, but it represents a portion of the substance of a Neumann's corpuscle outside the nucleus. This view of the constitution of a red corpuscle is the best that has yet been offered (Fig. 91).

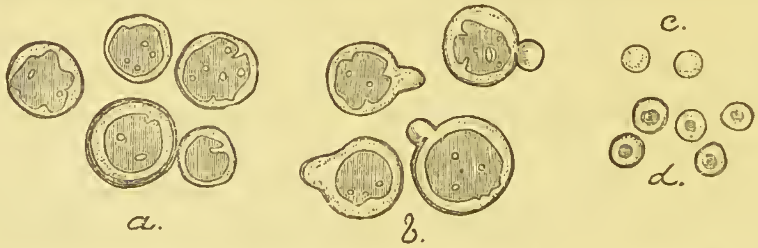

Fig. 91.—Formation of red corpuscles in a young goat. *a*, globuligenic or hæmoglobin cells without globuligenic buds; *b*, budding cells; *c*, spherical corpuscles; *d*, discoidal red corpuscles. (After Malassez.)

If then coloured are formed from certain colourless corpuscles, we are brought back to the question of the origin of the colourless corpuscles. These originate by the rapid multiplication by fission of lymph corpuscles in the lymphatic glands, and in the solitary and agminated glands of Peyer. Division, accompanied by karyokinetic phenomena, has been observed in these organs. Another locality in which the formation of colourless blood corpuscles occurs is in the pulp of the spleen, in which cell multiplication goes on with great rapidity. The fine adenoid tissue of this organ is always crowded with colourless corpuscles, and the blood flowing from the splenic vein is always much richer in white cells than the blood flowing in the splenic artery. Thus, in the blood of an ordinary vein, the ratio of colourless to coloured corpuscles is 1:350 or 400; in the splenic vein it may be 1:70 or 1:60. It is remarkable, in this connection, that the number of white to red corpuscles is also increased by the passage of the blood through the liver. For example, the ratio of white to red corpuscles in the blood of the portal vein is as 1:520 or 1:740, while in the hepatic vein it may be 1:170. In the case of the liver, this probably arises from the absolute diminution of the red blood corpuscles, but, in the case of the spleen, it is rather to be attributed to the absolute increase in the number of the white corpuscles. The red bone marrow is also the seat of the rapid formation of colourless corpuscles, and it is here also that transitional forms between colourless and coloured corpuscles have been traced.

The red blood corpuscles in the development of the chick are formed in large branched cells in the mesoblast. The processes of adjoining cells anastomose so as to form a protoplasmic network. Nuclei appear in the bodies of the cells (the so-called mother cells) and some of these nuclei, enclosed in a small amount of protoplasm, become blood corpuscles. They become tinted of a reddish colour. The protoplasm forming the wall of the space in which they lie, and the protoplasm of the anastomosing processes become hollowed out so as to form embryonic blood-vessels. The outer walls of the mother cells, with their nuclei, now constitute the walls of the vessels; fluid collects in these and washing away the corpuscles becomes embryonic blood. Some of the nuclei in the wall may also proliferate to form blood corpuscles and these become detached and are carried away with the fluid. At first colourless, these embryonic blood cells become coloured, show amœboid movement, and they multiply freely by fission. Similar large nucleated cells have been found in the liver, spleen, and red marrow during the embryonic life of mammals. In the early period of embryonic life therefore all the blood corpuscles are nucleated. Up to the close of the fourth week, only nucleated corpuscles are found in the human embryo. Then a change occurs. The nucleus becomes smaller and gradually disappears, and the corpuscle assumes the well-known biconcave disc form. For many weeks, up to the end of the third month, both kinds of corpuscles exist, the nucleated form however gradually becoming fewer in number, until they are rarely found at the end of uterine life. There is every reason to regard the liver, spleen, and lymphatic glands as the chief seat of their formation in the middle and later periods of embryonic life.

In birds, reptiles, amphibians, and fishes, the nucleated blood corpuscle, which is an embryonic condition in mammals, remains through the whole of life. Soon after birth, the formation of blood corpuscles has been traced in somewhat similar processes going on in connective tissues. Thus, Ranvier has seen in the omentum of young rabbits, a week old, large irregularly shaped cells having protoplasmic processes which become vacuolated so as to form vessels in which, by the separation of small bud-like portions of protoplasm from their walls, corpuscles are formed.

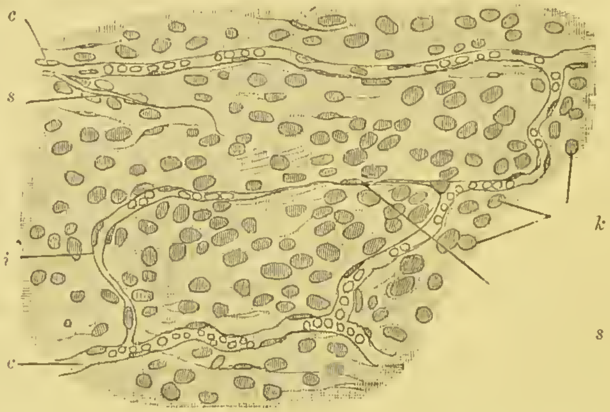

Fig 92.—Surface view of a portion of the great omentum of a rabbit 7 days old. × 240 d. *c*, blood capillaries, containing blood corpuscles; *s*, offshoot of a capillary running into a solid process; *i*, young capillary already hollowed out; *s*, capillary still solid; *k*, nuclei of endothelium of peritoneum.

This process is illustrated in Fig. 92. Schäfer has also traced the intra-cellular development of corpuscles in subcutaneous connective tissue cells of the young rat, and similar phenomena have been seen by other observers in other situations, all indicating that there is, in early life, a local formation of corpuscles in mesoblastic cells. After birth, red blood corpuscles are formed from certain nucleated colourless corpuscles, especially in the red marrow of the bones. (See Fig. 91, p. 170.) Here we find colourless cells and nucleated red blood cells, similar to those of embryonic life. It is highly probable that the same process occurs in the spleen, and, according to Norris, the lymph cells (those which in his opinion may be for a time invisible in the circulating blood) become tinted with hæmoglobin, and thus give origin to red blood corpuscles. It is evident, however, that our knowledge on this subject is still very imperfect, more especially as to the formation of a body so complicated in chemical constitution as hæmoglobin. The stages in the metabolism by which it is formed are at present unknown.

We have next to consider the function of certain organs often classed under the head of blood glands, although it is doubtful whether or not they have at any period anything to do with blood formation. It is not unlikely that in intra-uterine or early extra-uterine life, the thymus, thyroid body, and the supra-renal bodies may have a blood-forming function, while in later life their function may be more in the direction of using up, or destroying (by splitting up into simpler bodies) certain elements of the blood of an effete character. The matters thus formed, however, are not evacuated in the form of a secretion, as none of these bodies possesses a duct, but they are re-absorbed into the blood and probably are of further use in the body. Taking this view of the matter, we may now shortly state our imperfect knowledge regarding these organs.

1. **The Thymus.**—In the latter stages of embryonic life, and in the first epoch of extra-uterine life, when active development of tissue is going on, an abundant supply of blood corpuscles is evidently necessary, and accordingly we find that in this period the *thymus* is in a state of great activity, assisting the lymphatic glands, bone marrow, and spleen in the formation of blood corpuscles. In later life, when development has largely ceased, the thymus is not required, and it slowly undergoes absorption, disappearing from man about the beginning of puberty, and from the horse and ox soon after the second year. Reptiles and amphibians, which have no lymphatic glands, have a permanently active thymus body.

The minute anatomy of the thymus in relation to its function has been elaborately examined by H. Watney.[1] He found that "there are present in the lymph issuing from the thymus, cells containing coloured blood corpuscles and hæmoglobin granules; and that in the lymphatics of the thymus there are more colourless cells than in the lymphatics of the neck." He suggests that these colourless cells "form one source of colourless blood corpuscles," but he does not suppose that the thymic corpuscles are changed into coloured blood corpuscles. In the thymus, also, large colourless cells, containing bodies like coloured blood corpuscles, were seen, but Watney does not adopt the view of Von Kölliker, that these have absorbed the coloured cells as a step towards their disintegration, and he pertinently observes that similar cells have been found in the lymphatics, in the blood of leucocythæmia, in the thymus, the lymphatic glands, and in the marrow of bone, where we have no knowledge of any destruction of coloured blood corpuscles taking place.

2. **The Spleen.**—There are still many difficulties in the way of giving a satisfactory explanation of the functions of the spleen. It is undoubtedly a blood gland, but it appears to be concerned in the double process of the formation of colourless and of the destruction of coloured corpuscles. Probably it is the seat of other katabolic changes. Thus we find in spleen pulp evidence of the existence of many bodies resulting from the decomposition of albuminous compounds, such as leucin, tyrosin, xanthin, and hypoxanthin. Cholesterin, ferruginous pigments, and the organic acids, formic, acetic, butyric, lactic, and uric acids, have also been found in it. At the same time, it is not an indispensable organ, as it has been frequently extirpated without

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[1] Herbert Watney, M.A., M.D. (Cantab), *Phil. Transactions*, Part II., 1882.

apparent loss to the economy after the animal had recovered from the severe operation. In these cases, it has been discovered that the lymphatic glands enlarge, and that the red bone marrow shows more than a usual abundance of colourless cells, indicating that these organs may act vicariously for the spleen.

It has also been discovered by Roy that the spleen performs remarkable rhythmic movements. This he accomplished by enclosing the spleen *in situ* in the living animal in a box communicating with a recording apparatus.

The box, to which he has given the name *oncometer* (ὄγκος, bulk), is made of thin metal, and is composed of two symmetrical halves, joined by a couple of hinges. Each of these halves is composed of an outer and inner shell, and between the two is placed a thin membrane prepared from the peritoneum of the calf. An air-tight chamber is formed in each lateral half of the box, bounded on the one side by the membrane and on the other by the metallic side of the box. These chambers are filled with oil, and when the spleen is introduced and the box closed it is surrounded by the peritoneal membrane, on the other side of which, in each half of the box, is the chamber filled with oil. The interior of each chamber communicates by a tube with a common tube passing to the recorder, so that any change in volume of the spleen will be at once recorded, oil being forced into the tube connected with the recording tube when the spleen increases in volume, and when the spleen contracts, the oil will flow back into the instrument. The recording instrument, termed the *oncograph*, consists of a light piston moving in a box containing oil, the oil being prevented from escaping by a membrane tightly tied below the piston. The oil box has a horizontal tube near its lower part which is connected with the tube coming from the oncometer. In all the experiments made by Roy, the arterial blood pressure was recorded on the same paper as the changes in volume of the spleen. Specimens of the tracings thus obtained are shown in Plate A. Fig. 2, and in Plate B. Fig. 5.

By this method Roy has demonstrated (1) that the splenic circulation is carried on chiefly, if not exclusively, by a rhythmic contraction of the muscles contained in the capsule and the trabeculæ of the organ; (2) the rhythmic contraction is regular as to time, and in dogs and cats each contraction and expansion lasts about one minute; (3) variations in blood pressure produce only a slight influence on the volume of the spleen, so that arterial blood pressure is not the chief factor in carrying on the splenic circulation; (4) the rhythmic movement of the spleen is not the same as the peculiar rhythmic variation of blood pressure which produces the well-known Traube-Hering curves, which are recognized as being caused by rhythmic variations in the vaso-motor centre or centres, thus showing that the splenic movements do not depend on these centres; (5) stimulation of the central end of a sensory nerve or of the *medulla oblongata* causes a rapid contraction of the spleen; (6) stimulation of the peripheral ends of both splanchnics and of both vagi causes a rapid contraction of the spleen; and (7) even after section of both vagi and of both splanchnics, stimulation of a sensory nerve will still cause contraction of the spleen, showing that nervous influences pass to the spleen by some other unknown route.[1] The purpose subserved by these rhythmic movements is unknown. The organ increases in bulk after a meal, attaining its maximum size about five hours after finishing a meal, and it is also stated that when the volume of the spleen is diminished, that of the liver is increased. We are quite in the dark as to the influence of the spleen on the circulation in the abdominal organs. Its rhythmic movements depend on the presence of automatic nervous centres, in the form of small ganglia.

3. **The Thyroid.**—No definite information can be given regarding the functions of the *thyroid gland.* When much enlarged it gives rise to goître, a deformity sometimes associated with more or less marked idiocy, as in *cretinism.* It has also been stated that its removal from the human being has been followed by mental weakening. The operation of removal is much more serious in carnivora than in herbivora. Cats and dogs usually die, but horses, oxen, and sheep often survive. Many symptoms have been noticed after its removal, certain of which may be attributed largely to shock, but there are others bearing directly on the function of the gland. Thus, the red blood corpuscles undergo a great diminution and the white blood corpuscles are much increased in number. The salivary glands become enlarged, the parotid gland, which is normally a serous gland, begins to secrete mucin, and mucin may be found even in the blood. Victor Horsley states that thyroidectomy may be followed by three stages: (1) the *neurotic* stage, lasting from one to two weeks in dogs and from one to three weeks in monkeys, and characterized by muscular tremors and breathlessness; (2) the *mucinoid* stage, from one-half to one week in dogs and from three to seven weeks in monkeys, and showing a deposit of mucin in the tissues, or a mucinoid degeneration of the connective tissues, a condition known to pathologists as a *myxœdema*; and (3) the *atrophic* or *marasmic* stage, lasting from five to eight weeks in monkeys, and marked by atrophy of all the tissues except muscular tissue. The most remarkable of these effects is the increase in the amount of mucin in the tissues, but whether an excess of mucin is normally consumed in the gland, so that it increases when the organ is removed, or whether these changes indicate

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[1] Charles S. Roy, M.D., F.R.S., *The Physiology and Pathology of the Spleen. Jl. of Physiology*, Vol. III. No. 3, p. 203.

an interference with processes of complemental nutrition in which this organ is involved, are questions that cannot at present be answered. Enlargement of the thyroid is seen in Basedow's or Graves' disease, exophthalmic goître, in which there is protrusion of the eyeballs with increased rapidity of the heart's contractions due to stimulation of the accelerating fibres of the sympathetic. There is almost no evidence in support of the view that the thyroid is a blood forming gland, except that its enlargement from disease or its removal by operation is followed by anæmia, that is to say, a diminution in the number of red corpuscles in the blood, and by an increase in the coloured corpuscles.

The thyroid gland is of large relative size in fœtal life. From a phylogenetic point of view, it is the remains of an organ which was a diverticulum from the ventral wall of the pharynx or floor of the mouth, and it may then have had a secreting function of special importance in the ancestors of existing vertebrates.[1] That it still has a function is proved by the dire effects following its removal.

4. **The Supra-renal Bodies.**—There is still obscurity as to the functions of the *supra-renal bodies.* Their presence in fishes, amphibians, reptiles, birds, and mammals indicates their importance to the economy of the body. The history of their development supports the view that each supra-renal body is formed by the fusion of two organs, having independent functions. It has been established that the medullary part arises from the sympathetic ganglia while the cortical part is mesoblastic. The medullary portion is at first outside the cortical portion, but becomes gradually enclosed by it, so that in adult life the greater part of the body consists of cortical substance. It is important also to observe that the supra-renals are relatively large in fœtal life. At the end of the third month, they are as large as the kidneys.

As shown by Hoppe-Seyler, the medullary part of the supra-renal body contains albuminous bodies and pigmentary matters of various kinds. A watery extract exposed to sun-light acquires a red colour. On extracting the supra-renals with dilute hydrochloric acid and adding ammonia to the extract, a beautiful red colour is produced. The substance thus giving colour has not been isolated. Hippuric, taurocholic, and benzoic acids, taurin, and inosite have been found in these bodies. They must, therefore, be the seat of important metabolic changes.

Addison first made the observation that disease of these organs is often associated with a dark brown, or sallow, tint, or bronzing of the skin, accompanied by a number of symptoms, such as debility, giddiness,

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[1] F. M. Balfour, *Comparative Embryology*, vol. ii. p. 624.

vomiting, and breathlessness, grouped under the term *Addison's disease.* Extirpation, when successful, which it rarely is, owing to the unavoidable hæmorrhage and injury to nerves, has not brought to light any facts of importance. They cannot be regarded as nervous organs in the strict sense of the term, and even taking into account the existence of ganglionic cells in the supra-renal bodies, the fact remains that by far the larger portion of their structure is glandular in its nature.

The view that in some way they are concerned in the processes involved in pigmentation has been ably supported by the observations of MacMunn.[1]

He noticed that the spectrum of the supra-renals shows the bands of hæmochromogen or reduced hæmatin. This substance can be derived either from hæmoglobin or from histohæmatin. He supposes that the function of the supra-renals is "to pick out of the circulation these worn-out or effete colouring matters with their accompanying proteids," and that we should find incompletely metabolized pigments in the excretions when the supra-renal bodies do not perform their functions in consequence of disease. This evidence he finds in the detection in the urine of patients labouring under Addison's disease of a pigment named urohæmatoporphyrin. This pigment is a hæmochromogen. Other derivatives of histohæmatin or hæmoglobin, not metamorphosed by the diseased supra-renals, appear as the pigmentation of the skin, and, lastly, effete proteids may also accumulate in the blood, and by acting on the nervous centres produce the nervous symptoms, seen in Addison's disease.

5. **The Pituitary Body or Gland or hypophysis cerebri** consists of two genetically distincts parts : (1) a posterior and smaller portion belonging to the brain, and forming a continuation of the infundibulum. This part contains only a few nerve fibres, along with connective tissue and blood-vessels : (2) an anterior and larger part, which is developed from the layer continuous with the embryonic mouth. This portion contains small tubular glands, filled with cubical epithelial cells, sometimes clear, sometimes dark in hue. The tubular structures are often hermetically closed so as to form oval pouches or tubes sealed at each end, but a few open towards the surface. The structure also contains a large amount of connective tissue (Fig. 93). There are no grounds for classing this organ among the blood glands in the sense of being concerned in blood formation, but it may have a function in connection with the blood supply to the brain. V. Horsley has twice successfully removed it from dogs, and the animals

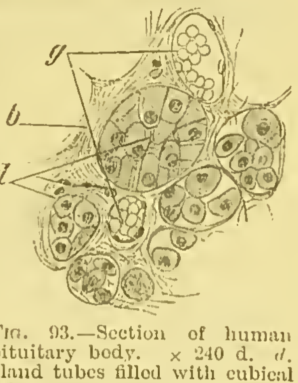

Fig. 93.—Section of human pituitary body. × 240 d. *d*, gland tubes filled with cubical cells; *g*, transverse section of vessels containing blood corpuscles; *b*, connective tissue. (Method No. 54, Appendix.)

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[1] C. A. MacMunn on "Addison's disease and the functions of the supra-renal bodies."—*Brit. Med. Journal*, Feb. 4th, 1888.

survived from five to six months without any symptoms indicating its loss. He observed that when the cortex of the brain was exposed and stimulated, there was increased excitability of the grey matter of the motor areas of the cerebrum, but this may have had no connection with the absence of the pituitary body.

6. **The Pineal Body.**—This organ, also sometimes erroneously classed as a blood-gland, is formed from a fold of the wall of the primitive brain, and it contains epithelial cells which have delicate processes issuing from them. The body has a sheath of connective tissue from which partitions pass into its interior. In the pineal body we find earthy matter or concretions, *acervulus cerebri*, of irregular form and granulated on the surface like a mulberry (Fig. 94). They are formed of an organic matrix impregnated with carbonate of lime and phosphate of magnesia. This is the structure of the body as determined in the human being, but it has now been conclusively established that the pineal body is the representative of an ancestral form of eye. In certain lizards (*Hatteria*, *e.g.*) the process of transition has not gone so far as in many other animals, so that histological elements belonging to the system of the eye can still be identified, such as corneal tissue, pigments, lens structure, and even retinal elements. It is also remarkable that the type of eye is not that existing now in vertebrates, but that of the compound eye found in invertebrates.

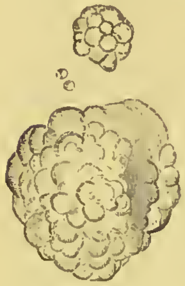

FIG. 94.—Earthy matter from the pineal body of a woman of 70 years of age. × 50 d. (Method, No. 55, Appendix.)

7. **The Coccygeal Gland, or Luschka's Gland,** situated in front of the tip of the coccyx, is composed of a plexus of minute arteries surrounded by polygonal cells like those in the thyroid and supra-renal bodies. A minute gland-like organ near the upper end of the common carotid, termed the *carotid gland*, shows a similar structure. The function of these bodies is unknown, but their general structure suggests that they may have to do with processes similar to those of the supra-renal bodies.

To recapitulate, it appears that the blood is frequently receiving new supplies of material from the following sources :—

1. Water, salts, sugar, peptones, etc., by vascular absorption from the alimentary canal.
2. Water, salts, peptones, fats, either free or as soaps, etc., by lacteal absorption from the alimentary canal.
3. Water, and possibly some volatile or soluble matters, by the skin.
4. Oxygen, and possibly some aqueous vapour and volatile matters by the mucous membrane of the lungs.
5. Water, salts, nitrogenous matters, etc., from the lymph or from shut sacs into which fluids had been previously effused.
6. Protoplasmic elements (lymph cells) from the lymphatic glands, mesenteric glands, and other blood glands, in which also no doubt exchanges (as regards fluids, gases, and soluble substances) occur between the chyle or lymph and the blood. From these protoplasmic elements, the coloured corpuscles are formed.

Chap. III.—THE BLOOD.

The blood, whilst in the vessels, is a fluid of a red colour, which may vary from a crimson, as seen in arteries, to a reddish purple, as in veins. A thin stratum spread on the surface of a sheet of glass is opaque, because the light is reflected by the concave surfaces of the corpuscles as from concave mirrors, but the addition of water, chloroform, ether, or bile, or extreme cold, or a temperature above 60° C., or a continuous current of electricity, causes such a layer to become translucent. Blood has usually an odour peculiar to each species of animal (*halitus sanguinis*). Soon after blood has been removed from the body, usually from two to fifteen minutes, it separates into two parts, a clot and a fluid, a process known as the coagulation of the blood. The coagulum *crassamentum*, or clot, contracts, and a clear or pink-coloured fluid is squeezed out of it, termed the *serum*. The specific gravity of blood from man varies from 1054 to 1062, from a dog, horse, or pig 1060, from a cat 1054, from a rabbit 1049, and from a goat 1042 (Munk). The density of the blood may be determined readily by a method proposed by Roy.

If a drop of blood is introduced by a fine hypodermic syringe into a mixture of glycerine and water of known density, it will sink if it be of higher density and it will float if it be of lower density than the fluid, and it will be stationary if the blood density is the same. A number of standard solutions of glycerine and water may be prepared for testing.

The blood is alkaline. This cannot be determined with red litmus paper in the usual way. It may be readily shown by the method of Zuntz.

Prepare a bit of fine silk paper by wetting it with solution of red litmus and with a strong neutral solution of sulphate of soda. Place a drop of blood on it for a few seconds, rapidly removing it with blotting paper. A bluish stain will be seen. The alkalinity corresponds to that of ·2 to ·4 per cent. of soda.

If we collect the blood of a horse, as it flows from the living body, in a tall cylindrical glass vessel, kept at a low temperature by being immersed in a vessel containing ice-cold water, the blood at first has its usual red colour, but as it does not clot in the cold the red corpuscles sink towards the bottom of the vessel, so that only about one half of the height of the column of blood is red, while the upper half is occupied by a clear amber-coloured fluid. This is the *blood plasma*, or *liquor sanguinis*. Between the two layers there is a delicate layer of a whitish colour, about ·02 of the height of the blood column. The fluid may be drawn off by a pipette or narrow syphon. About $\cdot 6\dot{6}$ of the total weight of the blood is represented by this fluid, the remaining $\cdot 3\dot{3}$ consisting of corpuscles. The plasma has a specific gravity of 1027 to 1030. It soon forms a translucent jelly-like clot, if placed in a cylindrical vessel, so adherent that the vessel may be inverted without the clot falling out. The clot separates from the sides of the vessel in the course of a few minutes, drops of a pale yellow fluid ooze from its surface and collect round its sides, so that the clot by-and-by floats free in the fluid. We thus see that blood plasma may be resolved into a clot and a fluid. The clot is composed of *fibrin*, and the fluid, the *serum*, is blood plasma from which fibrin has been removed.

Precisely similar changes occur when blood is collected from a living animal without any precautions to delay coagulation, but in this case the clot is red because blood corpuscles become entangled in it. The form of the clot is always that of the vessel into which the blood is received, and at first it completely occupies the volume of the previously fluid blood. In the course of a few minutes, the clot shrinks, and it soon separates itself from the sides and bottom of the vessel, and floats in a fluid of a straw yellow colour. The contraction of the clot terminates in from twelve to twenty hours. As the resistance to contraction of the clot is greatest where it touches the sides of the vessel, and least in the centre, the upper surface usually becomes concave, or, in the language of the old pathologists, *cupped*. When a clot formed in a tall cylindrical glass vessel, of narrow diameter, is examined, it will be seen that its colour increases in intensity from above downwards. Thus the surface may be nearly white, with a shade of pink, and the colour may become, by insensible gradations, deeper and deeper until the base of the clot is seen to be blood-red. The white layer thus formed was termed by the older physicians the *buffy coat*, or *crusta phlogistica*, because they saw it in the blood of patients suffering from inflammatory affections while it was absent from that of healthy persons on whom venesection was performed. It is due to the presence in the upper layers of a preponderance of colourless corpuscles. It is best seen in blood which coagulates slowly, as, when this occurs, the coloured corpuscles, from their greater specific gravity, sink towards the bottom, leaving the lighter colourless corpuscles nearer the top. If blood be whipped with a glass rod, or with a bunch of twigs, as it flows from a vessel, the fibrin will collect on the rod or twigs in the form of a fibrous elastic matter, and the red fluid thus obtained will not coagulate. This is *defibrinated blood*, that is, blood from which fibrin has been separated.

Whilst the blood was in the body it consisted of a fluid, the *liquor sanguinis*, in which the two kinds of corpuscles were immersed. When coagulation takes place, a new solid substance is formed called *fibrin*, constituting the fibrous matrix of the clot, in which the greater number of the corpuscles become entangled. Clot, therefore, consists of fibrin and corpuscles, and the serum consists of fluid, holding, in suspension, only a few corpuscles, and, in solution, salts, soluble organic substances, and gases. The process is illustrated by the following diagram—

CIRCULATING BLOOD. COAGULATED BLOOD.
Liquor sanguinis, or Plasma. } Serum ———————— Serum.
Fibrin-forming substance.
Corpuscles ———————————————— Clot.

The blood consists of about two-thirds of plasma and one-third of corpuscles. The following analyses show its percentage composition.

	Horse. *Hoppe-Seyler.*	Ox. *Bunge.*	Dog. *Hoppe-Seyler.*
Blood corpuscles, - - - -	33·45	31·87	35·7
Solids, - - - - -	13·03	12·75	15·38
Water, - - - - -	20·42	19·12	20·32
Plasma, - - - - - -	66·55	68·13	64·30
Solids, - - - - -	6·50	5·91	5·60
Water, - - - - -	60·05	62·22	58·7

The composition of 100 parts of the plasma of horses' blood is as follows—

Water, - - - - - - - -		90·8
Solids, - - - - - - - -		9·2
Fibrin, - - - - - - -	0·4	
Albumin, - - - - - - -	7·5	
Fat, - - - - - - - -	0·1	
Extractives, - - - - - -	0·4	
Salts, - - - - - - - -	0·8	9·2

The average of nineteen analyses of human blood, by Becquerel and Dodier, gave the following percentage results—

	Man.	Woman.
Water, - - - - - - - -	77·9	79·1
Solids, - - - - - - - -	22·1	20·9
Fibrin, - - - - - - -	0·2	0·2
Hæmoglobin, - - - - - -	13·5	12·3
Albumin, - - - - - - -	7·6	7·6
Fat, - - - - - - - -	0·2	0·2
Extractives and salts, - - - -	0·6	0·6
	22·1	20·9

The *serum* is a clear, slightly alkaline fluid of a pink or faint pink-yellow colour. Sometimes it may be amber-yellow or yellowish-brown, with even a tinge of green, as seen in that of the dog, and rarely it may be milky from the presence of numerous fatty particles absorbed after a meal rich in fat. Its specific gravity ranges from 1022 to 1029. Serum contains 90 per cent. of water and 10 per cent. of solids. The solids are composed of 3 to 5 parts of *serum albumin* (coagulating at 75° C.), along with another albuminous body, to the extent of 1·5 to 4 per cent., termed *serum globulin.* This substance is precipitated by adding to serum four times its volume of a saturated solution of sulphate of magnesia. In the serum of man and of the rabbit the albumin preponderates, but the reverse is the case in that of the horse and ox (Munk). *Fats* exist in small quantity, and consist of stearin, palmitin, and olein, with soaps. *Nitrogenous bodies* are also present, and include kreatin, hypoxanthin, urea, uric acid. With these we find *extractives,* such as cholesterin, lecithin, sugar, lactic acid, and a yellow pigment (lutein?[1]). The *salts,* amounting to about ·9 per cent., consist of chlorides, sulphates, phosphates, and carbonates of the alkalies (sodium, potassium), and alkaline earths (calcium, magnesium). Chloride of sodium is largely present, even to the extent of ·6 per cent.; chloride of potassium only in traces—·03 per cent.; disodium phosphate, Na_2HPO_4, and sodium carbonate, Na_2CO_3, abound, the first most largely in the serum of carnivora, and the second in that of herbivora, while both exist in about equal amounts in that of man. Both of these salts are the cause of the alkaline reaction of the blood, and as sodium carbonate is more alkaline than disodium phosphate, and as the former preponderates in the serum of herbivora, we have an explanation of the greater alkalinity of the blood of herbivora. As blood becomes more alkaline immediately after it has been shed, it has been supposed that an acid is formed at that time, which robs the sodium carbonate of a part of its base. Lastly, the serum contains the gases—carbonic acid, oxygen, and nitrogen (see Respiration).

We have now to consider the chemical composition of the *corpuscles.* The *colourless corpuscles* consist of protoplasm, the composition of which is little known.

Water, albumin, fat, lecithin, glycogen, lactic acid, and salts have been found in the white corpuscles. Pus corpuscles, which are colourless cells that have migrated from the blood in the inflammatory process, contain nuclein to the

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[1] Lutein gives an absorption band in the blue part of the spectrum. Bilirubin has been found in the serum of the horse and of calves.

extent of 2 per cent. See Vol. I. p. 78 and p. 210. Halliburton[1] has found the following proteids in lymph cells :—(1) a globulin coagulating at 48°—50° C. (cell-globulin α), (2) a globulin coagulating at 75° C. (cell-globulin β), (3) an albumin coagulating at 73° C. (cell-albumin), (4) mucin-like proteid rich in phosphorus, (5) mucin-like globules similar to those found in synovia and bile and in the cells of the submaxillary gland.

The *coloured corpuscles* are resolvable into a colourless *stroma* and into a reddish substance, the colouring matter, or *hæmoglobin*. The nature and chemical properties of hæmoglobin have already been fully described. (See Vol. I. p. 118.) Red blood corpuscles contain 60 per cent. of water and 40 per cent. of solids; of the 40 per cent. of solids no less than 39 per cent. consist of organic matters, chief of which is hæmoglobin, to the extent of 30 per cent. Further, we find about 1 per cent. of lecithin and cholesterin. The salts consist largely of potassium (·5 per cent.), calcium, magnesium (·15 per cent.), ·1 per cent. of chloride of potassium, and only traces of chloride of sodium. The chief acid is phosphoric acid (·2 per cent.), and this is combined chiefly with potassium, forming phosphates. The *stroma*, at ordinary temperatures, is insoluble in weak alkaline solutions. At 60° C. it dissolves. The nuclei consist of an albuminous matter having the chemical characters of mucin.

It is of practical importance to determine the amount of hæmoglobin present in a given specimen of blood. One method has already been described. (See Vol. I. p. 122.) Those usually followed by physicians are founded on the principle of comparing the colour of the blood, diluted with measured quantities of water, with a solution representing in tint a fixed quantity of hæmoglobin. One of the most convenient appliances for this purpose is the *hæmoglobinometer* of Gower, shown in Fig. 95. The following is a description of the apparatus and method :—

The *colour* of a dilution of average normal blood one hundred times is taken as the standard, and the quantity of hæmoglobin as indicated by the amount of distilled water needed to obtain this tint is taken as the standard of hæmoglobin. As a solution of hæmoglobin could not be preserved (decomposition soon taking place), glycerine-jelly tinted to the requisite extent is taken as a substitute. The two glass tubes D and C have the same capacity; the one, D, contains jelly tinted to that of a dilution of 20 c.mm. of blood in 2 c.cm. of water, that is, 1:100. The other tube, C, is graduated so that 100° = 2 c.cm (that is, 20 c.mm. × 100). The blood (20 c.mm) is measured by the capillary pipette B. This blood is placed in tube C, and a little water is added. Distilled water is then added by the dropper-bottle, A,

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[1] W. D. Halliburton, *Brit. Assn. Reports*, 1887; *Proceedings of Royal Society*, 1888.

until the tint of the fluid in C is the same as that of the standard D. As average human blood gives the required tint when diluted 100 times, the number of degrees necessary to produce the tint with the blood under examination is the percentage proportion of hæmoglobin, compared with the normal amount. Thus, if 20 c.cm. of blood give the standard tint at 30° of dilution, the blood contains 30 per cent. of the normal amount of hæmoglobin (average 13·3 per cent.). Gower states that "the instrument is only expected to yield approximate results, accurate within 2 or 3 per cent."[1]

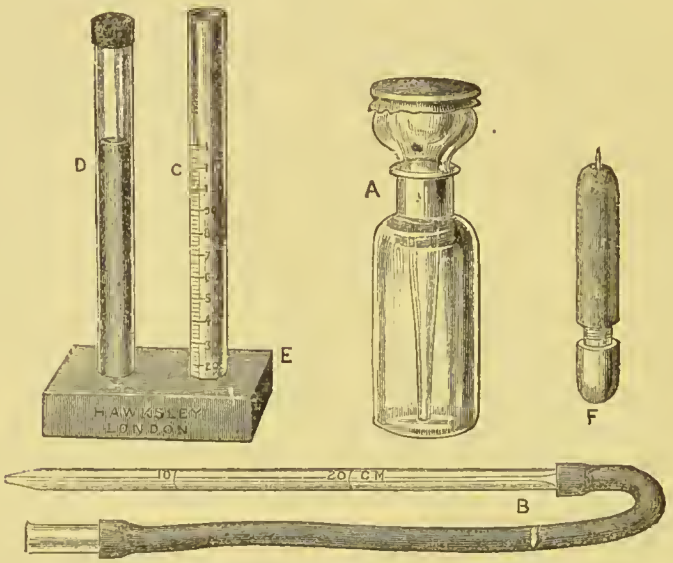

FIG. 95.—Gower's Hæmoglobinometer. A, bottle with pipette stopper for holding the diluting solution; F, puncturing needle; B, capillary pipette for measuring the blood; D, standard tint of normal blood; C, graduated tube for measuring the amount of hæmoglobin. E, wooden stand for D and C.

The blood of men contains from 13 to 15·7 per cent. (14·5 average) and of women from 12 to 13·7 per cent. (13·3 average) of hæmoglobin. About 10 per cent. exist in the blood of the dog, sheep, ox, and rabbit, and as much as from 15·6 to 17·6 per cent. in the blood of birds, such as the hen, duck, goose, and pigeon. It is of importance to note the amount of iron existing in the blood. In 100 grms. of human blood, taking the mean of 11 cases (men and women), we find ·05455 grms. of iron and 13·083 grms. of hæmoglobin. Taking the blood as amounting to $\frac{1}{14}$th of the body weight, it will weigh 4535·9 grms. Then $\frac{4536 \times 13·083}{100} = 593·44488$ grms. of hæmoglobin in the blood. To obtain the amount of iron: $\frac{4536 \times ·0546}{100}$ $= 2·476656$, or about 2·48 grms. (= 38·27 grains avoird.) of iron in the total blood. In this connection it may be mentioned that the amount of pure iron in 25 minims of the *Tinctura Ferri Perchloridi* of the Pharmacopœa, is about 1 grain.

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[1] A *hæmochromometer* has been constructed by Malassez on a similar principle, by which the richness of hæmoglobin can at once be read off in milligrammes. V. Fleischl has also invented an instrument on a somewhat different principle. Gower's method is simple, and easy of application.

The *number* of red blood corpuscles can be readily ascertained by the use of Gower's *Hæmacytometer*, Fig 96. It consists (1) of a small pipette holding 995 c. mm., A ; (2) a capillary tube, B, holding 5 c. mm. ; (3) a glass, D, for diluting the blood: (4) a glass spatula for stirring, E, and a brass stage plate bearing a glass slip, in which has been cut a cell $\frac{1}{5}$th mm. deep, C. The bottom of the cell is divided into $\frac{1}{10}$ sq. mm. A diluting solution of specific gravity 1025 is prepared by dissolving sulphate of soda in distilled water. The process is as follows :—995 c. mm. of sulphate of soda solution is placed by pipette, A, in mixing glass, D, 5 c. mm. of blood are drawn by pipette, B, from a puncture in the finger, made by the needle, F, and blown into mixing glass, D. The fluids are well mixed by stirrer, E, and a drop is placed in the cell, and a cover glass placed over it. The squares are examined under the microscope. The number of corpuscles in ten squares is then counted, and this multiplied by 10,000 gives the number of corpuscles in 1 c. mm. of blood. Each square is $\frac{1}{10} \times \frac{1}{10}$ mm. in area $= \frac{1}{100}$ sq. mm., and each square is $\frac{1}{5}$ mm. deep ; therefore the cubical content of one square $= \frac{1}{100} \times \frac{1}{5} = \frac{1}{500}$ c. mm. Therefore the number of corpuscles in 1 c. mm. of diluted blood = 500 times the number counted in one square = 50 times the number in 10 squares. But the blood is diluted 200 times ; therefore to find the number of corpuscles in 1 c. mm. of *undiluted* blood, we must multiply the number in 1 c. mm. of diluted blood by 200 ; therefore the number of corpuscles in 1 c. mm. of undiluted blood $= 50 \times 200 = 10{,}000$, the number seen in 10 squares. The average number of red corpuscles in healthy blood is 5,000,000 per c. mm., and blood of this richness will give 100 as the average number of corpuscles in two squares. Two squares contain ·00002 c. mm., and this may be taken as the hæmic unit. The number of corpuscles in two squares of any given specimen of blood (counting the corpuscles in 20 squares

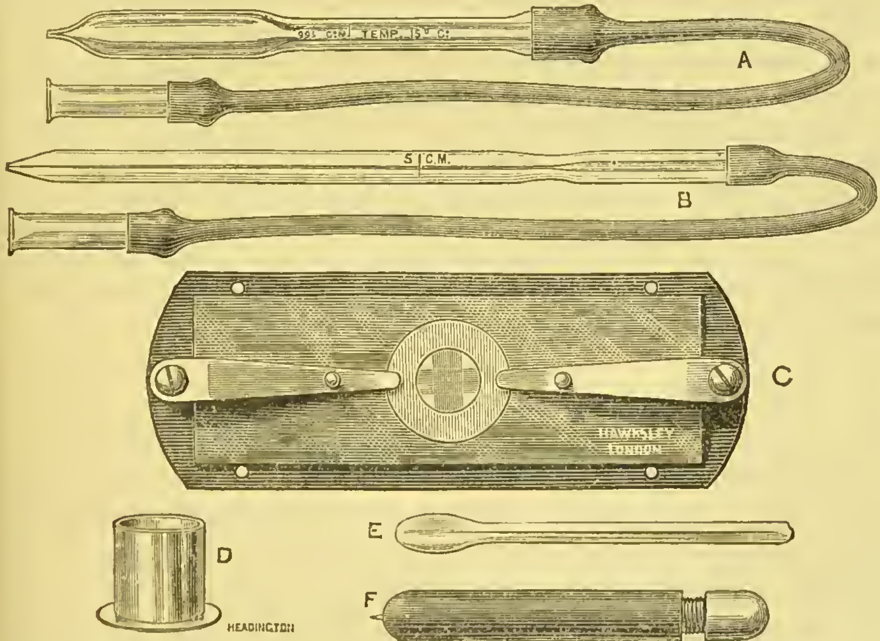

FIG. 96.—Gower's Hæmacytometer. A, pipette for measuring the diluting solution ; B, capillary tube for measuring the blood ; C, cell with divisions on the floor, mounted on a slide, to which springs are fixed to secure the cover glass ; D, vessel in which solution is made ; E, spatula for mixing blood and solution ; F, guarded spear-pointed needle.

and taking the mean) expresses the percentage proportion of corpuscles to that of health. The proportion of white corpuscles to the red, or the number per hæmic unit is best ascertained by observing the number of squares visible in the field of the microscope, and noting the number of white corpuscles in a series of 10 or 20 fields. The number of red corpuscles corresponding to the 10 or 20 fields is easily computed, and thus the proportion of white to red is ascertained. The normal *maximum* of white per two squares (hæmic unit) is ·3 (Gower).

As already mentioned, the average number of red blood corpuscles per 1 c. mm. of human blood in the male is 5,000,000. In the blood of women, the number is about 4,500,000. In some diseases the number may be reduced to 3,000,000 or 2,000,000, and in pernicious anæmia it may be as low as 500,000. The number is increased about one or two hours after a meal. The smaller the size of the blood corpuscles, as a rule, the greater is their number. Thus the blood of a goat has been found to contain 10,000,000 per c. mm. The number is diminished by bleeding. Malassez has estimated the number of corpuscles per 1 grm. of body weight, and termed the ratio the *corpuscular capacity*. In man this is about 341,000,000, that is, that number per gramme of body weight. He gives the total number as 22·5 milliards, that is 22·5 times 1,000,000,000, or 22·5 billions. Others have given the number in man at 25,000,000,000, that is 25 billions, and in the horse at 100,000,000,000 (one hundred billions). Taking the superficies of each corpuscle in man as $\frac{128}{1000}$ sq. mm., the total superficial area of the blood corpuscles amounts to about 2,880 sq. metres, that is the area of a square, each of whose sides is about 54 metres (about 59 yards square). This enormous surface is of much significance in connection with the respiratory functions of the coloured corpuscles. It will be evident also that the superficial area is much increased by subdivision of the corpuscles into smaller and smaller bodies. Hence in animals, in the blood and tissues of which respiratory processes are slow, we find a smaller number of large corpuscles (amphibians), while in those in whom respiratory processes are active, the corpuscles are small and numerous (birds, etc.). The weight of a coloured blood corpuscle is ·00008 milligramme ($\frac{1}{800000}$ of a grain). The volume is about ·00000072 or $\frac{7}{10}$ millionths of a cubic millimetre. The specific gravity of a red corpuscle is 1105, considerably above that of the plasma.

Chap. IV.—THE COAGULATION OF THE BLOOD.

This phenomenon has already been generally described, and we shall now consider some of the conditions that affect it, the nature of the process, and the theories that have been offered to explain it. The rapidity of coagulation varies in different animals. It is so rapid in birds that the blood of a pigeon, for example, clots almost immediately when it is shed. On the other hand, coagulation occurs in about fifteen minutes in the blood of a horse, in eight or ten minutes in that of an ox or pig, in four or five minutes in that of a dog, and in two or three minutes in human blood. The blood of the chick does not coagulate till about the twelfth or fourteenth day. The process is accelerated by the following influences:—(1) the presence of oxygen; (2) a temperature a little above that of the blood; and (3) contact with foreign bodies. The free access of air favours the change. This may be observed by contrasting the time required when the blood is collected in a flat vessel with that necessary in tubes or deep cylindrical vessels with narrow mouths. Blood will coagulate *in vacuo*, but the change is delayed if precautions are taken to avoid agitation and to have the temperature of the vessel nearly that of the blood in the vessels. On the other hand, the process is retarded:—(1) by the absence of oxygen; (2) by a temperature below zero or above 60° C.; (3) by saturation of the blood with carbonic acid; and (4) by the addition of neutral salts, such as sulphate of soda, carbonates of soda and potash, nitrate of potash, and the alkaline chlorides. A mixture of one volume of a concentrated solution of sulphate of soda or of sulphate of magnesia, with 3·5 volumes of horse's blood, prevents coagulation, and permits of the separation of the plasma from the corpuscles. To allow the plasma to form a clot in these circumstances, two or three times its volume of water should be added. Coagulation may also be delayed for a considerable time, so as to secure separation of the coloured corpuscles from the *liquor sanguinis*, by collecting blood from a horse in a tall vessel, surrounded by ice. The *liquor sanguinis*, thus obtained tolerably pure, on being removed from the vessel by a pipette, and submitted to ordinary temperatures, speedily coagulates into a translucent yellowish jelly. If frog's blood be collected in a two per cent. solution of sugar, and filtered, coagulation will be prevented, and a plasma containing only few corpuscles will be obtained.

In normal circumstances, coagulation does not take place whilst the blood is circulating through the vessels. It would thus appear that the living walls of the vessels prevent the change, a fact first shown by Hewson about 1772. Whilst the blood is in the vessels, many of the conditions, such as movement, friction, and temperature, are the same as those which favour coagulation when the blood is removed from the body; but in normal circumstances, in addition to these conditions, the blood is in contact with *living tissue*. For example, if a ligature be tied round the base of a frog's heart while it is pulsating (and under favourable circumstances it may continue pulsating for several days), the blood will remain fluid in the beating heart, but if the heart be punctured, the drop of blood that oozes out will quickly coagulate. Further, Brücke showed that the blood, thus isolated in the pulsating heart of the turtle, will remain fluid for days, but if a glass rod be introduced into the ventricle by the aorta, clotting will quickly take place on the glass rod. Brücke supposed that the living wall of the vessel had a restraining influence on a spontaneous tendency of the blood to coagulation; but Lister maintained that there was no such tendency, and that coagulation was caused by contact with a foreign body. In these cases the blood was agitated by the beat of the heart, and it might have been supposed that this condition was unfavourable to coagulation, but it has been ascertained that blood will remain fluid for hours in a portion of an artery or vein, isolated between two ligatures. When the vessel dies, in an experiment of this kind, coagulation soon occurs. Blood coagulates more slowly even in dead vessels than when collected in a glass tube. When we open the vessels of a dead animal, the blood is usually found coagulated, but occasionally blood may remain fluid for a lengthened period, even in dead vessels. Nor does the blood coagulate in the smaller vessels immediately after death. It may remain fluid for hours. Coagulation first commences in the heart and larger vessels, then in those of intermediate size; whilst in the smallest, decomposition may set in without any previous stage of coagulation. Foreign bodies introduced into the current of the circulation may become covered with a layer of fibrin, and it is well known that this may also occur on any surface roughened by inflammatory deposit either on the valves of the heart or in the interior of vessels. In some pathological states, also, there is a tendency to coagulation in the cavities of the heart, or in the vessels, leading to the formation of a *thrombus*, and a portion of this detached and whirled off by the stream of blood constitutes an *embolus*. It is not uncommon to find in the cavities of the heart large masses of fibrin of a pale colour, and often darker in tint in the most dependent part. These appearances are produced by the blood coagulating so slowly that there is time for the corpuscles to sink.

Up to the end of the 18th century, a blood clot was held to be made up of corpuscles only. Then Hewson, in 1772, advanced the view that a substance called fibrin was dissolved in the blood, and in some transudations from the blood, and that in certain conditions it coagulated to form a clot. In 1845, Professor Andrew Buchanan, of the University of Glasgow, first indicated that at least two substances were necessary for the production of fibrin, by demonstrating that certain fluids (such as that from a hydrocele), which do not coagulate spontaneously, undergo this change when a morsel of clot, or fluid expressed from the clot (serum), or a bit of muscle or of membrane, are added to it. Buchanan also recognized that two fluids, serum and hydrocele fluid, neither of which coagulates spontaneously, will form a coagulum when mixed together. He pointed out that if washed blood clot, which is a mixture of fibrin and colourless corpuscles, be added to hydrocele fluid, coagulation will occur, and he compared the action of washed clot to that of rennet in coagulating milk. He further found that the buffy coat of blood has strong coagulating properties, and he advanced the view that in blood plasma there is a substance which he termed soluble fibrin which, when acted on by the colourless blood corpuscles, produced fibrin. It will be seen later how near these views were to the truth. Since that date, numerous researches by Schmidt and others have supported Buchanan's theory: the elements of fibrin have been obtained analytically, and they have been synthetically combined to form fibrin.

In 1859, Denis mixed blood with a saturated solution of sulphate of soda, thus preventing coagulation. The corpuscles sank towards the bottom, and the salted plasma was decanted off. To the salted plasma, common salt was added until a whitish, cloudy precipitate fell. If this precipitate termed *plasmine* is re-dissolved in water, a coagulum quickly forms; and, according to Denis, plasmine divides into two parts, one forming a clot, true fibrin, and the other remaining in the plasma which he terms soluble fibrin. On the removal of the *plasmine of Denis* from the blood plasma, the latter loses the tendency to coagulation. It would therefore appear that the formation of fibrin depends on some change occurring in this substance. The question arises as to whether or not the plasmine of Denis is itself a simple substance.

Alexander Schmidt, in many researches dating from 1861, made important contributions to the subject. Recognizing that fibrin did not exist as such in the blood, he discovered what may be termed the parent substance, to which he gave the name *fibrinogen*, and he pointed out that it belonged to the globulin group of albuminous bodies. It is precipitated from plasma if we add to the latter several times its volume of a concentrated solution of sulphate of magnesia. Insoluble in water, it is readily soluble in a 10 per cent. solution of common salt, and in dilute alkalies, and in dilute solutions of carbonates of the alkalies. Schmidt also corroborated Buchanan's observation that the fluids of many transudations into serous sacs apparently spontaneously coagulate, if a drop of defibrinated blood is added to them, and he showed that fibrinogen also exists in these fluids. He further supposed that the defibrinated blood, or blood serum, contained another body which, by acting on fibrinogen, produced fibrin. To this substance he gave the name of *fibrinoplastin*, and after separating a substance he believed to be this body, he found it was also a globulin. The theory of Schmidt, as first promulgated, then was that fibrin is formed by the union of two fibrin-factors, fibrinogen and fibrinoplastin. He soon found, however, that occasionally both these bodies may be present in a fluid and yet coagulation may not occur, and it was seen that a third body was necessary, termed a *fibrin-ferment.* We shall now shortly consider the chief physical and chemical characters of the substances involved.

1. **Fibrin.**—We may readily obtain this substance by washing a blood clot, or by switching some blood with a bunch of twigs. It consists of white, structureless filaments, insoluble in water, alcohol, or mineral acids; soluble in lactic, phosphoric, and acetic acids; also soluble in potash, solutions of alkaline salts, and in a $\frac{1}{10}$th per cent. solution of common salt. It is decomposed by oxygenated water, splitting up into various substances. In 1874, Landois showed that a kind of fibrin is formed by disintegration of the stroma of red corpuscles. This stroma-fibrin is to be distinguished from the fibrin that forms the fibrous basis of blood clot.

2. **Fibrinogen.**—If some hydrocele fluid, diluted with 15 times its bulk of water, which coagulates on the addition of a little serum or defibrinated blood, is treated with common salt or, after large dilution, with a stream of carbonic acid, a precipitate is obtained, on the removal of which the fluid will not coagulate on the addition of serum; but if the precipitate is added to serum, a coagulum is formed. This substance is fibrinogen. It does not exist in blood serum but in blood plasma and chyle and lymph. It may be also thrown down from a serous fluid by the addition of powdered chloride of sodium. It coagulates at 56° C.

3. **Fibrinoplastin,** sometimes also termed *serum-globulin* or *paraglobulin.*—This exists to the extent of from 2 to 4 per cent. in the blood. The passage for a time of a stream of carbonic acid through serum diluted with twenty times its bulk of ice cold water throws down an amorphous precipitate of this substance. When collected and dried it forms a light granular powder. It may also be precipitated from diluted serum by neutralization with acetic acid—25 drops of a 25 per cent. solution of acetic acid to 120 cc. of dilute serum. The whole of it, however, is not precipitated by either method, and Hammersten showed that the remainder will be thrown down from serum by adding crystals of sulphate of magnesia to the point of saturation. As to the total amount, 100 cc. of serum of ox blood yield ·7 to ·8 grm., and of horse's blood ·3 to ·5 grm. of fibrinoplastin. The temperature of coagulation is about 75° C.

Both of these bodies are *globulins,* soluble in weak solutions of common salt, but precipitated by the salt in excess. Very weak hydrochloric acid converts them into a body like syntonin.

4. **Fibrin Ferment.**—Schmidt's method is as follows: Add to the serum of ox blood 20 times its volume of strong alcohol and set it aside for one month. Filter off the deposit, consisting of the ferment and insoluble albumin. This may be dried over sulphuric acid and powdered. Mix 1 grm. of the powder with 65 c.cm. of water, and filter after 10 minutes. The ferment alone appears in the filtrate. Gamgee has shown that if washed clot is digested in an 8 per cent. solution of common salt, a strong fermentive fluid is obtained. When fibrinoplastin is precipitated, the ferment is carried down with it. The ferment is destroyed at 70° C.

Arthur Gamgee was the first to make a careful examination of the true nature of the ferment,[1] and he established the points (1) that it is insoluble in distilled water, (2) that it is readily soluble in weak solution of chloride of sodium, and (3) that removal or precipitation of the globulins (by dialysis or saturation with magnesium sulphate) diminishes the activity of ferment solutions.

5. **Saline Matters.**—If fibrinogen, fibrinoplastin, and the ferment are deprived of salts, and dissolved in a very dilute solution of caustic soda, a coagulum will not be formed until common salt has been added to the extent of making a 1 per cent. solution of this salt. A small amount of sulphate of calcium produces the same result (Green). Hence it would appear that in the formation of fibrin, common salt (or some other saline substance) is necessary.

Thus it may be demonstrated: (1) that a fluid containing fibrinogen alone, such as hydrocele fluid, will not coagulate spontaneously; (2) that a fluid containing fibrinoplastin or paraglobulin alone, will not coagulate spontaneously; (3) that fluids from which either of the substances has been removed will not coagulate on the addition of the other substance, or of the fluid which contains it; (4) that occasionally both fibrinogen and fibrinoplastin may be present in a fluid and still coagulation may not take place; (5) that the addition of washed clot or of a solution of the fibrin ferment prepared as above quickly causes coagulation in a fluid containing the other factors; (6) that if the fluid supposed to contain the fibrin ferment is heated above 70° C. it may be added to the fluid containing the fibrin factors without exciting coagulation; and (7) that saline matters, and especially common salt, play a part in the process.

Many theories have been advanced to explain the process. As we have seen, Buchanan, who first aroused attention to this subject, took the view that fibrin

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[1] Gamgee. *Jl. of Anat. and Phys.* vol. ii. p. 145.

is formed from a soluble fibrinous body acted on by something in the colourless corpuscles, like the action of rennet in coagulating milk. Then came the more complicated view of Schmidt that two bodies took part in the process, but that they had to be wedded to form fibrin by the action of a third body, the ferment. Later, Hammersten went back to something like Buchanan's opinion that only one body was necessary, namely, fibrinogen, present in plasma, but acted on in the plasm in coagulation by the ferment so as to form fibrin, thus explaining why fibrinogen is absent from serum. The question next arises, What is the origin of these bodies? Schmidt held that all three factors are derived from the disintegration of colourless blood corpuscles. In the vessels, the blood is rich in these corpuscles (at least 15,000 per cub. mm.), but one can conceive that when the blood is shed large numbers of these at once disintegrate. Schmidt asserts that no less than 71·7 per cent.. of the white corpuscles thus disappear from the blood of the horse at the moment of coagulation. In this way then we can account for the three substances, fibrinoplastin, fibrinogen, and the ferment. Another view in entire opposition to that of Schmidt and his followers has been urged by L. C. Wooldridge.[1] He states that the white corpuscles are not necessary to coagulation, and that if they play any part at all it is a very insignificant one. After criticising the method of Schmidt for the separation of the colourless corpuscles, he points out that Schmidt did not take into account the granular matter found along with the corpuscles, which was assumed to be merely débris of corpuscles. Adopting the important observation of Fano that peptones introduced into the blood prevent coagulation in the usual way, Wooldridge injects peptone into the jugular vein of a dog, bleeds the animal, and separates the plasma by a centrifugal machine. The peptone-plasma "is spontaneously coagulable, for it coagulates when a current of CO_2 is passed through it, or when it is neutralized by other acids, *e.g.*, acetic acid. It also clots on dilution with water, or, though much less readily, with $\frac{1}{2}$ per cent. NaCl solution. Further, filtration through a clay cell will cause coagulation to a certain extent. These processes cannot be regarded as 'fibrin factors' in the ordinary sense of the word." He then finds that the process of cooling adopted by Schmidt and others removes from the plasma a substance which is of great importance in initiating coagulation. The next point he brings forward is that a weak salted plasma (1 vol. of dog's blood to 1 vol. of an 8 or 10 per cent. solution of NaCl) is always spontaneously coagulable, and retains this power in spite of long cooling, while a strong salted plasma (2 vols. of a half-saturated solution of $MgSO_4$ to 3 vols. of blood) does not coagulate spontaneously on dilution, and he infers that centrifugalized peptone-plasma, free from corpuscles, is spontaneously coagulable owing to the presence in it of a substance which can be removed "by cooling and by adding sulphate of magnesia of a certain strength." Wooldridge thus endeavours to eliminate the formed elements or corpuscles from the process, and it is clear that if plasma will coagulate when no cellular elements are present, the cause of coagulation must be looked for in the plasma itself. He then shows that leuco-

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[1] L. C. Wooldridge, *Report to the Scientific Committee of the Grocers' Company.* Section I. *The Nature of Coagulation.* The copy which Dr. Wooldridge sent me is marked "*under revision.*" A bibliography of his papers on the subject is given on p. 2. The above criticism was written before the lamented death of Dr. Wooldridge.

cytes from lymph glands when added to peptone-plasma soon cause clotting, that the amount of clotting bears a quantitative relation to the quantities of leucocytes used, and that this occurs without destruction of the leucocytes, as these can still be found by the use of the microscope. Next, he shows that although not altered morphologically the leucocytes do undergo a change, for if they have already caused clotting in strong plasma, they cannot cause it in weak plasma. He then found that injecting large quantities of washed leucocytes into the jugular veins of a dog did not produce clotting in the vessels, and he argues that clotting cannot be due to the death of leucocytes seeing "that extravascular plasma clots readily with dead isolated leucocytes, while intravascular plasma will not do so." Wooldridge attaches much importance to the interactions that take place between the colourless cells and the plasma, and the substance in the colourless cell which is the prime factor in coagulation is, in his opinion, lecithin. He finds that the addition of this substance causes coagulation. Thus, when the blood of a dog is received into a thick emulsion of lecithin, coagulation occurs more rapidly than when it is received into a considerable quantity of saline solution. If this substance diffuses into the blood, coagulation takes place, and it may be supposed that the action of peptone in arresting or delaying coagulation is that it interferes with the separation of lecithin. To put the theory in another form, in the plasma there are three ferment factors A, B, and C, fibrinogen. A and B fibrinogen are compounds of lecithin and proteid, and fibrin is produced by taking lecithin from A and giving it to B. C fibrinogen is also a compound of proteid with lecithin, and it is what has usually been known as fibrinogen.

The subject has also been ably investigated by Halliburton,[1] who strongly opposes the theory advanced by Wooldridge. He has arrived at the conclusion that the fibrin ferment is a globulin, derived from the disintegration of the white blood corpuscles and identical with cell-globulin, the chief proteid in the cells of lymphatic glands. His final statements are as follows : "(1) Lymph cells yield as one of their disintegration products, a globulin, which may be called cell-globulin. This has the properties that have hitherto been ascribed to fibrin ferment. (2) Fibrin ferment as extracted from the dried alcoholic precipitate of blood serum is found on concentration to be a globulin with the properties of cell-globulin. (3) The fibrin ferment as extracted by saline solutions from blood-clot is a globulin which is also identical with cell-globulin. (4) Serum-globulin as prepared from hydrocele fluid has no fibrino-plastic properties. It may be better named plasma-globulin. (5) Serum-globulin as prepared from serum has marked fibrinoplastic properties. This is because it consists of plasma-globulin, mixed with cell-globulin derived from the disintegration of white blood corpuscles, which are in origin lymph cells. (6) The cause of the coagulation of the blood is primarily the disintegration of the white blood corpuscles ; they liberate cell-globulin which acts as a ferment converting fibrinogen into fibrin."

It is impossible in this work to deal at length with the arguments and experiments adduced by Halliburton against the theory of Wooldridge. The chief are (1) that the lecithin employed was impure and that any finely divided foreign matter will hasten coagulation, and (2) that lecithin does not cause clotting "of pericardial fluid, of hydrocele fluid, of solutions of Hammersten's fibrinogen, of

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[1] W. D. Halliburton, "On the Nature of Fibrin Ferment." *Jl. of Physiology*, vol. ix. No. 4, p. 229.

dilute salted plasma, nor does it hasten the coagulation of pure plasma obtained by the living test tube experiment" (*i.e.*, retaining blood in a portion of living vessel between two ligatures). After carefully considering the question at issue, I feel bound to say that the evidence lies against Wooldridge's view. His method is open to the great objection that the peptone-plasma, on the reactions of which he relies, is abnormal plasma. Further, it has been satisfactorily demonstrated that fibrin ferment (produced from lymph corpuscles) contains no lecithin and still it causes coagulation in pure plasma and causes the formation of fibrin from Hammersten's fibrinogen. It is said that the latter contains no lecithin and it is admitted that fibrin ferment contains no lecithin, and yet fibrin is formed by the action of the one upon the other. We must, therefore, on the evidence adduced by these able investigations, accept the view that the formation of fibrin is due to the action of the fibrin ferment, cell-globulin, upon fibrinogen, and that both originate from colourless corpuscles of the blood. This is by no means the last word on the subject, as we know little or nothing of the conditions that cause the rapid destruction of colourless corpuscles antecedent to the formation of fibrin, nor can we explain why intravascular clotting is so rare an occurrence.

Chap. V.—THE QUANTITY OF BLOOD IN THE BODY.

Many methods have been employed for determining the quantity of blood in the body, but the most reliable is the colorimetric method of Welcker.

The animal is bled to death and the blood collected (a). The nozzle of a syringe is then introduced into a large vein and distilled water is injected until a colourless fluid flows from the vessels. The coloured washings are collected (b). The tissues and organs are cut into small pieces and washed with distilled water until not a trace of colour can be seen in the water used. These washings are also collected (c). The three fluids, a, b, and c, are now mixed, with the exception of a small portion of a (which we may term y) and the mixture may be designated x. Some of the original blood y is now mixed with distilled water until it has the same tint as x. We now know the quantity of distilled water added to the known portion y, the quantity of blood collected, and the quantity of water thrown into the veins, and from these can be determined the total quantity of blood less the first portion y, and the addition of these two figures gives the total quantity of blood. Gscheidlen has improved the method in several respects. In the first place he treats the blood with carbonic oxide so as to transform all the oxyhæmoglobin into carbonic-oxide-hæmoglobin, a more stable compound and having a tint more easily compared, because the tint of blood containing oxyhæmoglobin varies according to the amount of oxygen in it. He dilutes 2 cc. of defibrinated blood with 98 cc. of distilled water and treats this with carbonic oxide. This is placed in a vessel with parallel glass sides. A canula is now introduced into the carotid artery, and the vessels are washed out with a ·5 or ·6 per cent. solution of common salt under a feeble pressure, until the fluid flows colourless from the two jugulars and the inferior vena cava. The stomach and intestinal canal are emptied and all the organs and tissues are divided into small portions and treated with distilled water. At the end of twenty-four hours, the coloured water is poured off and the tissues are submitted to pressure so as to obtain all the fluid. This fluid is filtered, mixed with the washings of the vessels, and the mixture is treated with carbonic oxide. The washings are thoroughly mixed and a portion is placed in a vessel with parallel sides, A. Some of the first mixture of blood and distilled water B, say 1 cc., is placed in a vessel with parallel sides, and water is added from a burette until the tint of B is exactly that of A. Thus, suppose 100 cc. of blood were collected from vessels of animal (a), that 1 cc. of this is diluted with water to 100 cc. to make test (b), that the washings of the vessels amount to 200 cc. (c), that the washings of the tissues amount to 150 cc. (d), or the total washings to 350 cc. (e), that is ($c+d$), and that 50 cc. of water had to be added to 2 cc. of b to make the tint that of e. Call the latter mixture x. Then 50 cc. of x contain hæmoglobin equal to ·02 of blood. It follows that $\frac{350 \times \cdot 02}{49 \cdot 98} = \cdot 14$ cc. of blood (or hæmoglobin) in the washings. This added to the blood first collected gives 100·14 cc. as the total quantity of blood in the animal's body.

Another method applicable to a living man has been devised by Tarchanoff. The man is subjected to a Russian bath so as to cause profuse perspiration, and the amount of hæmoglobin in the blood is determined before and after the bath. Let p be the quantity of water lost by the blood, a the quantity of hæmoglobin in milligrammes in 1 cc. of blood before the bath, a^1 the quantity after the bath, x the total volume of the blood to be determined, then $xa =$ the total amount of hæmoglobin before and $(x-p)a^1 =$ the total quantity after the bath. Then $xa = (x-p)a^1$, or $x = \frac{pa^1}{a^1 - a}$; x will then represent in cubic centimetres the total volume of blood.

The method of Welcker, as carried out by many observers, has given the following general results: The ratio of the amount of blood in man and in the ox, to the body weight, is as $\frac{1}{13}:1$; in the cat, $\frac{1}{14}:1$; in the horse, $\frac{1}{15}:1$; in the rabbit and guinea-pig, $\frac{1}{19}:1$; in the pigeon, $\frac{1}{16}:1$; in the common fowl, $\frac{1}{12}:1$; and in the frog, $\frac{1}{17}:1$. In the newly-born child, $\frac{1}{19}:1$; in young whelps, $\frac{1}{17}:1$; and in kittens, $\frac{1}{18}:1$. In dogs, during pregnancy, the ratio of $\frac{1}{10}:1$ has been observed.

If the amount of blood is diminished by bleeding, the loss is quickly made up in a healthy animal. Thus Munk quotes an experiment of Tolmatscheff in which a dog, weighing 11·5 kilogs., during a period of seventy-one days, had as much blood removed by repeated bleedings, at intervals of ten to eighteen days, as ·87 kilogs., equal to one-thirteenth of its body weight, but it was found that the weight of its body, and the amount of hæmoglobin in its blood increased, between the first, third, and fourth venesections, although the amount of food it received was the same throughout the experiment. In this case, the dog must have produced in seventy-one days as many corpuscles as he lost. Again, four-seventh's of the total blood have been removed from a dog, and in thirty-four days the number of corpuscles was the same as at first. Colin states that horses have been known to lose twenty-five kilogs. of blood in eight days without any apparent injury.

SECTION IV.

THE CIRCULATION OF THE BLOOD.

The blood is contained during life in a continuous system of more or less elastic and contractile vessels. These are (1) the *arteries*, terminating in (2) the *capillaries*, from which originate (3) the *veins*, whilst a contractile organ (4), the *heart*, is placed at the commencement of the arteries and the termination of the veins. The general arrangement is seen in Fig. 97.

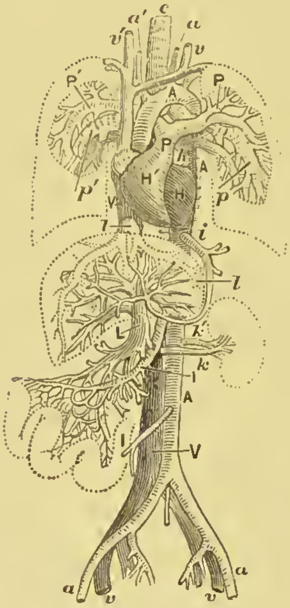

Fig. 97.—Diagram showing generally the course of the circulation and some of the principal vessels; H′, right ventricle; H, left ventricle; A, A, A, aorta; *h*, part of left auricle; P, pulmonary artery going to lungs; V, ascending or lower vena cava; *e*, trachea or windpipe; *a′*, *a*, right and left carotid arteries; *v′*, *v*, veins from root of neck (internal jugular and subclavian) joining to form descending or upper vena cava; *i*, hepatic artery; *l*, hepatic vein; I, superior mesenteric artery going to mesentery and bowels; L, portal vein going to liver; *k′*, renal artery; *k*, renal vein; V, inferior vena cava formed from the two iliac veins, *v*, *v*. (Allen Thomson.)

The heart is a double organ, each half consisting of an auricle and a ventricle, the right half containing blood which has been returned from the body to be sent to the lungs, and the left half containing blood which has been returned from the lungs to be distributed to the body. There are thus two circulations, the one, *pulmonary*, from the right side of the heart, by the pulmonary artery to the lungs, through the capillaries of the lungs, and back to the left side of the heart by the pulmonary veins, and the other, *systemic*, from the left side of the heart, by the aorta, and the arteries which ramify from it, to the capillaries throughout the tissues, and thence by the veins to the right side of the heart. Thus the course of the circulation may be traced (1) from right auricle to right ventricle, through the right auriculo-ventricular opening, guarded by the *tricuspid* valve; (2) from right ventricle by pulmonary artery, through the capillaries of the lungs, to the pulmonary veins which open into the left auricle; (3) from left auricle to left ventricle, through the left auriculo-ventricular opening, guarded by the *mitral* valve; (4) from the left ventricle into the greater arteries, the medium-sized arteries, and the arterioles into the capillaries of the tissues and organs; and (5) from them by the veins, opening into larger and larger trunks so as ultimately to constitute the superior and inferior venæ cavæ, which open into the right auricle, the point from which we started. Remembering that the walls of these tubes are all more or less elastic, imagine them to be so filled with blood as to be distended. There would then be a condition of permanent tension, which would be varied if pressure were applied to any part of the system. Such a variation of pressure would produce a movement of the fluid in the direction of less pressure, and as the fluid cannot escape, there would be a *circulation*, which would be carried in one direction by mechanical arrangements of valves. In the living body, the contractions of the heart force blood into the arterial system so as to increase pressure in that part of the circulation; the arteries empty part of their contents into the capillaries, which carry the blood to the veins, so as to tend to an equalization of pressure between the venous and arterial systems; if the pressure in both systems became equal, there would be no circulation, but as the veins pour a portion of the blood back again into the heart, this organ, refilled, again contracts, forces more blood into the arterial system, again raising the pressure there, and thus prevents the possibility during life of an equalization of arterial and venous pressure. Thus the movement or circulation of the blood is carried on in a definite direction.

A. The Heart.

Chap. I.—PHYSIOLOGICAL ANATOMY OF THE HEART.

The form, position, and general arrangements of the heart are fully described in anatomical works, and it is only necessary here to allude to points of physiological importance. In Figs. 98 and 99 we have views of the anterior and posterior aspects of the heart, and in Fig. 100 the interior of the cavities is displayed.

The heart is a hollow muscular structure, of which the external surface is covered by a serous membrane, the *serous layer of the pericardium* or *epicardium*, whilst the interior is lined by another serous membrane, the *endocardium*, continuous with that of the blood-vessels. Enclosed in a membranous sac, the *pericardium*, the heart is placed behind the sternum and the costal cartilages, the base being directed upwards, backwards, and to the right, and extending from the level of the fifth to that of the eighth dorsal vertebra; the apex is directed downwards, forwards, and to the left, and in the living man may be felt beating in the space between the cartilages of the fifth and sixth ribs, a little below and to the inner side of the nipple. The heart, therefore, is placed obliquely in the chest, and it projects further into the left than into the right half of that cavity.

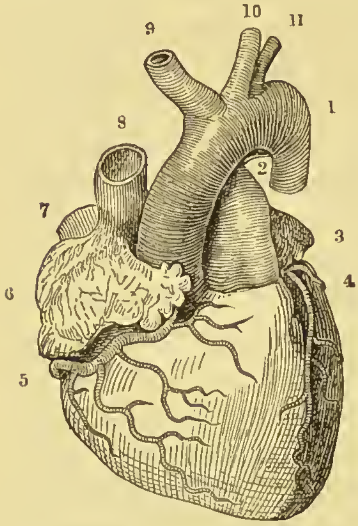

FIG. 98.—Heart in the condition of diastole, seen from the front. One-third natural size. 1, End of aortic arch; 2, tissue binding the aorta to the pulmonary artery; 3, left auricle; 4, anterior branch of the left coronary artery, running in the groove between the right and left ventricles; 5, right coronary artery; 6, right auricle; 7, inferior vena cava cut off short; 8, superior vena cava; 9, innominate artery; 10, left carotid; 11, subclavian. (Krause.)

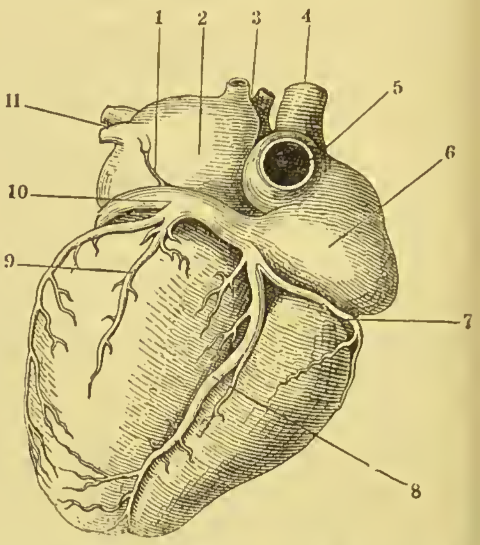

FIG. 99.—Heart in condition of diastole, with the veins injected and seen from behind. One-third natural size. 2, Left auricle; 3, right pulmonary veins; 4, superior vena cava; 5, inferior vena cava; 6, right auricle; 7, posterior branch of the right coronary vein, in the groove between the right auricle and the right ventricle; 8, small coronary vein; 9, branch on the posterior surface of the left ventricle; 10, great coronary vein; observe the entrance of a small vein from posterior surface of left auricle, 1; 11, left pulmonary veins. (Krause.)

The substance of the heart is composed of a special variety of muscular tissue, along with connective tissue, blood-vessels, lymphatics, nerves, and ganglia. The muscular fibres of the heart substance have already been described and figured. · See Vol. I. p. 312, and Fig. 172, p. 313. Cardiac fibres may be regarded as intermediate, both as to structure and function, between involuntary or non-striated muscle, and voluntary or striated muscular fibre. Underneath the endocardium in the sheep and ox, polyhedral clear cells exist containing granular protoplasm, usually containing two nuclei. These are known as *Purkinje's fibres* and are believed to be transitional forms of the cardiac muscular fibre. They are not found in man.

A large mass of fibrous tissue and fibro-cartilage (which in some animals, as the ox, is bony) is found at the base of the heart in the angle between the aortic and two auriculo-ventricular openings, and from it processes pass in various directions. These processes form the basis of the *fibrous* or *tendinous rings* of the auriculo-ventricular and arterial openings, and to these many if not all of the bands of muscular fibre are attached. These bands are arranged in layers. The embryonic heart is tubular and has an outer circular and an inner longitudinal layer of fibres. The tube is by longitudinal growth thrown into a folded or curved shape, and as the bend increases the venous is doubled back upon the arterial end, and the auricular cavity is placed dorsally and to the left of the ventricular part. Still later, there is the division of each original single cavity of the ventricle and auricle into two compartments by the formation of the septum. Hence some of the fibres must be common to the two auricles, whilst others belong to the two ventricles. The primitive arrangement persists in the auricles, but in the ventricles the layers become twisted in a spiral manner and appear more complicated. The fibres of the auricles are completely separated from those of the ventricles by the fibro-cartilaginous rings above mentioned; they are in two layers, an outer transverse passing over both auricles and an inner longitudinal, for each auricle. The outer transverse may be traced from the openings of the venous trunks, whilst there are circular layers of striated muscle around the orifices of the great veins, more especially around the superior vena cava. Similar circular fibres surround the pulmonary veins, and in man these may be traced to the hilum of the lung. According to Pettigrew, there are seven layers of fibres forming the wall of each ventricle, namely, three external, a fourth or central, and three internal, and they are so arranged that the first or outer external layer is continuous with the seventh or inner internal layer, the second with the sixth, and the third with the fifth. Ludwig describes a simpler arrangement: (1) an *outer* longitudinal layer extending from the base where the fibres are attached to the tendinous structures around the orifices, and passing obliquely to the apex where

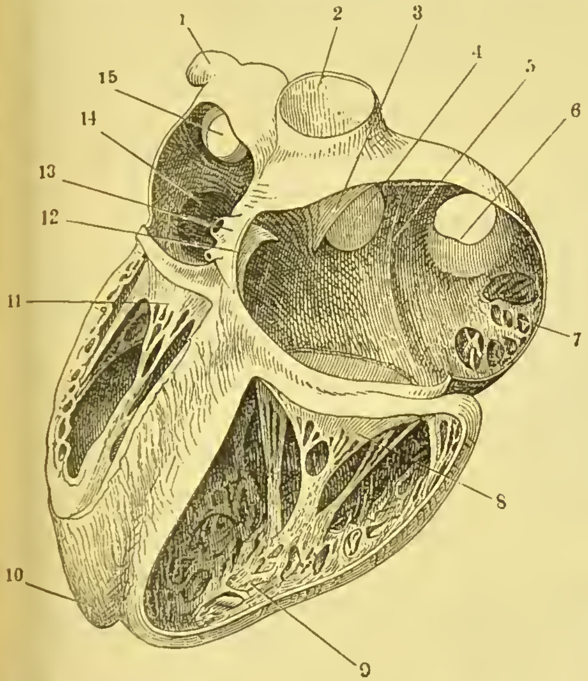

FIG. 100.—View of the cavities of the heart opened from behind. Half natural size. 1, Left superior pulmonary vein; 2, inferior vena cava; 3, Eustachian valve; 4, fossa ovalis; 5, tubercle of Lower; 6, superior cava; 7, right auricle; 8, tricuspid valve, with *musculi papillares* and *chordæ tendineæ*; 9, *trabeculæ* in right ventricle; 10, apex of heart, left ventricle; 11, bicuspid or mitral valve; 12, *valvulæ Thebesii*; 13, great coronary vein; 14, left auricle; 15, left inferior pulmonary vein, the right pulmonary veins are not seen. (Krause.)

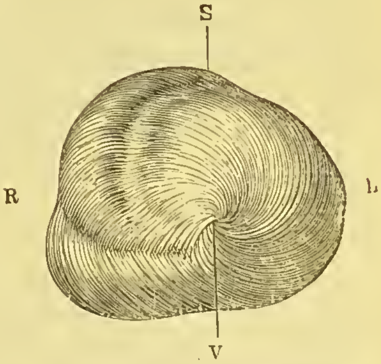

FIG. 101.—Apex of ventricle. One-third natural size. R, right ventricle; L, left ventricle; S, longitudinal groove; V, apex; (Krause)

they enter by a twist into the interior of the ventricle; (2) an *inner* longitudinal layer composed of the same fibres as the outer layer,—some of these becoming continuous with the papillary muscles, and others forming an irregular stratum of fibres, which terminate in the fibrous rings at the base of the ventricle; (3) an *intermediate* or transverse layer, the thickest of the three, formed of fibres passing with less and less obliquity until they are transverse.

The following phenomena are shown by the beating heart: (1) the auricles contract independently of the ventricles. Whilst the rhythmic movement is normal the auricular contractions are equal in number to the ventricular; but as the heart dies, there may be several beats of the auricle for one of the ventricle, and at last only the auricles contract. The auricular portion of the right auricle is the last to cease beating, hence it is termed the *ultimum moriens.* Sometimes, also, contractions of the vena cava and pulmonary veins may be noticed after the heart beats have ceased. (2) The contraction of the circular fibres around the orifices of the veins empties these vessels into the auricles and no doubt also has a sphincter-like action during the contraction of these cavities, preventing the regurgitation of blood, and thus doing away with the necessity for valves at these orifices. (3) The double arrangement of fibres around the auricles produces, when the fibres contract, a uniform diminution of the auricular cavity; (4) the spiral arrangement of the fibres in the ventricular walls expels the blood with great force, as if it were propelled by wringing or twisting the walls of the cavity.

The Pericardium and Endocardium.—The *Pericardium* is a membranous sac of a conical form, its base resting on the diaphragm whilst the upper and narrower part surrounds the roots of the great vessels. It consists of two layers, an outer, composed of connective tissue intermingled with elastic fibres, and an inner or serous. The inner or serous layer not only lines the fibrous layer but is reflected over the surface of the heart. There is thus a space between the two layers, the *pericardial space*, containing a small quantity of lymph, the *pericardial fluid.* The layer of the pericardium covering the heart is a thin membrane covered with a single layer of irregularly polygonal endothelial cells. The membrane is supplied with lymphatics, which communicate with other lymphatics in the sub-serous coat and with still deeper lymphatics in the muscular structure of the heart. The *Endocardium* is not merely the lining membrane but the entire wall of a viscus consisting of several layers. It consists of connective tissue containing many elastic fibres. These are strongly developed near the entrances of the vessels, and they form either reticulations or fenestrated membranes. (See Fig. 181, p. 324, Vol. I.) It is lined by a single layer of endothelial cells. Bundles of non-striped muscular fibres are scattered in the elastic coat. These resist the distension which occurs when the heart contracts and great pressure is put upon the endocardium.

The *valves* of the heart are: (1) The *tricuspid*, guarding the right auriculo-ventricular opening (Figs 100 and 103), consisting of three flaps formed of fibrous tissue (containing many elastic fibres) covered with endocardium. These flaps are continuous at their base, forming an annular membrane surrounding the auricular opening, and they are kept in position by the *chordæ tendineæ* which are attached to their ventricular surfaces and free margins: (2) The *biscuspid* or *mitral*, at the left auriculo-ventricular orifice, consisting of two pointed segments or cusps, having the same structure as those of the tricuspid valve (Figs. 100 and 103). The *chordæ tendineæ* are connected with the *musculi papillares*, small papillæ projecting from the walls of the ventricles. A section of a papillary muscle is shown in Fig. 102.

Fig. 102.—Transverse section of papillary muscle of human heart. × 240 d. *m*, transverse sections of bundles of muscular fibres; *p*, perimysium with small nuclei; *v*, blood-vessel. (Method No. 56, Appendix.)

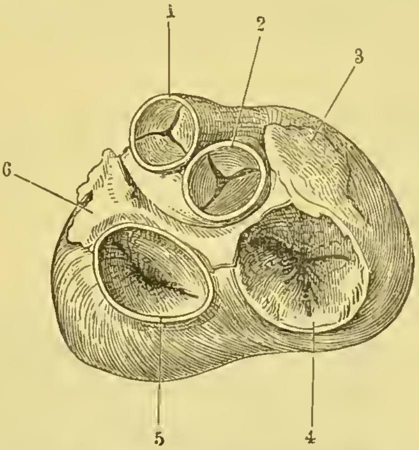

Fig. 103.—Transverse section through the heart above the level of the valves. The epicardium has been removed, thus exposing the muscular fibres. All the valves are shut, and they are seen from above. Half nat. size. 1, Pulmonary artery; 2, aorta; 3, right auricle still covered with epicardium; 4, tricuspid valve; 5, mitral valve; 6, left auricle. (Krause.)

The auriculo-ventricular valves contain striated muscular fibres, radiating from the auricles into the segments of the valve. These shorten the valves towards their base and make a larger opening for the passage of the blood into the ventricles. A concentric layer of fibres is found near the base of the segments which has a sphincter-like action, approximating the base of the valves. Some of the larger *chordæ tendineæ* contain striated muscle, whilst a delicate muscular network exists in the *valvulæ Thebesii* (guarding the openings of small veins from the substance of the heart into the right auricle, Fig. 100) and in the *Eustachian valve* (a crescentic fold of membrane in front of the opening of the inferior vena cava, Fig. 100).

The aortic and pulmonary openings are guarded by the *sigmoid* or *semilunar* valves. Each of these consists of three semicircular flaps, and each flap is attached by its convex border to the wall of the artery, whilst its free border projects into the interior of the vessel. The segments consist of fibrous tissue covered with endocardium. At the middle of the free border there is a fibro-cartilaginous thickening, the *nodulus* or *corpus Arantii.* From this nodulus numerous tendinous fibres radiate to the attached border of the valve, but along the margin of the valve, the membrane is thin and destitute of such fibres. These thin parts are called the *lunulæ.* Opposite each semilunar flap there is a bulging of the wall of the vessel, called a *sinus of Valsalva.* In the aorta these sinuses are situated one anteriorly and two posteriorly (right and left). From the anterior arises the right coronary artery ; from the left posterior the left coronary artery, the vessels supplying blood to the substance of the heart.

Cardiac Measurements.—The size of the heart is about equal to the closed fist of the individual. Its mean weight is about 269·3 grms. The average weight in the adult male is 312 grms., and in the female 255 grms. The proportion of the weight of the heart to that of the body is from 1 to 150 to 1 to 170. There is scarcely any difference between the capacities of the two ventricles, although in the ordinary modes of death the right is apparently more capacious than the left, probably because it is distended with blood ; the left ventricle, after death, is usually empty and more contracted. It is important to note the much greater thickness of the wall of the left ventricle than of the right. The thickness of the left ventricle in the middle is 11·25 mm., and of the right 3·8 mm. The average circumference of the tricuspid orifice in man is 118 mm. ; in woman 111·2 mm. ; of the mitral, 106·1 mm. and 97 mm. respectively. The average circumference of the pulmonary artery is 75·5 mm., of the aorta 71·1 mm., of the superior vena cava, 18 to 27 mm., of the inferior vena cava 27 to 36 mm., and of each pulmonary vein, 12 mm.

Chap. II.—THE ACTION OF THE HEART.

1. Modes of examining the Heart.—When the hand is applied to the side, a little to the right of the left nipple, and in the interval between the fifth and sixth ribs, a shock or impulse is felt. In some rare cases, where there is a congenital fissure of the sternum, the finger can be applied to various parts of the heart's surface, with only the integuments and pericardium intervening. This mode of examination is termed *palpation.* Again, when the ear is applied either directly, or indirectly by means of the stethoscope, over the position of the heart, sounds are heard, the duration and rhythm of which are of physiological significance. This mode is known as *auscultation.* By *percussing* over the region of the heart the anatomical limits of the organ may be defined, and information obtained as to its actual size, and as to any alterations in the relation of the lungs to the heart, and as to the presence or absence of fluid in the pericardium. The *direct registration* of the movements of the heart has been accomplished with the aid of recording instruments.

2. **Movements of the Heart.**—These consist of a series of contractions which succeed each other with a certain rhythm. The contraction is termed the *systole*, whilst that of the relaxation is the *diastole.* The two auricles contract and relax synchronously, and these movements are followed by a simultaneous contraction and relaxation of the ventricles. Thus there is a systole and a diastole of the auricles, and a systole and diastole of the ventricles. On the other hand, if we consider each half of the heart, the contractions and relaxations of the auricle, and the contractions and relaxations of the ventricle, are successive. Finally, there is a very short period in which the whole heart is in diastole. The series of movements, from the commencement of one auricular systole to the commencement of the one immediately following, is known as the *cardiac cycle*, or *period of revolution* of the heart. The sequence and duration of the various movements are shown in Fig. 104.

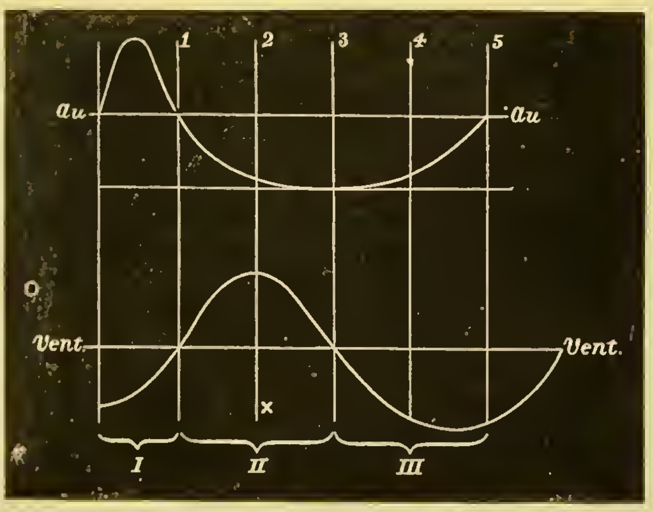

Fig. 104.—Diagram of the movements of the Heart.

In this diagram the systole is represented by a curve above, and the diastole by a curve below, the horizontal lines; the auricular changes are traced on the upper line, *au-au*, and those of the ventricle on the lower line, *vent-vent.* The length of the lines represents the total duration of a cardiac revolution. It will be seen that the auricular systole occupies $\frac{1}{5}$th of the total time of a revolution of the heart, the ventricular systole $\frac{2}{5}$ths, and that the auricular systole immediately precedes the ventricular systole; that the commencement of the ventricular systole coincides with the commencement of the auricular diastole, and that during $\frac{2}{5}$ths of the total period, both auricles and ventricles are in a state of diastole. There are thus three periods:—(1) a period of auricular systole, $\frac{1}{5}$th; (2) a period of ventricular systole, $\frac{2}{5}$ths; and (3) a period of repose, $\frac{2}{5}$ths. The impulse of the apex against the wall of the chest, the moment of which is indicated by a ×, occurs at the middle of the time occupied by the ventricular systole.

In 1861, Chauveau and Marey obtained a record of the various movements of the heart of a horse, determining the duration of the events happening in the heart, and measuring the endocardiac pressure, by employing an instrument termed a *cardiac sound,* so named from a resemblance to the instrument called a sound employed by surgeons in the detection of stone in the bladder. The sound consists of a tube containing two compartments, and in connection with each compartment is an oval elastic bag. One bag is at the end of the sound, and the other is at such a distance above, that when the lower bag is in the ventricle, the upper is in the auricle (Fig. 106). Each bag and air tube is placed in communication with a recording tambour. These tambours, along with a third tambour, connected with a cardiograph (an instrument to be afterwards described) applied to the chest over the apex of the heart, are adjusted in the same plane to a blackened surface on a revolving cylinder. Thus any variation of pressure within the auricle or ventricle affects the elastic bag, and will raise or depress the lever of the recording tambour, and care is taken, at the beginning of

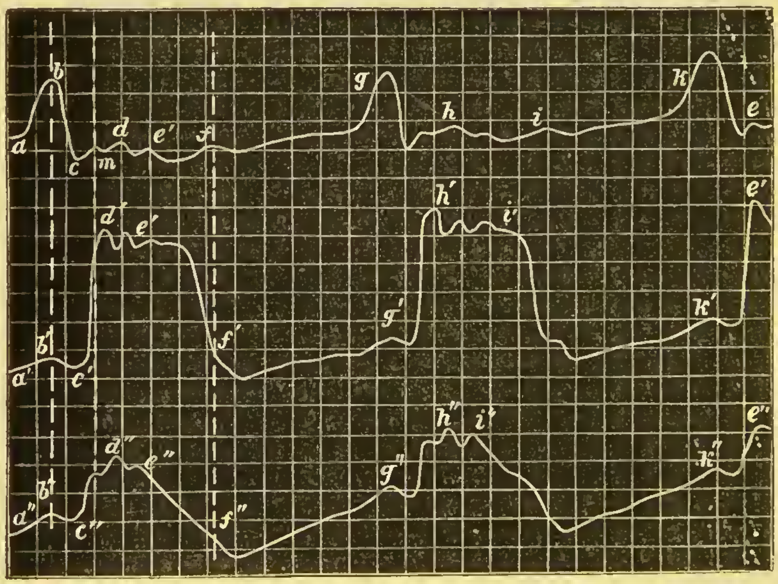

Fig. 105.—Tracings obtained from the heart of a horse by Chauveau and Marey. The upper tracing is from the right auricle, the middle from the right ventricle, and the lowest from the apex of the heart. The horizontal lines represent time, whilst the vertical represent amount of pressure. The vertical dotted lines mark coincident points in the three movements. The breadth of one of the small squares represents the one-tenth of a second.

the experiment, that the points of the levers are placed exactly in the same vertical line. The animal having been anæsthetized, the sound is then passed into the right side of the heart through the jugular vein and superior vena cava, one bag is left in the right auricle, whilst the tube bearing the other is passed through the right auriculo-ventricular opening into the right ventricle.

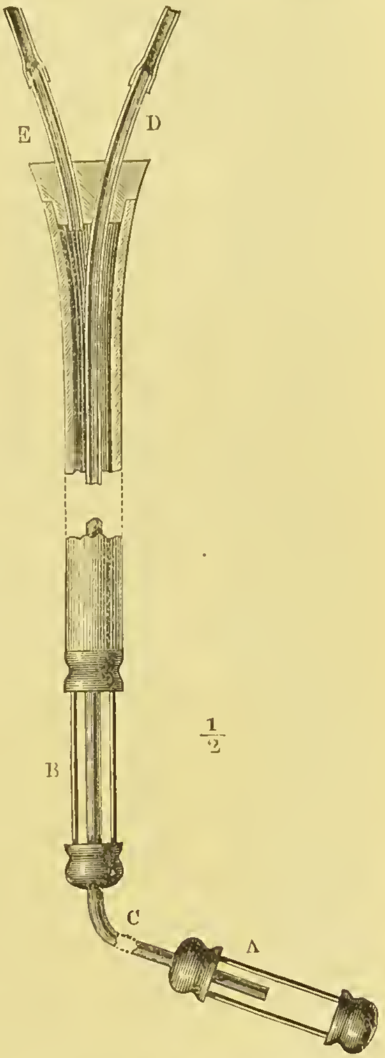

FIG. 106.—Chauveau and Marcy's cardiac sounds. Section of compound sound for right heart. A, framework of bulb for ventricle; B, framework of bulb for auricle. A and B are covered with fine india-rubber, stretched over a thin metallic capsule, in which there are four rectangular windows, through which pressure is communicated to the air in the bag or capsule. C, connecting tube; E and D, tubes to be connected by india-rubber tubing with tambours.

The tracing thus obtained is shown in Fig 105, and it illustrates the following points:—(1) The auricular contraction is less sudden than the ventricular, as indicated by the line *a b* being more oblique than the line *c′ d′*; (2) The auricular contraction lasts only for a very short time, as shown by the curve beginning almost immediately to descend, whereas the ventricle remains contracted for a considerable time, and then slowly relaxes; (3) The times of the contraction of the auricle, and of its relaxation, are about equal, but the time of the relaxation of the ventricle is nearly twice as long as the time of its contraction; the movements of the auricle are thus uniform and wave-like, whilst those of the ventricle are more of a spasmodic character; (4) The auricular movement, as already stated, precedes the ventricular, and the latter coincides with the impulse of the apex against the wall of the chest, as may be seen by allowing the eye to follow the second vertical dotted line; (5) The contraction of the auricle, by forcing blood onwards, affects the pressure for an instant in the ventricle, as indicated by the little elevation seen immediately before the ventricular contraction; and, lastly, (6) During the period of contraction of the ventricle, there are oscillations of pressure affecting both the auricle and the ventricle, which are indicated by the little waves *d*, *e*, *d′*, *e′*, *d″* and *e″* on the three lines,—similar waves are seen in the other curves at *h*, *i*, *h′*, *i′*, and *h″*, *i″*.

With these facts in view, one may now attempt to describe the phenomena happening in a complete cardiac cycle. Suppose the blood to be pouring from the venæ cavæ and from the pulmonary veins into the two auricles. At that time, the auricles are passing into a state of complete diastole, and their cavity is increased by the funnel-shaped aperture at the auriculo-ventricular openings formed by the segments of the valves guarding these orifices. The distension of the auricles is due partly to the pressure in the venæ cavæ and pulmonary veins being greater than in the interior of the auricles, and partly to the aspirating action of the thorax during inspiration sucking the blood from the veins outside the chest to those inside the chest, and thus favouring the flow of blood to the heart. During this time both ventricles are filling with blood, the auriculo-ventricular orifices being open. When the distension of the auricles is complete (which happens before the distension of the ventricles, as the capacity of the auricles is smaller than that of the ventricles), the auricular systole commences by the contraction and emptying of the auricular appendix towards the general cavity of the auricle, and by the mouths of the veins becoming narrowed by contraction of the circular fibres in their coats. These rhythmic movements are propagated quickly over the auricular walls, and these contract simultaneously towards the auriculo-ventricular orifices. The contracting wall forces the blood chiefly in the direction of least resistance, that is into the ventricle, which at the same time is only partially full of blood, and is passing into a state of complete relaxation. The pressure in the veins, aided by the rhythmic contraction made by them at the commencement of the auricular systole, is sufficient to prevent the blood from passing backwards, but there is a momentary arrest of the flow of blood into the large venous trunks. It is thus seen that the auricles act not only as passive reservoirs for the blood in its passage from the veins to the auricles, but as rhythmic cavities tending to keep up a mean pressure in the veins, diminishing by their extensibility the pressure which tends to increase during the ventricular systole, and increasing the pressure by their contraction at a time when the venous pressure would diminish, that is, towards the close of the ventricular diastole. Both auricles and ventricles exercise, during their diastole, a feeble aspirating or sucking action, like that seen during the relaxation of a compressed india-rubber bag.

The amount of blood discharged into the ventricles (already partially filled during the diastole of the auricles) by the auricular systole is sufficient to fill their cavities, and consequently the ventricular systole immediately follows the contraction of the auricles. During the inflow of blood from auricles to ventricles the auriculo-ventricular valves are floated upwards into a more or less horizontal position, and the assumption of this position is aided by contraction of the longitudinal muscular fibres that pass from the auricles into the cusps of the valves. When the ventricular walls contract, the margins of the auriculo-ventricular valves are closely pressed together and the cusps are kept from being folded backwards into the auricle by the simultaneous contraction of the *musculi papillares* pulling on the *chordæ tendineæ* which are affixed to the ventricular aspect of the valves. The close apposition of the cusps is also increased along their margins by the arrangement that the *chordæ tendineæ* of one papillary muscle always pass to the adjoining edges of two cusps. Thus the valves, tricuspid on the right side and mitral on the left, are tightly closed, and the blood cannot regurgitate into the auricles. The blood thus compressed can only pass into the pulmonary artery from the right, and into the aorta from the left, ventricles. The positive pressure in the ventricles is at its maximum at the beginning of their contraction, and it diminishes during the contraction, reaching a minimum, or even becoming negative, at the close of the systole. At this moment there is an aspiration, due to the formation of an empty space in the ventricle caused by the energetic expulsion of the blood through the aorta and pulmonary artery. During the diastole immediately following, the pressure is negative. As the blood passes from the ventricles into the pulmonary artery and aorta, the segments of the sigmoid valves are forced open and stretched across the sinuses behind each cusp, without being actually pressed against the walls of the vessels, and as both the pulmonary artery and aorta contained a certain amount of blood before, the pressure in these vessels is increased, and the walls of both yield to a considerable extent. As already stated, the ventricle continues in the contracted state for a brief space of time, and then it relaxes. Simultaneously with the commencement of relaxation, the auriculo-ventricular orifices open, thus permitting the passage of blood from the auricles; and at the same time, the elastic walls of the aorta and pulmonary arteries recoil so as to force a portion of the blood backwards towards the cavities of the ventricles, in which, as they are passing into diastole, the pressure is much less than in the vessels. This blood, however, by filling the sinuses of Valsalva and the crescentic pouches of the sigmoid valves, closes these valves so as to prevent any blood from passing into the ventricles. From the end of the ventricular contraction to the moment when the auricles are again full, all the cavities of the heart are in a condition of dilatation, and the cavities are filling with blood. This is the period of the *pause*, during which the heart may be supposed to be in a state of rest.

In the left ventricle the great anterior flap of the mitral valve lies between the orifice of the aorta and the orifice of the auricle, and as the papillary muscles do not extend higher than the middle third of the cavity, there is a space above them and below the flap of the valve which may be called the *supra-papillary space.* When the ventricular wall contracts, the blood lifts up the flaps of the mitral valve and the large mitral flap shuts off the auricular opening, and swells out the root of the aorta, making it continuous with the supra-papillary space. The supra-papillary space contains blood even at the end of systole, and in this residual blood the flaps of the sigmoid valves have free play

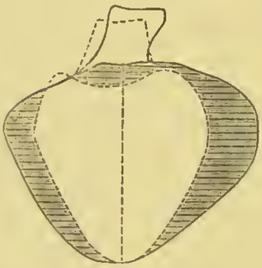
FIG. 107.—Projection of a dog's heart, posterior surface. Shaded portion indicates appearance in diastole, white portion in systole.

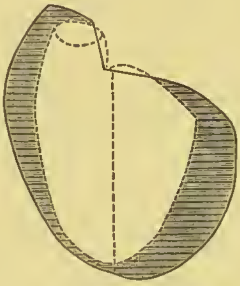
FIG. 108.—Left lateral surface. Shaded, diastole; unshaded, systole.

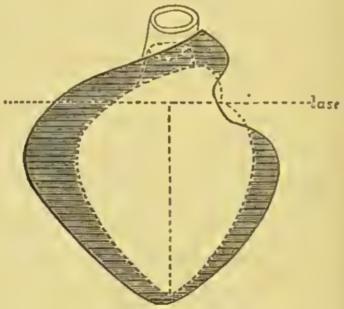

FIG. 109.—Anterior surface. Shaded, diastole; unshaded, systole.

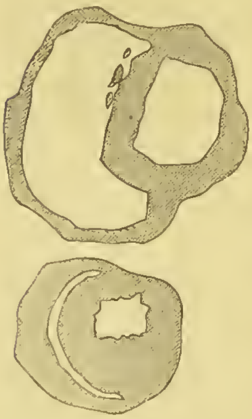
FIG. 110. — Sections through upper third of ventricles. Upper figure in diastole; lower in systole.

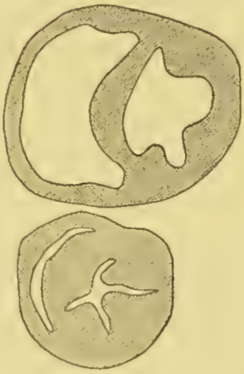
FIG. 111. — Sections through middle third of ventricles. Upper figure in diastole; lower in systole.


FIG. 112. — Projections of the base in systole and diastole of the same heart. The disposition of the ostia in systole is indicated.

(Macalister). According to Sandborg and Worm Müller,[1] the elasticity of the *musculi papillares*, and especially of the *chordæ tendineæ*, has a regulative function, adjusting the position of the flaps of the tricuspid and mitral valves, according to the amount of shortening or lengthening of the axis of the ventricles from base to apex.

3. **Change of Shape of the Heart.**—When one watches an actively beating heart, the movements are so rapid that the eye cannot follow them so as to give to the mind a correct conception of the changes in form that the organ undergoes. Owing to this, knowledge of the changes in the form of the heart has been derived from an inspection after death.

Recent investigations by Ludwig and Hesse have shown that the *post mortem* form is not the natural shape of the living heart either in diastole or in systole. They succeeded in distending the ventricles of the still living heart of the dog (the animal being unconscious) by a pressure equal to that of the arterial pressure, and in taking a plaster cast of the ventricles when thus distended. This condition represents the diastolic phase. To obtain the form at the end of a systole a similar living heart, empty of blood, was suddenly plunged into a hot (50° C.) saturated solution of bichromate of potash, which caused it to give one strong, rapid, and final contraction, and fixed it in the contracted form. From this casts were made, representing the systolic phase. To obtain the shape of the cavities two hearts of similar size were taken: one was filled with blood and placed in a cold solution of bichromate of potash, which slowly hardened it in the diastolic state, whilst the other was treated with the hot solution. Casts were then made of the cavities. The results are shown in Figs. 107, 108, 109, 110, and 111.[2] The base of the relaxed ventricle is an ellipse, the greater axis running from left to right and the shorter obliquely from before backwards. The axis running from apex to base forms an obtuse angle with the plane of the base, so that the heart has an inclination to the apex. When systole occurs, the ellipse becomes a circle, by the transverse axis of the ellipse diminishing by ⅓rd. The longitudinal axis becomes shorter and it now forms a right angle with the plane of the base, so that the apex is now opposite the centre of the base (Figs. 112, 113).

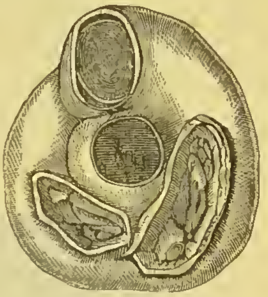

FIG. 113.—Base of the ventricles in systole, according to Ludwig. ⅓rd natural size.

4. **The Apex Beat or Shock of the Heart.**—This is the impulse felt in the fifth left intercostal space 2 inches below the nipple and 1 inch to its sternal side, or at a point 2 inches to the left of the sternum. It is synchronous with the systole, and is caused by a movement of the

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[1] Sandborg and Worm Müller. *Études sur le Méchanisme du Cœur.* Christiania. 1880.

[2] For an account of this subject see a paper by Dr. Donald Macalister in the *British Medical Journal* for October 28th, 1882.

apex of the ventricle by which it is pressed more firmly against the chest wall, from which it is separated, when the heart is at rest, by the thin margin of the lung. At the time of ventricular systole the form of the heart changes; in place of being an oblique cone having an elliptical base, as in rest, it becomes a regular cone, having a circular base; when contraction occurs, the apex is carried from below and behind, upwards and forwards, and is forced into the intercostal space; and at the same time the ventricular portion twists on its long axis from left to right, partially exposing the left ventricle. It is the twisting motion that gives the impulse, and it is caused by the contraction of the oblique fibres in the ventricles which lift up the apex, but it is assisted by the spiral arrangement of the aorta and pulmonary artery. Some have supposed that the movement is partly due to the recoil of

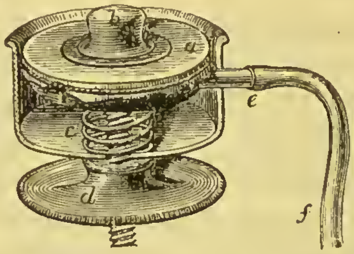

FIG. 114.—Section of the cardiograph of Marey for recording the movements of the heart of man or of animals. *a*, india-rubber membrane; *b*, vulcanite or ivory knob applied over the apex of the heart, resting on a thin aluminium plate; *c*, spiral, which may be tightened or relaxed by turning the milled head *d*, thus increasing or diminishing the sensibility of the instrument; *e*, *f*, tube leading to the recording tambour. (Marey.)

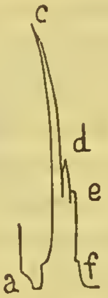

FIG. 115.—Normal curve from man. (Landois.)

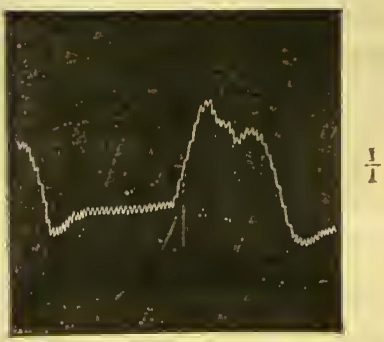

FIG. 116.—Normal curve from man, registered on a vibrating glass-plate with each indentation = ·01613 of a second.

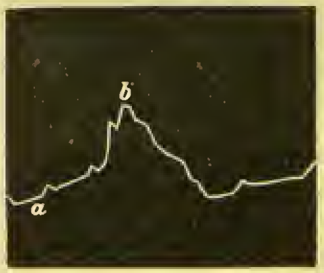

FIG. 117.—Tracings of the cardiac pulsations of a healthy man. (Marey.)

the ventricles on discharging their blood (like that of an exploded gun), causing the apex to go in the opposite direction, downwards and outwards, whilst others have held that the discharge of blood into the pulmonary artery and aorta causes an elongation of these vessels, whereby the apex is pushed downwards and forwards. Both of these mechanisms have only a slight effect as the cardiac impulse occurs even when from hæmorrhage the heart is empty.

5. **Cardiographic Tracings.**—To obtain a tracing of the apex beat instruments of various kinds, termed *cardiographs*, are employed. One of the most serviceable is that of Marey, seen in Fig. 114.

Tracings obtained by such instruments are termed *cardiograms*. In Fig. 117 is seen a tracing of the apex beat of a healthy man, and a diagrammatic tracing is given in Fig. 115. This tracing should be studied along with the tracing obtained by Landois on a vibrating glass plate by means of the apparatus shown in Fig. 118. In Fig. 115, *a* represents the time of the pause and the contraction of the auricle, and it is evident that the latter phenomenon causes the apex of the heart to move slightly towards the intercostal space. The portion *a*, *c* corresponds to the contraction of the ventricles and is synchronous with the first sound. The curve then rapidly falls as the ventricles relax and during the descent there are two elevations, *d* and *c*, synchronous with the second sound. As already shown, when the ventricles relax, the blood in the aorta and pulmonary artery, driven backwards by the elastic recoil of the walls of these vessels, closes the semilunar valves. This shock is propagated to the apex of the ventricles and causes a vibration of the intercostal space. The elevation *d* is synchronous with the closure of aortic valves and *e* with the pulmonary valves, and it will be seen that these valves are not closed at the same moment, but are separated in time by the ·05 to ·09 of a second, an effect due to the greater blood pressure in the aorta than in the pulmonary artery. Finally, the portion *e f* corresponds to the remaining part of ventricular diastole.

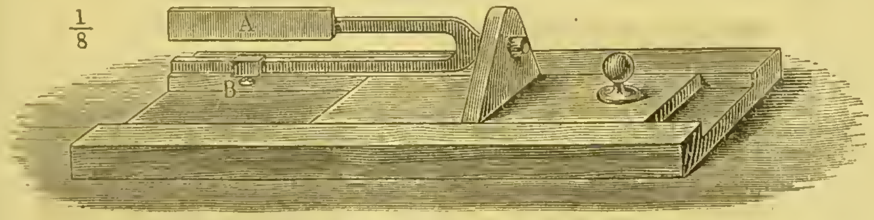

FIG. 118.—Tuning fork carrying smoked glass-plate on one limb, counterbalanced by weight B, and moved horizontally while tracing is being taken. (Gscheidien.)

6. Time occupied by Cardiac Movements.—This has been measured by various observers by tracings obtained from the impulse against the wall of the chest, recorded by cardiographs. If the velocity of the surface on which the tracings are obtained is known, and if a correct interpretation is given of the causes of the various parts of the curve, it is not difficult to determine the time occupied by the phases of a cardiac revolution. Rollett gives the following results in fractions of a second as determined by Landois.[1]

Events in the Heart.	Rate of Heart-beat per minute.				
	55	55	74·2	109·7	113·1
	Duration of phases in fractions of a second.				
1. From beginning of pause to end of auricular contraction, - - - - - -	·563	·584	·494	·213	·247
2. Contraction of ventricle, - - - - -	·243	·274	·079	·006	·057
3. Relaxation of ventricle to closure of semilunar valves, - - - - - -	·066	·072	·144	·194	·133
4. From close of pulmonary valves to beginning of pause, - - - - - -	·259	·200	·092	·090	·103
5. Between 1st and 2d sounds, - - -	·309	·346	·223	·244	·190
6. Between 2d sound and next 1st sound, -	·822	·784	·586	·303	·394
7. Time from 1 to 4 inclusive (complete cardiac revolution), - - - - -	1·133	1·133	·809	·547	·539
8. From closure of aortic valves to closure of pulmonary valves, - - - -	...	...	·780	·100	·057

This table shows (*a*) that the faster the heart beats, the shorter the pause (1); (*b*) that the faster the heart beats, the shorter the ventricular contraction (2); (*c*) that the time between the 1st sound and the next 1st sound is that occupied by a cardiac revolution (compare the summations of 5 and 6 with 7); and (*d*) that the time between the closure of the aortic and pulmonary semilunar valves varies considerably (a fact due to the difference of pressure in the aorta and pulmonary artery, so that if the pressure in the aorta greatly exceeds that in the pulmonary artery the second sound of the heart may be doubled). Observations have also been made on an individual with a cleft sternum (*ectopia cordis*) by G. A. Gibson, who gives the following figures in fractions of a second; auricular contraction, ·100 to ·130; ventricular contraction, ·325 to ·395; difference between closure of valves, ·09; ventricular diastole, ·11; and pause, ·455 to ·690. Fuanther also made observations as to the time between the first and second sounds, and the duration of these and of the pause, by listening to the heart and registering the time by a delicate chronometrical arrangement, and obtained results closely agreeing with those above detailed.

7. Frequency of the Cardiac Pulsations.—These, in the adult man, number from 65 to 75 per minute. The heart beats per minute are—in the elephant, 25 to 28; horse, 25 to 40; ox, 45 to 50; pig, sheep, goat, 70 to 80; dog, 70 to 120; cat, 120 to 140; rabbit, 130 to 160; and birds, 120 to 180; fishes, 20 to 24; and amphibian, 60;

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[1] Hermann, *Handbh. d. Physiol.* vol. iv. p. 157.

frog, tortoise, 20; crab, about 50. Stallions, have 28 to 30; very old stallions, 23; and mares and castrated horses, 36 to 40; foal, 60; calf, 56 heart beats per minute (Munk). The heart of a human fœtus pulsates from 140 to 150; and that of a newly-born foal, 150 to 160 times per minute. There is a relation between the amount of blood in the circulation and the frequency of the heart beats. Thus, as the beats of the heart increase in frequency the quantity of blood which passes per minute in one kilogramme of body weight also increases, as shown in the following table by Vierordt.

	Quality of blood per minute and per kilogramme of body weight.	Number of pulsations per minute.
Horse, - - - -	152	55
Man, - - - -	207	72
Dog, - - - -	272	96
Rabbit, - - - -	620	220
Guinea-Pig, - - -	892	320

In man, about the tenth year, there are eighty-seven heart beats per minute; it falls to seventy to seventy-five till the twentieth year; remains about this amount till the sixtieth year, and then rises a little in advanced age. In a healthy adult man, the number of heart beats will be seventy-three in the morning, sixty-nine in the forenoon, eighty-one to eighty-three an hour or two after a mid-day dinner, then it will fall to about seventy towards night. During sleep the heart beat is slowed. Prolonged fasting may bring the number down to forty or fifty; the number of strokes is greater while standing than while sitting, and while sitting than while lying down. Quickened breathing increases the number of beats. Mental excitement also quickens the heart beats.

8. **Quantity of Blood in the Heart.**—It has been determined, both by direct measurement and by calculation, based on the velocity of the blood in the aorta and the cross-section of the orifice of that vessel, that from a heart of average size, each left ventricular systole ejects about 180 cc. of blood, weighing about 188 grms. This is the figure usually given, but it must be regarded as approximative.

The left ventricle of the horse, sheep, goat, and dog can contain, of blood, in weight, about $\frac{1}{376}$ of the weight of the body. Thus, in a horse weighing 400 kilogs, the capacity of the ventricle is about 1 litre, or 1·07 kilogs. of blood. Each ventricle holds about $\frac{1}{30}$ of the total blood, so that, when both contract, about $\frac{1}{15}$ of the total blood is ejected. In man, the auricles have a capacity of about 103 cc.

The amount may vary, even in the same individual, according to the state of vigour of the muscular walls of the organ.

9. **Sounds of the Heart.**—When the ear is applied over the cardiac region of the chest of a healthy man, two sounds are heard, the one with greatest intensity over the apex, and the other over the base of the heart. The dull long sound heard with greatest intensity over the apex has received several names, such as the *first*, the *long*, the *inferior*, and the *systolic* sound; whilst that over the base—clearer, sharper, shorter, higher—has been called the *second*, the *short*, the *superior*, the *diastolic* sound.

Suppose the sounds expressed by the syllables *lupp*, *dupp*, when one listens over a healthy heart, it will be noticed that the accent is on *lupp* (the first sound) when the stethoscope is over the apex: thus—lúpp, dupp; lúpp, dupp; and on dupp (the second sound) when over the base: thus—lupp, dúpp; lupp, dúpp. One will also observe a pause between the second sound and the next succeeding first sound, and a much shorter pause (almost inappreciable) between the first and second sounds: thus—

At apex—lúpp dupp (pause), lúpp dupp (pause), lúpp dupp.
At base—lupp dúpp (pause), lupp dúpp (pause), lupp dúpp.

These relations are well seen in diagram (Fig. 119). Walshe states, that if the cardiac cycle be divided into tenths, the first sound will last $\frac{4}{10}$; the short pause, $\frac{1}{10}$; the second sound, $\frac{2}{10}$; and the long pause, $\frac{3}{10}$. As the measurement of the duration of the sounds depends on the

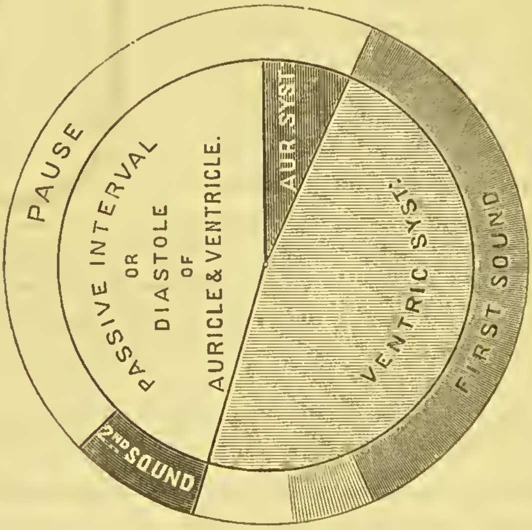

FIG. 119.—Scheme of a cardiac cycle after Gairdner and Sharpey. The inner circle shows what events occur in the heart; and the outer, the relation of the sounds and silences to these events.

auditory sensations of the listener, it is to be expected that considerable differences of opinion exist on this question. Thus some observers state that the first sound occupies, of a cardiac cycle, $\frac{2}{10}$; a short pause immediately following, $\frac{1}{10}$; the second sound, $\frac{2}{10}$; and the long pause, $\frac{5}{10}$. The so-called short pause is practically inappreciable.

There are differences of opinion as to the cause of the *first* sound. Some have supposed it to be due to vibrations of the auriculo-ventricular valves; others, that it is muscular, owing to the contraction of the ventricles; not a few have attributed it to movements of the blood through the aortic and pulmonary orifices; whilst the remainder have thought that the sound might be the result of a fusion of these effects. It is certainly not due to the impulse against the chest wall, as it has been heard after removal of the heart from the chest, by an arrangement shown in Fig. 120. The sound has not the quality produced by vibrating membranes or by the rush of fluid through an orifice, and it is difficult, on acoustical principles, to conceive a fusion of the supposed causes. There is no doubt it is a *muscular sound*, varying in quality from the ordinary sound of a contracting muscle, from the arrangement of the cardiac fibres. The sound is modified by the vibrations of the tense auriculo-ventricular valves. The fact that the sound has been heard from an excised heart, still pulsating, but empty of blood, supports this explanation, and there is further the pathological evidence that in cases where muscular walls have been weakened by fatty changes (as in the advanced stages of typhus, fatty degeneration, etc.), the first sound may disappear. It may be said to this view, that derangements of the valves affect the first sound, and that, therefore, it cannot be due to muscular action alone. But the passage of fluid through an orifice, such as is formed by diseased mitral valves, is quite sufficient to produce a sound which will entirely mask the normal muscular sound; and it has always appeared to the present author that the blowing sound, heard with disease of the valves, is an abnormal sound different from the normal first sound, and of sufficient intensity either to conceal it, or to produce

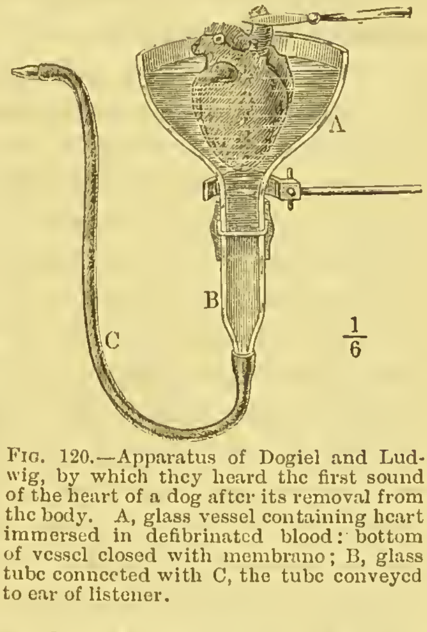

Fig. 120.—Apparatus of Dogiel and Ludwig, by which they heard the first sound of the heart of a dog after its removal from the body. A, glass vessel containing heart immersed in defibrinated blood: bottom of vessel closed with membrane; B, glass tube connected with C, the tube conveyed to ear of listener.

a sound of the intensity and quality characteristic of a blowing murmur.

No doubt exists as to the cause of the *second* sound. This is produced by the sudden sharp closure of the sigmoid valves. If one of the valves at the aortic orifice is hooked up by a curved needle as was done by Williams and Hope, the sound disappears or is replaced by an abnormal murmur, whilst it returns when the needle is withdrawn. As already mentioned, the aortic and pulmonary valves do not close simultaneously, but the difference in time is inappreciable in normal circumstances to the ear, and can only be detected by special chronometric arrangements.

For practical purposes, we must bear in mind what is happening in the heart whilst listening to its sounds. Thus, with the *first* sound, we have (1) contraction of the ventricles; (2) closure of the auriculo-ventricular valves; (3) rushing of the blood into the aortic and pulmonary artery; (4) impulse of the apex against the chest; and (5) filling of the auricles: with the *second* sound, (1) closure of the semilunar valves from the elastic recoil of the aorta and pulmonary artery; (2) relaxation of the ventricular walls; (3) opening of the auriculo-ventricular valves so as to allow the passage of blood from auricle to ventricle; and (4) diminished pressure of apex against chest wall: with the *long pause* (1) gradual refilling of the ventricle from the auricle, and (2) contraction of the auricle so as to entirely fill the ventricle. As already mentioned, the so called *short pause* between the first and second sounds is so short as, in normal circumstances, to be inappreciable, but we may suppose that during that short period the ventricle is in or nearly at a condition of maximum contraction. The sound of the *tricuspid valve* is loudest at the junction of the lower right costal cartilage with the sternum; of the *mitral* at the apex beat; of the semilunar valves at the *aortic* orifice in the direction of the aorta where it is nearest the surface at the second right costal cartilage, and of the valves at the *pulmonary* orifice over the third left costal cartilage, to the left and external to the margin of the sternum.

10. **Nutrition of the Heart.**—The heart is nourished by the blood flowing through its cavities in some of the lower vertebrates, as the frog, but in the hearts of larger animals, in which nutritional changes are more active, there is a special arrangement of vessels or *cardiac circulation.* The coronary arteries originate at the aortic orifice in the region of the sinus of Valsalva, rather above the upper border of the semilunar valves, so that when the ventricle contracts, the mouths of these arteries are not covered by the segments of the valves. The small branches of the coronary arteries penetrate the muscular substance and

end in a plexus of capillaries, which carries arterial blood to the structure of the heart. From these the radicles of the cardiac veins originate, which carry the blood, now venous, into the right auricle by larger vessels called the *anterior cardiac veins* and by numerous small veins constituting the *foramina of Thebesius* or the *venæ minimæ cordis.* The coronary vein is dilated before entering the auricle, forming the *coronary sinus*, and at the junction of the vein with the dilated portion there is a valve consisting of one or two segments. Other veins enter the coronary sinus, each having a valve.

These valves serve two purposes : (1) they interrupt the flow of blood during the contraction of the right auricle, preventing regurgitation and venous congestion of the wall of the heart, and (2) as the valves open towards the right auricle they prevent the backward flow of blood during contraction of the ventricles, and favour its onward flow, and thus the stream of blood is accelerated, as in the veins of a contracting muscle. The blood is sent through the cardiac circulation by the systole of the ventricle, and not during its diastole. Brücke supposed that when the left ventricle contracted the segments of the aortic semilunar valves covered the openings of the coronary arteries, and that the diastolic filling of these arteries assisted in the dilatation of the ventricles. This view has been disproved by the observations that filling the coronary vessels with fluid under high pressure caused a diminution and not a dilatation of the ventricular cavity, that the coronary arteries, when wounded, spout with each ventricular contraction, like an ordinary artery, that the pulse of the coronary artery is synchronous with that of the pulmonary artery, and that the pulse in the coronary artery is simultaneous with that in the carotid artery in the neck. No doubt there is always enough of blood in the sinuses of Valsalva to fill the arteries at the beginning of the ventricular systole, and when the semilunar valves are raised they do not cover the orifices of the coronary arteries. Further, it is known that during the contraction of an ordinary skeletal muscle the arteries dilate and the flow of blood is quickened. The walls of the coronary arteries are thick in proportion to their calibre, probably to resist the great pressure to which they are subjected during the systole.

It is to be expected that an organ so active as the heart will have the *lymphatic system* largely developed. These vessels are found in great numbers both beneath the pericardium and the endocardium, and also throughout the muscular tissue. Amongst the muscular fibres there are lacunæ or spaces lined by endothelial cells, representing the origins of the lymphatics. The lymph is carried into lymphatic glands found between the aorta and the trachea, and ultimately finds its way into the right innominate vein and the thoracic duct.

11. Persistence of Cardiac Movement.—It has been known from early times that the heart will continue to beat after removal from the body. This is more especially the case with the hearts of cold-blooded animals. The frog's heart may continue to pulsate for two and a half days, whilst that of a rabbit will do so only for a period of from three to thirty minutes. The average duration of the beats of the warm-blooded heart is said to be eleven minutes. The right auricular appendix, termed the *ultimum moriens*, beats longest, and it has been observed pulsating in the rabbit fifteen hours after death, in the mouse forty-six hours, in the dog ninety-six hours. After the heart has ceased beating, it may again be caused to contract by direct stimulation or by heat. The injection of arterial blood into the coronary vessels restores excitability in the mammalian heart after it has ceased to beat.

12. **The Cardio-Pneumatic Movement.**—If a wide glass tube filled with smoke be inserted into one nostril while the other nostril and the mouth are closed, the smoke will be seen to move with each pulsation of the heart. The phenomenon is explained by the fact that when the heart contracts it occupies less space in the chest, and consequently if the glottis be open air will be drawn into the lungs. The reverse will happen during the diastole. Landois has designed an instrument (the *cardio-pneumograph*) by which a tracing of these movements may be obtained. These tracings show (1) an expiratory movement at the moment of the first sound in consequence of the dilating branches of the pulmonary artery compressing the bronchi; the blood of the right ventricle having entered the pulmonary circuit; (2) this is succeeded by an inspiratory movement in consequence of more blood leaving the chest by the aorta and its branches than passes simultaneously into it by the venæ cavæ; (3) after the closure of the semilunar valves and the second sound the arterial blood accumulates in the chest, and hence there is again a slight expiratory movement of the air in the lungs; (4) again the blood empties quickly from the arteries in the chest into those outside, and there is another inspiratory flow of air into the lungs.

13. Influence of the Respiratory Movements on the Action of the Heart.—The heart and lungs being contained in the air-tight cavity, the chest or thorax, it is evident that the increase and decrease in the size of the chest during inspiration and expiration must exercise an influence on the amount of pressure on the outer surface of the heart, and consequently on its movements. When an inspiration is made by the descent of the diaphragm and the elevation of the ribs, the lungs expand, there is less pressure on the outer surface of the heart, and the heart is in a state of distension in diastole. In consequence also of the removal of pressure during inspiration from the great veins entering the chest and reaching the right side of the heart, the flow of venous blood towards the heart is favoured. These effects are more marked if, after a deep expiration, the glottis be closed, so as to prevent air entering the lungs, and if then the chest be dilated by a powerful inspiratory effort. This, which may be called Müller's experiment, causes a dilatation of the heart, venous blood flows freely into the right side, this sends it on to the lungs, causing them to become engorged, whilst at the same time the dilated left side of the heart is unable to send out a sufficient amount of blood into the arterial system. The pulse may then disappear, and there is an intense feeling of distress. On the other hand, expiration increases the pressure on the outer surface of the heart and on the outer surface of the great veins, only a small amount of blood flows into the right side, the heart is contracted, the systole is small and the pulse is also reduced in volume. This condition is intensified in what is termed *Valsalva's experiment*, in which, after a deep inspiration, the glottis is closed, and a powerful expiratory effort is made. When this is done, the flow of venous blood into the heart is interrupted, the veins in the face and neck swell, the blood is forced out of the compressed lungs into the left side of the heart, which throws it into the arterial circulation. The pulse and heart sounds disappear, and there is the risk of syncope or fainting. Both of these experiments, Müller's and Valsalva's, are dangerous, and should not be often repeated. They are extreme conditions of the normal state of things in which inspiration favours the flow of blood into the heart and the dilatation of the heart, while expiration has the opposite effect, and they also explain the mechanism by which air may be sucked into the veins from wounds in the neck or armpit. This is most likely to occur during inspiration, and when it does occur speedy death is the result.

14. **The Work of the Heart.**—This may be ascertained by the following calculation:—Each systole of the left ventricle forces into the aorta ·188 kilog. of blood; the pressure in the human aorta has been estimated at 250 mm. of mercury—that is, it would support a column of mercury of that height. But 250 mm. of mercury = 3·2 metres of blood, for 1·06 is the specific gravity of the blood, and 13·6 that of mercury, therefore $250 \,.\, \frac{13{\cdot}6}{1{\cdot}06} = 3210$ mm. or 3·2 metres. We have next to consider the rapidity, v, with which blood is drawn into the aorta. With a uniform pressure, h, the rapidity of efflux is equal to the rapidity a falling body would reach if it fell from the height h, therefore $v = \sqrt{2gh}$, in which g is the accelerating force of gravity = 9·81 metres; h therefore $= \frac{v^2}{2g}$. The force of the rapidity of the current, v, on the quantity of blood, q, is equal in work to $q\,\frac{v^2}{2g}$, for, falling

from the height $h=\frac{v^2}{2g}$ would produce the same rapidity. The rapidity, v, in the aorta is ·5 metre. The work of the left ventricle, therefore, is

$$\cdot 188 \times 3\cdot 2 + \cdot 188 \left(\frac{\cdot 5^2}{2 \times 9\cdot 81}\right) \text{ kilog. m.} = \cdot 188(3\cdot 2 + \cdot 0127).$$

Taking the pulse beat at 70 per minute, then

$$3\cdot 2127 \times \cdot 188 \times 70 = 42\cdot 279 \text{ kilog. m.}$$

for left ventricle per minute. The right ventricle does about $\frac{2}{5}$ths of this amount, or 16·911 kilog. metres, or together, as the work of both ventricles, 59·190 kilog. metres. Then 59·190 × 60 × 24 = 85,233 kilog. m. is the work of the heart (Robert Mayer). As 1 horse power = 75 metre-kilogrammes per second (or 550 foot-pounds per second), the daily work of the human heart is $\frac{1}{75}$th of a horse power. Munk, by a similar calculation, gives the work of the heart of the horse as $\frac{1}{30}$th of a horse power. To produce $\frac{1}{75}$th of a horse power requires the combustion of 28 grms. of carbon. The work done is thus enormous, amounting to more than $\frac{1}{5}$th of the total work accomplished by the body.

CHAP. III.—MODES OF STUDYING THE ISOLATED HEART.

Many methods have been devised for the study of the movements of the hearts of amphibians by which important facts have been brought to light. One of the simplest of these is to curarize a frog, place the animal upon its back on a cork plate, on the edge of which a delicate lever is so adjusted as to be brought over the beating heart exposed by removing the anterior wall of the thorax. A very convenient form of double lever arrangement has been devised by Cash.[1]

A simple method of observing the effects of *heat* on the heart, as devised by Lauder Brunton, is shown in Fig. 121. The heart is placed below the light lever C, moving on a pin inserted into cork B, a counterpoise E being attached. On heating copper-plate A, the heart beats more and more quickly till it passes into a condition of heat-tetanus, from which it may recover on cooling the plate A by means of a lump of ice.

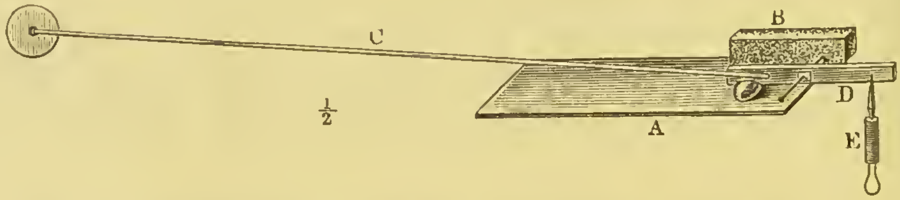

FIG. 121.—Lauder Brunton's arrangement for observing effects of heat on the heart.

The *movements* of the heart may also be registered, and the effects of *electrical stimulation* observed, by using Marey's *cardiac forceps*, as shown in Fig. 122. It consists of two small cups, one to be placed on each side of the heart. Each cup is connected with a little vertical arm attached at the top to a horizontal bar. One arm is fixed and the other is movable, the latter carrying a delicate horizontal lever. The two vertical arms have a small india-rubber ring slipped over them. Each systole opens the forceps and moves the lever, which records on a drum

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[1] *Jl. of Physiology*, vol. iv.

moving on a horizontal axis. Wires may be led to the forceps, as shown in the diagram.

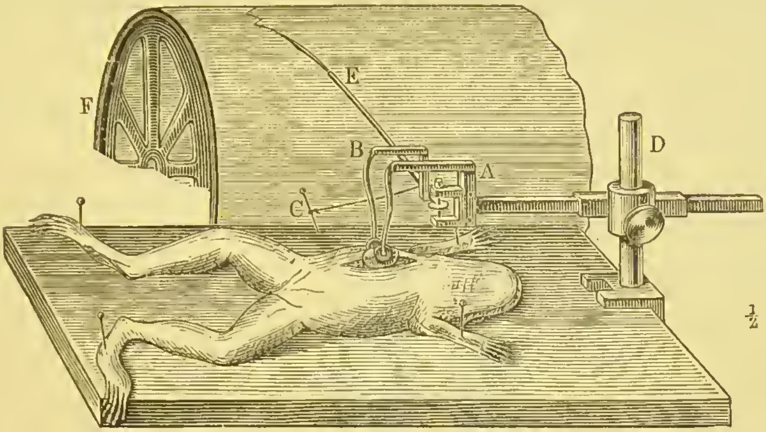

Fig. 122.—Cardiac Forceps of Marey.

The study of the *work* accomplished by the isolated beating heart has been facilitated by various ingenious instruments. The most complete of these appliances is the *Frog-Heart Apparatus* of Ludwig and his pupils, shown in Fig. 125. It consists of two graduated burettes, *b* and *c*, communicating with one outlet, *a*, guarded by a two-way stopcock. The tubes are supported on a stand, along with a small frog-heart manometer (Fig. 123), one limb of which passes downwards so that it opens at the level of the burette opening. Another branch of this limb passes upwards and backwards, and is guarded with a stopcock.[1]

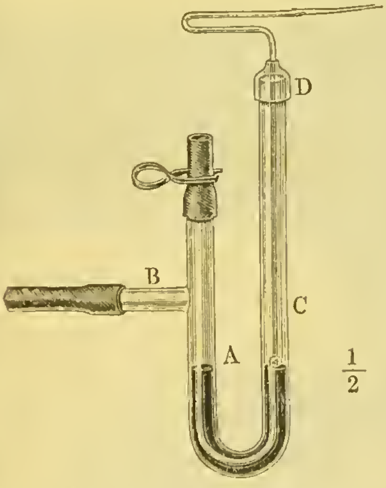

Fig. 123.—Frog-heart manometer, containing mercury. Half nat. size. Diameter of tube, 2 mm. Observe the glass float carrying a delicate glass marker in limb C

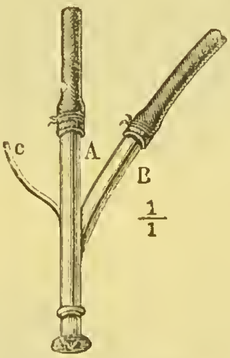

Fig. 124. — Kronecker's canula for the frog's heart.

The limb C, Fig. 123, contains a fine stem of glass floating on mercury

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[1] The description here given is from M'Gregor-Robertson's *Physiological Physics*, p. 236.

by a bulbous extremity, the projecting end being bent at right angles and terminating in a point for writing on a blackened revolving cylinder.

For fixing the frog-heart to the apparatus, the Kronecker heart canula (Fig. 124) is used. It is divided into two compartments, one communicating with the branch *a*, and the other with the branch *b*. To each of the branches is attached

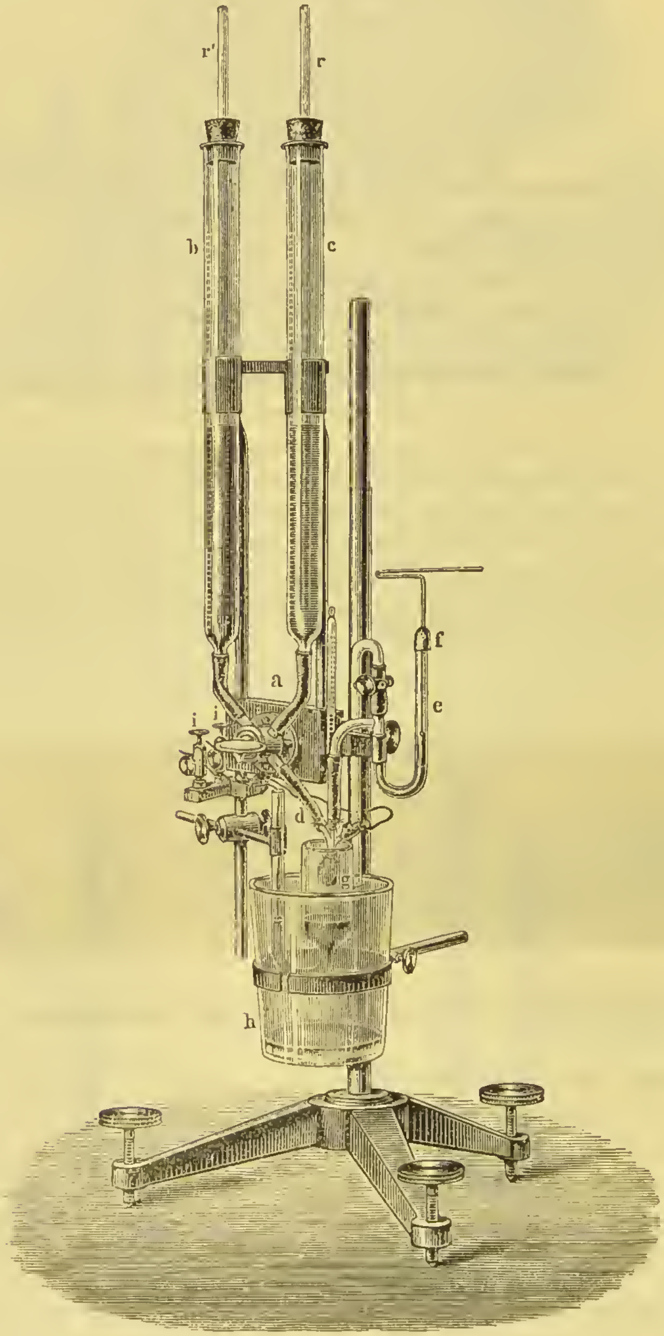

Fig. 125.—Frog-heart apparatus. For description, see Text.

a short bit of caoutchouc tubing. The pericardium is opened in front, the heart turned over, and a fine vessel, passing from the pericardium to the back of the heart, ligatured. The *sinus venosus* is opened by a snip, and the canula passed through it, and through the auricle into the ventricle, where it is bound above the auriculo-ventricular furrow. The heart, attached to the canule, is then separated from the body, and the canule connected, on the one hand, with the outlet tube of the burettes, on the other with the manometer tube. Into one burette is placed a solution of one part of defibrinated rabbit's blood and two parts salt solution (·6 per cent.). The burette is closed with a cork, through which passes a tube which dips into the fluid, and so maintains a constant pressure, on the principle of Mariotte's bottle. On opening the stopcock connected with the burettes and that of the manometer, the blood will flow into and fill the heart, pass through it into the limb of the manometer, and, if allowed to flow, will issue by the upward branch, below which a vessel (*h*) should be placed to receive it. If, however, the manometer cock be closed, the blood will dilate the heart, and if, when it is fully dilated, the burette cock be closed, then, on the heart contracting, the blood, finding no other way of escape, will be forced into the short limb of the manometer, and will depress the column of mercury there. The column in the long limb will consequently be raised, and the glass float with it, the recording point of the float marking the ascent on the blackened surface. When the heart relaxes, the blood will return, the mercury will fall to its original level, and the descent will be recorded. An example of tracings obtained by Marckwald, with this apparatus, of the movements of the heart of a mammal, a hybernating marmot, is shown in Fig. 126.

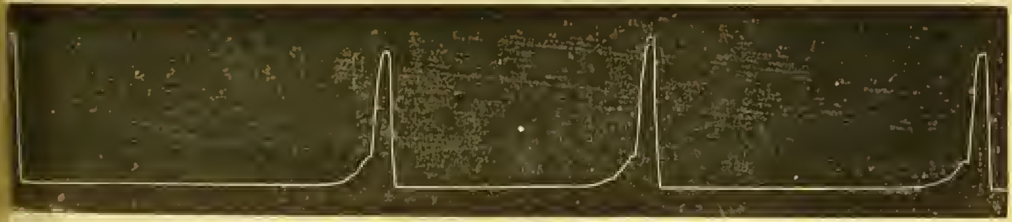

FIG. 126.—Beat of the heart of a marmot, at the rate of 5 to 6 beats per minute. (Marckwald.)

More recently, Roy has invented an apparatus termed a *tonometer*, for the study of influences affecting the work done by the beating heart. This instrument, shown in Fig. 127, possesses several advantages over those already described. It consists of a small bell jar, the rim of which rests in a well-greased groove in a brass plate. A perfusion canula passes through the stopper of the jar, and to this the frog's heart is attached, so that blood may flow through the heart. In the centre of the brass plate is a circular opening, or short cylinder, in which an aluminium piston moves. Round the edge of the lower end of the cylinder a thin animal membrane is loosely stretched; the centre of the membrane is connected to the upper surface of the piston, so that when the piston moves up and down it carries the membrane along with it. The piston is connected by a delicate rod with a lever adjusted underneath. The glass vessel is filled with olive oil, and this may be allowed to flow out by the small side tube, guarded by a stopcock, seen on the right of the figure. The heart is immersed in the oil. During diastole it expands and forces down the piston, and along with it the lever, the point of which has been previously adjusted to the surface of a blackened cylinder, and when systole occurs the piston rises. In this way tracings are taken, two of which are given in Plate B, Fig. 6 and Fig. 8. In Fig. 6 we see the peculiar grouping of contractions described by Luciani, and in Fig. 8 we have a tracing illustrating the effects of electrical stimulation of the auricle.

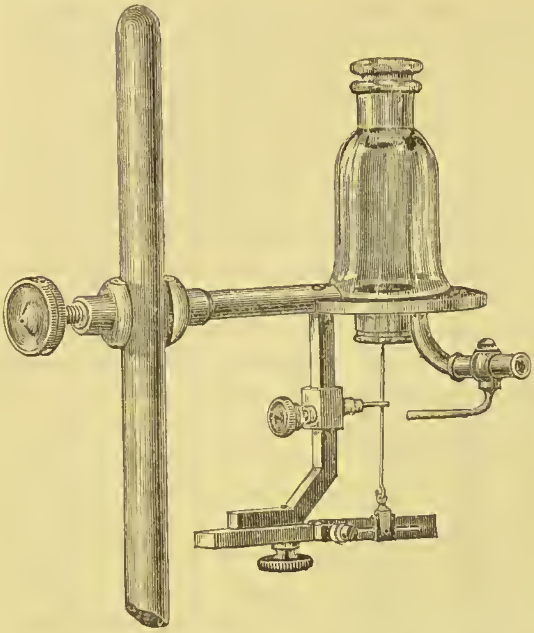

Fig. 127.—Roy's Tonometer, for measuring changes of volume during contraction of the heart.

The experiments on the isolated heart have been performed chiefly with the heart of amphibians. In 1882, Newell Martin[1] described a method by which the heart and lungs of a dog or cat may be completely isolated from the remainder of the body of the animal, and be kept alive for some hours. All the vessels of the systemic circulation, except those supplying the heart itself, were occluded, while the pulmonary circulation was left intact. Thus a circulation was kept up. By this method several important observations, to be afterwards referred to, were made as to the effect of heat on the mammalian heart. Waller and Reid[2] have also succeeded in making observations on the isolated mammalian heart, relating to the nature of its contractions and its electrical phenomena.

CHAP. IV.—THE INNERVATION OF THE HEART.

The nervous arrangements of the heart have been investigated by many observers, both on account of the importance of accurate information regarding the influence of the nerve centres on the heart, and also because the facts obtained throw light on many difficult questions as to the relations of nervous and muscular actions. The investigations may be divided into two groups: (1) those relating to the influence of

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[1] Newell Martin, "The Direct Influence of Gradual Variations of Temperature upon the rate of Beat of the Dog's Heart." *Philosophical Transactions*, Part II. 1883.

[2] A. D. Waller and E. W. Reid, "Action of the Excised Mammalian Heart." *Philos. Transactions*, 1887. B.

the great nerves connecting the heart with the central nervous organs, or what may be termed the *extrinsic nervous mechanism;* and (2) those relating to the nervous arrangements in the heart itself, or the *intrinsic nervous mechanism.*

A. THE EXTRINSIC NERVOUS ARRANGEMENTS.

The *extrinsic* arrangements, consisting of the nerves given off by cardiac plexuses derived partly from the cerebro-spinal and partly from the sympathetic system, have been investigated chiefly in the larger animals, such as the tortoise, rabbit, and dog.

1. **Action of the Vagus**.—In 1845, the Webers[1] made the remarkable discovery that excitation of the trunk of the pneumogastric in the neck produces, if the excitation be feeble, a diminution of the number of cardiac beats, and if it be strong, arrest of the heart in diastole with repletion of all its cavities. Section of the nerves they found to be followed by an acceleration of the pulse. The slowing and the arrest of the heart may be produced by electrical, mechanical, or chemical stimulation. In man, Czermak observed that compression of the carotid at the anterior border of the sterno-mastoid was followed by slowing of the heart, an effect which he attributed to irritation of the pneumogastric. The arrest of the heart produced by electrical stimulation of the pneumogastric lasts from fifteen to thirty seconds in the dog. During arrest, the heart has not lost its excitability, and it will respond to direct stimulation. The stoppage cannot be regarded as a reflex act; it is direct, inasmuch as it will take place on stimulating the distal end of the cut nerve. One of the early investigations which gave precision to our knowledge on this subject was by Rutherford, who showed especially that the inhibiting action is not constant, as was supposed by Von Bezold, but "a state of activity seems to be the exception."[2] The acceleration of the beats of the heart which follows section of the pneumogastrics may be readily observed in animals of slow pulse, such as frogs, tortoises, turtles, etc. The right vagus exerts a more powerful influence on the heart than the left. Nuël observed that the weakening of the systole caused by gentle stimulation of the vagus affects the contraction of the auricles chiefly.

But the pneumogastric acts not only on the frequency of the cardiac

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[1] Müller's *Archives*, 1846, p. 497.

[2] William Rutherford, "Influence of Vagus on the Vascular System." Communicated to Royal Society of Edinburgh, 3rd May, 1869. See *Journal of Anatomy and Physiology*, vol. iii. p. 432.

beats, but upon the amplitude of the pulsations. When stimulated, the pulsations not only become fewer, but also more feeble, so that, according to Coats, the work of the heart, in a given time, is diminished.

Section of the spinal cord, and of the two sympathetics in the neck, increase the excitability of the pneumogastric, so that an extremely feeble irritation is sufficient to arrest the heart's action.

Thus, certain fibres in the pneumogastric exercise an *inhibitory* or restraining influence over the cardiac pulsations. The action as recorded by a cardiograph, is shown in the following tracing, Fig. 128. See also Plate B, Fig. 15.

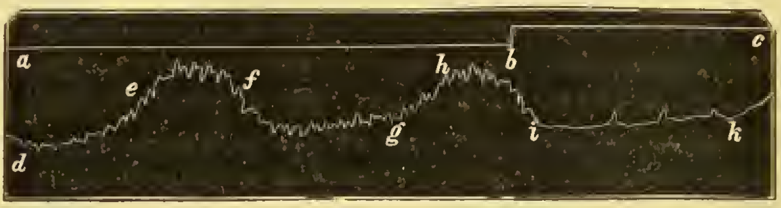

FIG. 128.—Cardiographic tracing from a rabbit. The two pneumogastrics had been cut. At the point *b*, as indicated by the inflection of the electric signal, *a*, *b*, *c*, the peripheral end of one pneumogastric was stimulated, and the effect, from *i* to *k*, is almost complete arrest of the movements of the heart. The tracing is to be read from left to right. (Marey.)

2. **Action of the Sympathetic.**—This nerve contains fibres which act antagonistically to the inhibitory fibres of the vagus, that is, they are *accelerators.* Section of the sympathetic, even on one side, is followed by slowing of the heart's action, whereas stimulation of the peripheral end causes the beats to become faster. Stimulation also of the delicate fibres passing to the heart from the inferior cervical ganglion causes an acceleration of the beats of the heart. These accelerating fibres originate in the spinal cord, as it has been found that even after dividing all nervous communications between the heart and the cerebro-spinal centres, and leaving only the accelerating fibres of the sympathetic intact, even then stimulation of the upper end of the cord will cause acceleration of cardiac beats. It has also been ascertained that stimulation of the two first dorsal ganglia of the sympathetic quickens the beats of the heart. The accelerating fibres, then, augment the number of the heart's pulsations, but they do not appear to alter the amount of work done by the heart. Consequently, in a strict sense, they cannot be regarded as the *motor* nerves of the heart. Moreover, severe excitation does not produce tetanus as it would do if they were motor nerves distributed to muscular fibres. They end in intra-cardiac ganglia.

The accelerator fibres come from the inferior cervical and first thoracic ganglia, forming two branches which form a ring round the subclavian artery (the *annulus of Vieussens*). The superior cervical ganglion receives fibres from the anterior roots of the 1st and 2nd spinal nerves ; the trunk of the sympathetic receives fibres from the 3rd cervical nerves ; the first thoracic ganglion receives fibres from the 4th, 5th, 6th, 7th, 8th, 9th, 10th, and 11th, and perhaps the 12th and 13th, spinal nerves. Accelerator fibres may also pass from the superior cervical ganglion into the vagus, and running down the trunk of that nerve reach the cardiac plexus, either directly or indirectly, through the anastomosis of Galen, between the superior and inferior laryngeal nerves.

3. **Reflex Action of some Sympathetic and Cerebro-Spinal Fibres.**—The sympathetic, in addition to accelerating fibres, contains also centripetal fibres, which excite reflex activity through the vagi. If, in a rabbit, the two sympathetic nerves are divided in the lower part of the neck, and the cephalic end is excited, there is slowing of the pulse, a result which will not take place if the vagi have been previously cut. The sympathetic in the abdominal region also contains fibres, the excitation of which slows the heart's beats, through the medium of the vagi. Thus, as shown by Goltz, a sudden stroke on the stomach may, in this way, stop the action of the heart, a fact which may account for sudden death from syncope after a blow on the epigastrium, or after swallowing ice-cold liquids or corrosive poisons. François-Franck has also shown, in an elaborate research on the effect on the heart of excitations of sensory nerves, that sudden and severe stimulation of almost any nerve may produce such an effect. The following is one of his illustrations :—

FIG. 129.—Slowing of the action of the heart caused by pinching of the posterior auricular nerve at the point indicated by the vertical dotted line. Tracing to be read from left to right. At *e*, the irritation was removed.

Schiff showed long ago that strong irritation of the sub-orbital nerve (branch of the fifth) of a rabbit arrests the heart in diastole.

4. **Action of the Spinal Cord on the Heart.**—As already stated, the accelerating fibres originate in the upper part of the cord. The *medulla oblongata* contains the inhibitory centre for the pneumogastric, but the exact situation of the centre has not been well determined. Stimulation of the *medulla* is said to be followed by arrest of the cardiac beats. It appears, therefore, that in the *medulla* and upper part of the cord there are two centres related to the heart—(1) an *inhibitory* centre, which gives origin to the inhibitory fibres of the vagi ; and (2) an

accelerating centre, which is connected with those fibres passing through the sympathetic that quicken the heart's movements. It has also been observed that the inhibitory centre is at once excited by the presence of an undue amount of carbonic acid in the blood. For example, if the nostrils of a rabbit are compressed for a few seconds, the heart beats more slowly. Again, oxygen excites the accelerating centre. Thus the two centres may each be excited either by the state of the blood or by nervous influences. These nervous influences may be of two kinds: (1) those coming from the periphery of the body (*sensory nerves*), from the abdominal cavity (*splanchnics*), or from the heart itself by a special nerve, the *depressor*; and (2) those coming from the higher cerebral centres, the action of which explains the influence of emotional states in the heart.

5. **Action of Depressor Nerve.**—The action of this nerve, sometimes called the *nerve of Ludwig and Cyon*, will be better understood after studying the circulation in the vessels and the innervation thereof.

B. THE INTRINSIC NERVOUS ARRANGEMENTS.

These have been investigated more especially in the heart of the frog, views of which are given in Figs. 130 and 131.

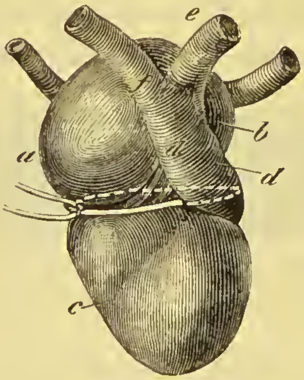

FIG. 130.—View of Frog's heart from the front. See description of Fig. 131. (Cyon.)

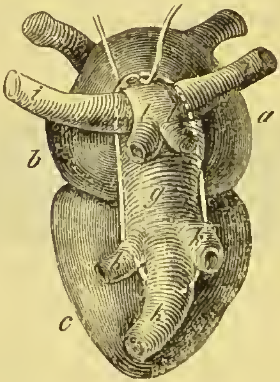

FIG. 131. — View of Frog's heart from behind. *k*, vena cava inferior; *g*, sinus venosus; *i*, venæ cavæ superiores: *a*, right auricle; *b*, left auricle; *c*, ventricle; *l*, pulmonary vein; *d*, truncus or bulbus arteriosus; *e*, ductus caroticus, ductus aorticus, and ductus pulmo-cutaneus. (Cyon.)

It is important to bear in mind that the frog's heart is far more under the control of intrinsic nervous mechanism than the heart of the mammal, or to put the statement in another form, it is less under the control of extrinsic nerves. For example, although cardio-inhibitory fibres pass from the *vagi* to the frog's heart, they are probably in action only under exceptional circumstances, as is shown by the fact that when the vagus of a frog is cut, the heart does not beat more rapidly. It will be seen that the frog's heart possesses two auricles, communicating by a foramen in the septum, and a single ventricle. The venous blood from the body is poured in the first instance into a cavity called the *sinus venosus*, which communicates with the right auricle. The left auricle receives the arterial blood from the pulmonary veins. Both auricles empty into the common ventricle, which contains therefore a mixture of arterial and venous blood, and when the ventricle contracts some of this blood is again sent to the lungs, whilst the remainder passes into a dilatation at the commencement of the arterial system, called the *bulbus arteriosus*, and thence into the aorta. The nervous arrangements in the frog's heart are comparatively simple. The two cardiac branches of the *vagi* (*nervi cardiaci*) pass along the wall of the *vena cava inferior* to the posterior surface of the *sinus venosus*, and where the latter joins the right auricle they unite to form a small knot of nervous matter called *Remak's ganglion*. The fibres then pass along the auriculo-ventricular groove, joining the two ganglia, known as *Bidder's ganglia*. Numerous slender nerve fibres pass from immediately below the endocardium to these ganglia, whilst others pass outwards and end in the muscular tissue. Small unipolar nerve cells, and larger bipolar pyriform cells having each two processes, one straight and the other spiral, have been found in the frog's heart. Nerve cells occur chiefly in the basal and middle parts of the ventricles of the hearts of the dog, sheep, calf, and pig, chiefly in the anterior and posterior inter-ventricular grooves and on the left ventricle.

C. RESULTS OF EXPERIMENTS.

If the heart of a decapitated frog be removed from the body, it will continue to beat, although it has been thus removed from the influence of the great nervous centres. Rhythmical movements, therefore, may continue for some time independently of these centres. If the apex of the heart be then cut off, it will remain motionless whilst the larger part will still beat rhythmically. Successive slices may then be removed from the larger portion without affecting rhythmical contraction until a section is made through the auriculo-ventricular groove, when the ventricular portion of the heart ceases to beat. If the motionless apex, or the separate portions rendered motionless by the above procedure, be mechanically irritated, a single contraction, not a series of ryhthmic contractions, follows. These are phenomena that may be easily observed ; to analyze them skilfully is a matter of much greater difficulty.

1. **Experiment of Descartes.**—When the ventricle is separated from the rest of the heart by a ligature, or by an incision at the level of the auriculo-ventricular groove, the ventricle stops, but the auricles and the sinus go on beating. To continue rhythmic movement of the ventricular it is necessary to have attached to it a small portion of the auricular part of the heart, especially the lower margin of the septum. It would therefore appear that impulses passed from this auricular portion into the ventricular and caused the latter to pulsate. Gaskell has tested this by the ingenious method of passing over the auriculo-ventricular groove (or over any other part of the heart) a delicate clamp, regulated by a fine screw, by which he could tighten or relax the pressure of the clamp at pleasure. Thus he found it possible to "block" the passage of the nervous impulses with the effect of altering the ratio of the ventricular to the auricular beats. Normally, there is one ventricular beat for each auricular, but the clamping causes 2, 3, or 4, auricular beats for each beat of the ventricular, thus—$\frac{A}{V}, \frac{1}{1}, \frac{2}{1}, \frac{3}{1}, \frac{4}{1}$. (See Plate A, Fig 4.)

2. **Experiment of Stannius and Rosenberg.**—If the *sinus venosus* is separated from the auricles by incision or ligature, the veins and the sinus continue to beat, whilst the auricles and ventricles are arrested in diastole (Fig. 131). Suppose then an incision is made through the auriculo-ventricular groove, the ventricle frequently then begins to beat, but the auricles remain in diastole. It is also observed in these circumstances that the ventricle now beats more slowly than normal.

The experiment may be performed as follows :—Lay bare the heart, open the pericardium, cut through a little connective tissue between the pericardium and the ventricle (often containing a small vessel), and lift up the ventricle. Pass a thread below the heart and draw a ligature exactly between the *sinus venosus* and the right auricle. A thin white line indicates the position. Keep the ligature rather on the side of the *sinus* than of the auricle, because if a bit of the auricle has been enclosed, we may have the heart beats quickened, as occurs after a section through the auriculo-ventricular groove. Next tie a ligature or make a section in the auriculo-ventricular furrow, and the ventricle, and often the auricle, begin to beat anew. The experiment may also be performed when the heart is connected with a manometer, the canule being inserted not further than the very beginning of the *sinus venosus*. Allow the heart to rest a little before applying the ligature.

When the heart cavities have thus been inhibited, it is important to avoid touching, or even shaking the heart, as a slight mechanical irritation may provoke contractions.

We have seen that certain of the fibres of the vagus have an inhibitory action on the heart, so that, when they are stimulated, the heart stops in diastole. Is this effect due to a direct influence of the vagus on the muscular fibres of the heart, or is there an intermediate ganglionic mechanism between the terminal fibres of the vagus and the muscular fibres? Experiments with various poisons appear to favour the latter view. Thus, it is well known that if a large dose of curare has been given, stimulation of the vagus is not followed by diastolic cessation, while, in these circumstances, a direct electrical stimulus applied to the *sinus venosus* at once produces it. Again, if atropine has been administered, then neither stimulation of the trunk of the vagus nor of the *sinus venosus* is followed by diastolic cessation. The explanation offered, is that curare in large doses paralyses the terminal fibres of the vagus without paralysing the inhibitory mechanism in the *sinus venosus*, and that atropine paralyses the inhibitory mechanism itself. The phenomenon of inhibition (that is, of diastolic cessation) is brought about by the application of muscarin or pilocarpin, and the effect may be antagonized by atropine. Here, then, there appears to be a physiological antagonism: muscarin and pilocarpin stimulating, while atropine paralyses, the inhibitory mechanism. The experiment of Stannius may be explained, by supposing that Remak's ganglion in the *sinus venosus*, in the normally beating heart, has some influence over Bidder's ganglion in the auriculo-ventricular groove. When Remak's ganglion is cut off by the ligature between the *sinus venosus* and the auricle, the auricle and ventricle stop because the ganglion of Bidder has not sufficient energy to excite the movements. Stimulation of Bidder's ganglion, however, as may be carried out by dividing (or applying a ligature) in the auriculo-ventricular groove, causes both auricles and ventricle to pulsate, if a portion of the ganglion remains attached to the auricles and the other portion to the ventricles.

Although the rhythmical contractions of the heart are influenced by the nervous arrangements, it cannot be said that ganglionic nerve cells and nerve fibres are a necessary part of the mechanism. Thus, if the ventricle of a frog's heart is cut into two or more strips in a zigzag, so that the individual parts still remain connected with each other by muscular tissue, the strips still beat in a regular progressive manner, provided one strip is caused to contract. The rapidity of the transmission is about 10 to 15 mm. per sec., showing that the conducting paths for the impulse are not nervous, but exist in the contractile substance itself. This is in accordance with the fact that rhythmical movements occur in structures devoid of any nervous apparatus such as: (1) the embryonic heart at an early period of development; (2) the heart of many invertebrates; (3) the tissue of the medusæ; and (4) the heart apex in certain circumstances.

If the canule of Kronecker's or Roy's apparatus (p. 222 and p. 224.) is introduced into the ventricle and a ligature is applied so that the heart-apex is attached to its lower end, the apex, at first motionless, begins to pulsate when it is distended by the pressure of the saline solution. As no nervous elements can be seen in the apex, the rhythm must depend on its muscular structure, and the apex preparation is of great value in the study of the cause of rhythm and of the action of active substances on the muscle of the heart. If, however, the ligature has been applied above the auriculo-ventricular groove, and especially if the heart is fed with serum, groups of contractions make their appearance, as was first shown by Luciani. A diastolic pause occurs between the groups and the successive contractions in each group become shorter and shorter. (See Fig. 6, Plate B, as taken by Roy with the Tonometer, but without the staircase character.) These groups disappear when the heart is fed with defibrinated blood or with saline solution.

CHAP. V.—ACTION OF PHYSICAL AND CHEMICAL AGENTS ON THE HEART.

Many physical and chemical agents act on the living heart, and it is evident they may have an influence on the muscular structure, or on the intrinsic nervous arrangements, or on both.

1. **Heat.**—In 1644, Descartes showed that heat increased the number of the pulsations of an eel's heart. The experiment may be readily performed on the frog's heart with the apparatus shown in Fig. 121, p. 220. As the temperature rises up to about 40° C., the heart-beats become quicker and quicker, until the organ passes into a state of heat-rigor. Up to about 20° C., the amplitude of the contractions increases; above this limit it diminishes, while the contractions occupy a shorter and shorter time. As already mentioned, heat-rigor may be removed by cooling. A frog's heart beats more and more slowly in the cold, and it will stop a few degrees above 0° C., but if gradually warmed it will again begin to beat. It may be even frozen throughout, and yet recommence its pulsations after slow thawing. As regards the heart of the higher vertebrates, Bernard and others found a slow pulse in animals artificially cooled. Hybernating animals have a slow pulse. Lauder Brunton found the heart-beats quicker than normal in rabbits artificially heated, but this did not prove any direct action of heat in the heart. Cleland and others observed that the heart of the chick in the 3rd day of incubation beats faster when warmed. By far the most complete observations as to the effect of heat on the heart of mammals have been made by H. Newell Martin, by the method referred to on p. 224. He found that the mammalian heart, when cut off from all extrinsic nervous control, beats more quickly when warm blood is supplied to it, and more slowly when it gets cooler blood. The dog's

heart in this respect behaves like that of the frog, and its activity is controlled by its temperature. Further, it is the temperature of the blood in the cardiac capillaries that influences the rate, not the temperature of that in its cavities, showing that the warm blood must act directly on the muscle fibres and nerve cells of the organ. These results are of great importance in relation to the question of the cause of the rapid pulsations of the heart in fever.

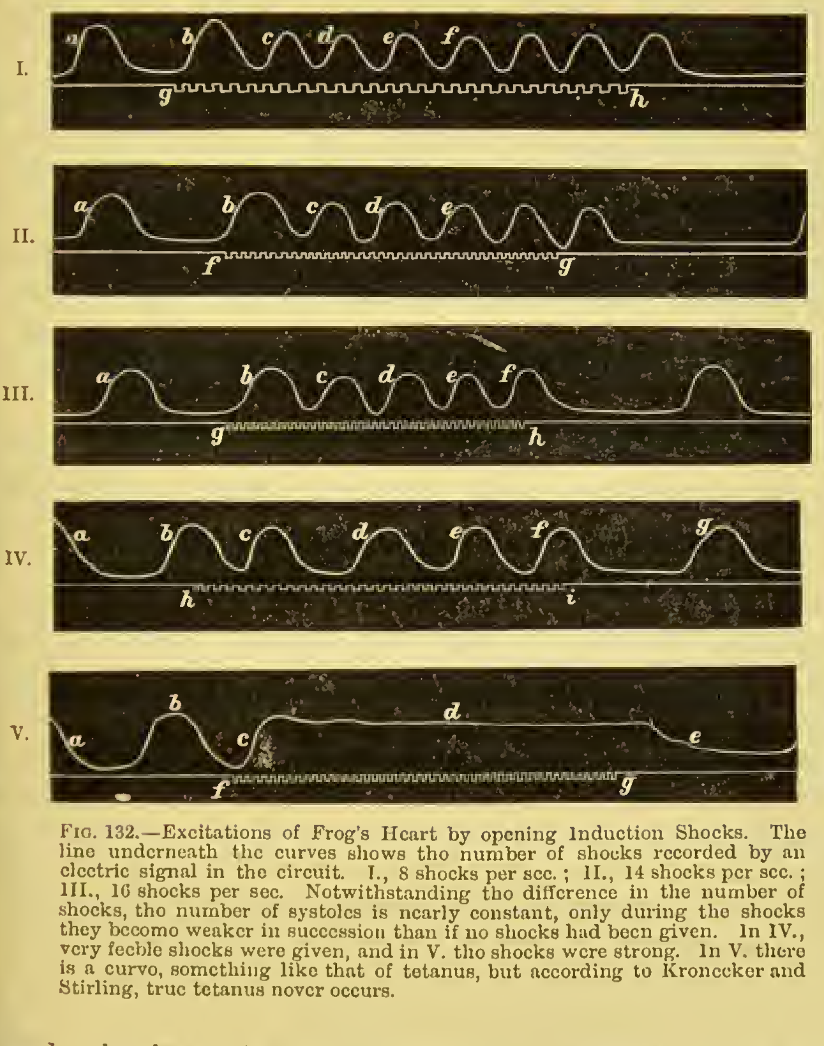

Fig. 132.—Excitations of Frog's Heart by opening Induction Shocks. The line underneath the curves shows the number of shocks recorded by an electric signal in the circuit. I., 8 shocks per sec.; II., 14 shocks per sec.; III., 16 shocks per sec. Notwithstanding the difference in the number of shocks, the number of systoles is nearly constant, only during the shocks they become weaker in succession than if no shocks had been given. In IV., very feeble shocks were given, and in V. the shocks were strong. In V. there is a curve, something like that of tetanus, but according to Kronecker and Stirling, true tetanus never occurs.

2. **Electricity.**—A *constant* current of moderate strength passed through the heart *in situ* quickens the heart-beats, and if it be strong it may cause fibrillar contractions. A slowly interrupted current is more effective *cæteris paribus*, than one quickly interrupted—that is to say, interruptions at the rate of 5 per second applied to a quiescent ventricle are more effective than a series of 100 per second

of the same strength (M'William). When the frog's heart is stimulated by the apparatus shown in Fig. 122, p. 221, we find (1) that a single *induction* shock applied during systole has no effect; (2) that a single induction shock given during diastole brings on the next systole sooner; (3) that a shock may be so weak as to produce no systole, but if the strength of the shock is gradually increased until it is sufficient to cause a contraction, then there is a *maximal* contraction—that is to say, as shown by Kronecker and Stirling, a minimal stimulus produces a maximal contraction, or, whatever be the strength of the excitation, if it cause a contraction at all, the response is always maximal; (4) even a rapid series of induction shocks does not produce true tetanus; (5) the production of one contraction, by a weak stimulus, as shown by Bowditch, so affects the excitability of the heart that a considerably weaker stimulus will now be sufficient to excite a contraction; and (6) to secure contractions with feeble stimuli, Kronecker has shown that they must come at the proper time—that is to say, they must come at intervals longer than the time required by the heart for its complete systole and diastole, and if they come too quickly they will produce no effect. This is well illustrated by the following tracings taken by Marey.

Induction currents have not been observed to have any effect on the human heart, but this was probably due to the difficulty of transmitting the shocks at the proper rhythm. An important series of experiments bearing on this point has been made by M'William[1] on hearts of cats, dogs, rabbits, hedgehogs, guinea-pigs, and rats. He finds that with the mammalian, as with the amphibian heart, minimal stimulation produces maximal contraction; and he points out that the effect of a strong stimulus depends to a great extent on the time that has elapsed since the last contraction. If this time has been sufficient for recovery to take place, a weak stimulation or a strong stimulation produces a contraction; but if the time has been too short, so that complete recovery has not taken place, then a minimal stimulus may not be able to secure a response, but a maximal one will "force" it. To quote his words:

> "Hence it is obvious that there occurs a rhythmic rise and fall in the excitability of the heart; a fall immediately succeeding the occurrence of an effective stimulation, followed by a gradual rise extending through the phase of active relaxation and to a variable extent into the phase of quiescence. This rhythmic

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[1] M'William, "On the Rhythm of the Mammalian Heart." *Jl. of Physiology*, vol. ix. p. 167.

rise and fall affects the cardiac excitability both as regards (*a*) the force of contraction, and (*b*) the facility with which a contraction may be elicited, as measured by the strength of stimulus required to induce a beat."

Strong constant currents or faradic currents applied to the ventricles cause an abolition of the normal beat, and the ventricular muscle shows rapid twitching movements, the dilated ventricles being unable to expel their contents. The auricles are not affected. This has been termed *fibrillar contraction*, *delirium cordis*, etc. [1]

3. Chemical Substances.—Many substances, soluble in the blood, directly affect the heart. Thus, a small quantity of ether accelerates the beats of the frog's heart while a larger dose may arrest them, and if the heart be then supplied with blood containing no ether, the beats will be renewed (M'Gregor-Robertson). Chloroform and ethidene dichloride diminish the number of heart-beats, Plate A, Fig. 1. Weak solutions of bile or the bile salts quicken, while stronger solutions diminish the number, or may even paralyse the heart. Sulphuretted hydrogen and carbonic oxide paralyse the heart; large excess of carbonic acid weakens the heart, or may even arrest its action; sulphurous acid quickly kills it; and weak solutions of chlorine stimulate while strong ones destroy it. Salts of potash arrest the heart in diastole. The action of the specific poisonous substances on the heart is shown in the accompanying table, modified from one first compiled by Kronecker.[2]

CARDIAC POISONS.

1. Excitors of the inhibitory centres without influence on the vagus. *Muscarin*[3] (·029 to ·5 mg., frog; ·5 mg., dog and rabbit). Physostigmin antagonizes muscarin. Diastolic cessation caused by stimulation of vagus and *sinus*.
2. Paralyse inhibitory centres. (*a*) Cardiac ganglia, *atropin* (·005 mg., frog), *hyoscyamin* (2 mg., dog), *daturin* (2 mg., dog), *physostigmin*, *aconitin* (·5 to 1 mg.), *pseudaconitin*, *delphinin*, *veratrin*, *duboisia*, *pilocarpin*, (antagonizes *muscarin*). (*b*) The terminal fibres of *vagus* passing to cardiac ganglia, *coniin*, *curarin*, *nicotin* (·2 mg., frog), pituria.
3. Excitors of motor centres: *aconitin*, *muscarin*.
4. Excitors of muscle-substance, and in large doses paralysing same: *Aconitin*, *delphinin*, *veratrin*, *antiarin* (¼ drop), *digitalin* (5 mg., dog).

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[1] Fully investigated by M'William, "Fibrillar Contraction of the Heart." *Jl. of Physiology*, vol. viii.

[2] Cyon's *Methodik der Physiologischen Experimente*, p. 171.

[3] According to W. H. Gaskell, muscarin does not act as an excitor of the inhibitory centres, but as a deterrent to motor activity. *Jl. of Physiology*, vol. viii. p. 408.

CHAP. VI.—NATURE AND CAUSES OF RHYTHMIC CARDIAC CONTRACTION.

Hitherto we have considered some of the more obvious phenomena of the heart. It is true that even these appear to be so complicated as almost to baffle investigation, so that when William Harvey watched the beating heart, he wrote : *ita ut modo hinc systolen illinc diastolen, modo e contra, modo varios, modo confusos, fieri motus, me existimarem cernere.*[1] But beneath these phenomena, many of which have now, by the use of the graphic method, been carefully investigated, there are others of a molecular character, on which the rhythm of the heart depends, and the explanation of which is the key to some of the secrets of vital action. A few of these hidden phenomena may now be shortly considered. Much discussion has taken place as to whether the contraction of the heart is to be regarded as a simple contraction, like the "twitch" of a muscle obtained by a single stimulation, or a tetanic contraction, like cramp, such as is caused by a number of stimuli in rapid succession. It is true that many of the phenomena of a cardiac contraction resemble those of a skeletal muscle. Thus fatigue diminishes the amplitude and increases the duration of the contraction and the effects of changes of temperature are similar. The period of latent stimulation of a cardiac muscle ($\frac{1}{3}$ sec.) is much longer than that of skeletal muscle ($\frac{1}{100}$ sec.). The systolic contraction, as regards duration, is more like a tetanic spasm than a twitch, being from eight to ten times longer. The electrical phenomena on the other hand, resemble more those of a twitch than of tetanus. Thus, when the heart is examined with a galvanometer, it is found that there is a "negative variation" with each beat. It has also been pointed out that if the nerve of a rheoscopic limb is laid across a pulsating heart there is a simple secondary twitch and not a tetanic spasm, as would have probably occurred if the beat of the heart had been of the nature of tetanus. These facts, however, demand closer scrutiny.

In the study of the electrical phenomena of muscle, we saw that each contraction, whether it is a simple twitch or a tetanic spasm, is preceded by a short period of diminished excitability and electrical disturbance, and that the latter condition is an expression of molecular changes occurring before contraction, but intimately related to it. The electrical disturbance is the well known phenomenon of the *negative variation.* In 1856, Kölliker and H. Müller showed that this variation may also be seen in the beating heart, when the base of the ventricle (cut off from the

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[1] William Harvey, *De Motu Cordis.*

auricle a little above the auriculo-ventricular groove) is placed against the one cushion of the galvanometer and the apex against the other. Engelmann, in 1873, discovered that the surface of the uninjured heart exhibits no difference of electrical tension, and that the negative variation occurred in relation to the systole. The negative wave was propagated at a rate of usually 20 mm. per second. The subject has been elaborately investigated by Burden-Sanderson and Page.[1] They find that the variation, as observed in a heart rendered motionless by the method of Stannius, passes through two phases: (1) what may be termed an *initial phase*, immediately following excitation, when the excited part becomes negative to other parts; and (2) a *terminal phase*, coinciding with the relaxation of the ventricle, and the opposite to that by which the systole of the ventricle was ushered in. In other words, there is a double variation of negativity first at the apex and then at the base, seen in the systole of the excised heart. The state of excitation of each muscular element of the ventricle does not coincide in time with the period of latent stimulation, but it lasts from the beginning of the initial phase to the beginning of the terminal phase, a period, at 12° C., of about 1·8 sec. In six experiments, the initial phase began about ·03 sec. after excitation, rose rapidly, and was over by ·07 to ·08 sec. The total duration of the initial time may be stated at ·13 sec. Engelmann noticed a positive condition immediately following the initial phase, but Burdon-Sanderson and Page have not been able to corroborate this observation. The E. M. F. of the initial stage is from ·03 to ·04 Daniell. By touching the apex of the heart with a hot platinum wire it was found that the increase of temperature of the apex was without effect on the initial, but increased the terminal phase. They also found "in the inhibited ventricle, if either of the leading off contacts be injured the terminal phase disappears and the initial phase is followed by an electric condition, in which the injured surface is more positive, or less negative relatively to the uninjured surface." The rate of propagation of the exciting stage is about 125 mm. per sec. The general conclusion is that if we suppose a part of the ventricle to be excited, it at once becomes negative to every other part, and this excitory condition is propagated in all directions at a rate of 125 mm. per sec. Contraction of the fibres immediately follows this wave of excitory disturbance, so that a wave of contraction passes through the heart. This method of

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[1] Burdon-Sanderson and Page, "Time Relations of the Excitatory Process in the Ventricle of the Heart of the Frog." *Jl. of Physiology*, vol. ii. p. 384. The subject has also been investigated photographically by these observers. *Jl. of Physiology*, vol. iv.

inquiry has been applied to the mammalian heart by Waller and Reid.[1] By laying levers on the quiescent heart (removed from the body but still alive) at different points, they find that a wave of contraction passes from the point of excitation. They have also found a wave of negativity in the form of a diphasic variation (as in the frog's heart). In the frog's heart the wave of contraction passes from base to apex, but in the heart of mammals it would appear that contraction usually begins at the apex. The rate of propagation was much more rapid than in the frog's heart (100 mm. per sec. at 9°C.), being in the heart of a sheep about 8 metres per sec. It is interesting to note that with the mammalian heart the effects of excitation are precisely similar to those observed on the frog's heart, showing that the molecular process is of the same kind in both. There are, however, certain differences. Thus, in the frog's heart, we have first negativity of base followed by negativity of apex, the wave of contraction passes from base to apex, and the inference is that both waves are propagated through the muscular structure. The action of the mammalian heart is more irregular in this respect. Sometimes Waller and Reid observed a diphasic, and at other times a monophasic variation, and when the former occurred, the base at one time might be negative and the apex at another. A monophasic variation shows that the muscular structures must be the seat of excitatory processes almost at the same moment of time, and that the excitory impulses are propagated with such great rapidity as to indicate that they must be transmitted by nervous channels and not by the muscular structure, in which the rate of propagation is much slower. The wave of contraction sometimes travels from apex to base, another point of difference from the behaviour of the mammalian heart. Finally, Waller has been able to observe the variation in the normal and unexposed human heart by dipping the hand and foot in two vessels connected with a sensitive capillary electrometer.[2] Here again, as one would expect from a consideration of the facts stated above, the variation precedes the cardiac impulse.

The events constituting a *cardiac contraction*, considered as a whole, begin near the termination of the great veins in the right and left auricles. In a slowly contracting heart, the wave of contraction begins at the junction of the veins with the auricles, passes a little way along

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[1] Waller and Reid, "Action of the Excised Mammalian Heart." *Phil. Trans.* 1887, B.

[2] Augustus D. Waller, "Electro-motive Properties of Human Heart." *British Medical Journal*, October 6th, 1888.

the veins and then onwards over the auricles, and from these over the ventricles. If this portion of the vein, which seems to be the starting point, be cut off by a clamp from the auricles, rhythmic movements still continue in the veins. Both sides contract simultaneously. This I have frequently seen demonstrated by placing light levers over the exposed heart, and bringing them into contact with a rapidly moving cylinder.

The question as to whether the rhythmic movement of the heart depends on molecular processes in muscle, or in nervous tissue, or in both combined, is very difficult to answer, but it lies at the foundation of any theory that will explain the cardiac beat. We know that rhythm occurs in many tissues that are apparently non-nervous, such as pulsating organs of many invertebrates, the contractile tissue of *medusæ*, the early embryonic heart, the cardiac muscle of the heart of the tortoise, the non-striped muscle in the ureter, etc.; but in all these situations the tissue may be regarded as a compound nervous and muscular substance, so that it is impossible to dissociate the two. Both tissues, in certain conditions, discharge rhythmic impulses, and it is not unlikely that the rhythm of the purely muscular structure may only be called into action by rhythmic impulses starting from truly nervous tissue. In the heart, every element of muscular tissue may respond in this way. Thus, as shown by Waller and Reid, rhythmic contractions occur in the excised heart of the rabbit and dog, and the beat of the auricles is independent of that of the ventricles. The ventricles can keep up an independent rhythmic movement even after they have been divided from the auricle. From certain experiments by Wooldridge, Tigerstedt, and M'William, it would appear that independent rhythmic movement occurs in ventricular tissue, as, for example, near the apex, where no nerve cells can be found. The origin of this rhythm is therefore *myogenic* and not *neural* but the rhythmic power is probably not the same in all parts, so that, if we conceive one part of the heart substance to have a higher power of rhythm than another part, the rhythm of the former will supersede the inherent rhythm of the other parts, and determine the rate of contraction of the whole organ (M'William). Thus the rhythm of the ventricle and of the auricle is the same in rate while they are connected, but when disjoined the ventricle beats more slowly than the auricle, and the latter retains the rate of the normal rhythm. Again, the rhythm of the veins would appear, in a sense, to govern that of the auricles, and it may be regarded as the dominant rhythm. Starting then in the veins, the rhythmic movement sweeps downwards by muscular conduction into the auricles; but it is not easy to understand how the rhythm is propagated into the ventricles, as these are histologically separated from the auricles. One can conceive that the electrical variation in the auricular part acts as a stimulus to the ventricular tissue. Thus, suppose an ordinary muscle supplied by a nerve. The nerve breaks up into finer and finer branches until the terminal fibres end in *end-plates* in certain of the muscular fibres, but not in all. Many muscular fibres have no nerve termination, there are muscular areas destitute of nerves, and still these fibres contract by some kind of stimulus propagated to them from the fibres that received the nerve stimulus. Kühne[1] has suggested that a nerve only throws a muscle into contraction by means of its currents of action, and that the negative variation of one muscular fibre is, as in Matteucci's experiment of the induced contraction (see Vol. I. p. 452), the stimulus of those lying near it. M'William suggests this hypothesis as applicable to the heart, but rejects it, and holds to the ordinary explanation that the propagation of the contraction from auricles to ventricles is effected through nerve fibres. It is difficult to imagine any kind of nervous arrangement which would account for the transmission of nervous impulses from auricle to ventricle, so that the beat of the ventricle immediately follows that of the auricle, without assuming the existence of ganglia in which nervous energy is stored up and liberated at certain intervals of time. No ganglionic mechanism is necessary to explain the rhythm in the veins and in the auricle, and the rhythmic movements of the wall of the latter will go on even when the wall has been cut into the form of a ribbon with transverse incisions so made as to leave only slender bands connecting the consecutive parts. Suppose then rhythmic impulses to arise in the auricle, it is not easy to see how these can affect any ganglionic centres in the ventricles so as to cause an accumulation of energy in these which, in turn, bursts out at intervals so as to control the rhythm in the tissue of the ventricles. The electric hypothesis appears to me to be less free from difficulties than the nervous one.

Roy is of opinion that the nervous elements in the walls of the *sinus venosus* and of the auricles regulate the work of the heart,[2] while those in the ventricles have only the power of regulating the rapidity with which the contractions follow each other. He attaches great importance to the fact discovered by the use of his tonometer, that the elasticity of the ventricular wall is remarkably perfect, and that the ventricle is most distensible with the forces of such a strength as act on it

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[1] W. Kühne. Croonian Lecture. "On the origin and the causation of vital movement." *Proceedings of Royal Society*, vol. xliv. p. 427.

[2] C. S. Roy, "Influences modifying the work of the heart." *Jl. of Physiology*, vol. i. No. 6.

in the living animal. It follows that the force distending the ventricle depends on the strength of the auricular contraction, and, in turn, it is the auricular contraction that is mostly under the influence of the nervous system. From this point of view, the auricle is a more highly developed organ than the ventricle, and the molecular changes in the auricle are of the greatest importance in determining not merely the rhythm but even the work of the heart in the living animal. From this point of view, it will be seen that the *intracardiac pressure* forms an important factor among the causes of the heart-beat.

So long ago as in 1880, Gaskell[1] investigated this question by a study of the behaviour of the apex of the frog's heart, which contains no ganglion cells, and in his experiments he endeavoured to vary the stimulus both as to strength and character. He showed (1), that the spontaneous beats of the apex depend upon the pressure in the cavity rather than on the blood supply; (2), that a weak alkali added to the blood with which the apex is fed brings it from a position of relaxation to one of contraction; (3), that a weak solution of lactic acid brings the apex to a stand-still in diastole; and that antiarin and digitalin act like an alkaline solution, while the influence of muscarin is more like that of lactic acid. These experiments indicate that a slight change in the character of the fluid bathing the tissue elements of the heart may affect its rhythm, or in other words, that the heart beat depends on *phenomena of nutrition.*

In a suggestive paper dealing with an experimental inquiry into the innervation of the heart, more especially that of the tortoise, Gaskell[2] makes the following statement:

> (1) The power of independent rhythmical contraction decreases regularly as we pass from the *sinus* to the ventricle; (2) The rhythmical power of each segment of the heart varies inversely as its distance from the *sinus*; (3) A strip cut from the apex of the ventricle can be caused to beat rhythmically at the same rate as that of the sinus or auricle by the trophic action of nutrient material or of the interrupted current; (4) A wave of contraction passes along the auricle and induces a ventricular contraction when it reaches the auriculo-ventricular groove; (5) By cutting up the auricle so as to have one portion attached to the *sinus* and the other to the ventricle, a wave of contraction passes up the strip stretching from the *sinus* to the thin bridge, across the bridge, and then after a slight pause down the strip from the bridge to the ventricle, and then the ventricle contracts (see Plate A, Fig. 4, on the left, in which a ventricular follows each auricular beat); (6) If the auricle be slit so as to make the bridge narrower, only *every second* contraction passes over, and then it excites a ventricular contraction, but the ventricle never responds to the beat of the auricle that does not pass across the

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[1] W. H. Gaskell, "Tonicity of the heart." *Jl. of Physiology*, vol. iii. No. 1.

[2] W. H. Gaskell, "The innervation of the heart, with special reference to the heart of the tortoise." *Jl. of Physiology*, vol. iv. No. 2.

bridge (see Plate A, Fig. 4, on the right, where evidently a ventricular beat is lost); and (7) When the bridge is made very narrow then the "block" is complete, and any contractions the ventricle may then make are independent of those of the *sinus* and of the auricle.

It thus becomes clear that the ventricle contracts after the auricle only when an impulse travels to the auriculo-ventricular groove. Further, from observations made on the cardiac nerves in the heart of the tortoise, in which he finds that they have no power on the force of the ventricular contractions (see Plate B, Fig. 7), but that nervous arrangements exist by which the ventricle regulates the force of the auricular contraction, Gaskell makes the important suggestion that many of the nerve fibres passing from auricle to ventricle may convey impulses from the latter to the former, regulating the amount of blood thrown into the ventricle, and thus also regulating the work done by the heart. Thus there is a correlation established between auricle and ventricle, the one reacting on the other. Gaskell has also demonstrated that stimulation of the cardiac nerves increases the conductive power of the auricular substance, so that after a partial "block" had been caused by division of the auricle as above explained, so that only every second contraction passed, after stimulation of the nerves every contraction passed. Sometimes, however, such stimulation seemed to increase the block, see Plate B, Fig. 10, in which every second contraction passed before stimulation of the right vagus and coronary nerves, while no contraction passed during stimulation. Thus the action of the nerve stimulus may be usually and normally to *hasten* the recovery of the conducting power of the muscular tissue, and thus facilitate the transmission of the contraction wave. This view leads the way to the valuable suggestion of Gaskell that the influence of the vagus (the so-called inhibitory influence) is to intensify function and that it may be regarded as the *trophic* nerve of the heart, that is to say, it depresses or exalts the different functions of the heart-muscle, as regards rhythm, contraction, tone, conduction, or excitability. Gaskell thus contrasts the properties of the three varieties of muscle found in the body :

I. *Striated muscle of vertebrates:* (1) rapidity of contraction most highly developed ; (2) tonicity rudimentary ; (3) rhythmic action still more rudimentary: II. *Cardiac muscle:* (1) rhythmic action most highly developed ; (2) rapidity of contraction well marked ; (3) tonicity well marked : III. *Unstriped muscle:* (1) tonicity most highly developed ; (2) rhythmic action well marked ; (3) rapidity of contraction most rudimentary.

This comparison shows in a striking manner that the behaviour of cardiac muscle may be accounted for if we regard it as not only structurally but physiologically intermediate between plain and striated muscle. Considering contraction alone, we find the three varieties: (1) rapid contraction, most marked in striated fibre; (2) tonic contraction, most marked in plain fibre, and (3) rhythmic contraction, most marked in cardiac muscle. In some circumstances, however, each variety may manifest the predominant characteristic of one or other of the remaining two, as when the unstriped muscle of the ureter contracts rhythmically, or when the striated *sartorius* of the frog beats rhythmically in Biedermann's fluid,[1] or when the cardiac muscle develops a tonicity similar to that of unstriped muscle when tetanized, or shows rapid fibrillar contractions like those of striated muscle.

To return to the ganglionic nerve cells. The heart of the tortoise, (although each part of this heart possesses the power of spontaneous rhythmical contraction, as shown by Gaskell,[2]) contains two kinds of nerve cells:[3] (1) *motor*, most excitable in the *sinus* and at the junction of the sinus with the auricles, less excitable in the wall between the auricles, and least excitable at the junction of the auricles and ventricle; and (2) *trophic*, which are distributed throughout the course of the nerve fibres passing from the sinus to the ventricle. The vagus acts on both of these classes. If the impulses reach the motor group the rate of rhythm is affected, and if they reach the trophic, they affect the force of the contraction, the conduction, and the tonicity. These views are generally supported by Wesley Mills.[4]

Following out the indications afforded by these and other inquiries, Gaskell has been led to the profound conception that the apparently opposite action of the fibres of the vagus and of the sympathetic on the heart is due to their influence on the nutritive processes occurring in the cardiac tissue. It is well known that prolonged stimulation of the sympathetic nerve soon exhausts the energy of the beating heart so that the beats become weaker. Gaskell observed on the contrary, that while stimulation of the vagus diminishes the energy of the heart beats for a time, when the stimulation ceases the heart beats as strongly, or more strongly than before. The action of the vagus is apparently to improve the condition of the heart, so that the sympathetic may, in consequence of stimulation of the vagus, regain some of its lost power over the heart.

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[1] See Vol I. p. 420.

[2] W. H. Gaskell, "On certain points in the function of cardiac muscle." *Proceedings of the Cambridge Philosophical Society*, vol. iv. 1882.

[3] W. H. Gaskell, "On the innervation of the heart of the tortoise." *Jl. of Physiology*, vol. iii.

[4] T. Wesley Mills, "The innervation of the heart of the Slider Terrapin." *(Pseudemys rugosa.) Jl. of Physiology*, vol. vi.

Thus we may compare the action of the sympathetic fibres to that of a motor nerve in a muscle, leading to destructive metabolism, or *katabolism*, while on the other hand the action of the vagus fibres has to do with constructive metabolism, or *anabolism*. The sympathetic fibres excite processes of decomposition by the splitting up of the complex muscle-protoplasm into simpler bodies, and the vagus fibres, on the other hand, excite processes of repair. The vagus fibres are, therefore, *anabolic*, while those of the sympathetic are *katabolic*. These are terms more expressive than *inhibitory* and *motor*, because they indicate the nature of the processes in which the nerve fibres are engaged.[1] Is inhibition an indication of katabolism? How can this be discovered? Only by minutely examining the molecular processes occurring in connection with it, and as the most convincing proofs of molecular processes in muscle are derived from an investigation of the electrical phenomena connected with them, it is to this field of inquiry we must turn.

It is well known that the action of a nerve-ending on the protoplasm of muscle is to cause a katabolic change, which finds a physical expression in a fall of electrical potential at the stimulated point, that is to say, the stimulated point becomes negative to any other part of the muscle substance. On the other hand, an anabolic change might be reasonably expected to cause a rise of electrical potential, so that when the change occurred the part would become positive to any other part of the muscle. In the case of the heart, Gaskell has shown that when the vagus is stimulated in the neck of the tortoise, and when a preparation has been made from the heart by cutting away the sinus and part of the auricles without cutting the coronary nerve, there is always an *increase of positivity*. Here the nervous influence which causes *inhibition* produces positivity, so that "the cardiac muscle under the influence of an inhibitory nerve becomes positive to the quiescent muscle, just as the contracted muscle becomes negative to the uncontracted."[2] He has further shown that by stimulating the sympathetic nerve negativity of the tissue is produced.[3] This important observation strongly confirms Gaskell's theory of inhibition.

A consideration of these facts enables us to offer the following explanation of the phenomenon of the heart beat. By long-continued hereditary transmission, the variety of muscle constituting the heart

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[1] W. H. Gaskell, "Structure and Function of Visceral nerves." *Jl. of Physiology*, vol. vii. See also "The inhibitory actions and inhibitory nerves in general." *Trans. of the Eighth Session of the International Medical Congress in Copenhagen*, 1884.

[2] W. H. Gaskell, "Ueber die Elektrischen Veränderungen, welche in dem ruhenden Hertzmuskel die Reizung des Nervus Vagus begleiten." *Beiträge zur Physiologie. Carl Ludwig's Festschrift.* See also *Jl. of Physiology*, vol. vii.

[3] W. H. Gaskell, "Muscarine and Cardiac Electric Changes." *Jl. of Physiology*, vol. viii.

manifests the fundamental property of rhythmical contraction to a greater extent than any of the other properties of muscle. This tendency to rhythm is located chiefly towards the base of the heart; that is to say, the tissues in the region of the ends of the great veins and in the auricle manifest this property to the greatest extent. The rhythm thus induced is propagated along the auricles to the auriculo-ventricular groove, and the electrical variation caused by the rhythm of the auricles, aided by the increased cardiac pressure produced in the ventricles by the flow of blood into them, causes these also to contract, or, in a sense, calls into play the rhythmic tendency which is also a characteristic of ventricular tissue. In the hearts of fishes and amphibians these arrangements, depending ultimately on nutritional changes, are almost all that is necessary to carry on the pulsations of the slowly moving heart; but in birds and mammals there is added a mechanism of nerve centres, influenced in turn by extrinsic nerves, to secure more rapid and more simultaneous contractions. This intra-cardiac nervous mechanism appears in the hearts of fishes and amphibians, but it probably does not assume so much importance in these as it does in the heart of the bird or mammal, and it is at all events certain that the heart of the fish and amphibian is less influenced by the extra-cardiac nerves. Even in the heart of the bird and mammal, however, it is probable that the intra-cardiac ganglia have more of a co-ordinating function than that of the generators of nervous energy that keep up the rhythm. Thus they may influence the intra-cardiac pressure, and thus control the work of the heart, by securing that the walls of its cavities contract to the extent required under ever-varying circumstances. The rhythm, however, is influenced by the direct action of extra-cardiac nerves on the nutritive changes going on in the muscular elements of the heart, influences passing along fibres of the sympathetic which act like the motor fibres of a muscle, and hence causing katabolic processes, while other influences occasionally pass along certain of the fibres of the vagus which have an opposite effect producing anabolic changes, by which the molecular processes for building up the muscular tissue are facilitated. As katabolism is known to be associated with action, that is contraction, so anabolism must be associated with rest, or with that kind of action we have hitherto termed inhibition. Finally, the electrical variations are not only one of the physical expressions of the molecular changes occurring in the cardiac tissue, but in all probability they play their part by acting as stimuli to cardiac fibres. Thus the ultimate processes of nutrition constitute the basis of all cardiac phenomena.

B.—The Blood-Vessels.

Chap. I.—GENERAL PHYSICAL CONSIDERATIONS.

Before studying the complicated phenomena of the flowing of the blood in the arteries, capillaries, and veins, it is necessary to take a brief survey of those general principles that regulate the pressure and the flow of fluids in tubes, rigid and elastic.

One of the fundamental propositions of hydrostatics (the principle of the equal transmission of pressure) is that a pressure on any area, A, of the surface of a fluid is transmitted equally and at right angles to every portion of the surface having an area equal to A. Suppose a vessel of any shape to be filled with water, the pressure exerted upon its bottom will be equal to the weight of a vertical column of water, the base of which is equal to the area of the bottom and the height of which is equal to the height of the fluid. The sides of the vessel are also subject to pressure, and the pressure exerted on any area on the side of the vessel will be equal to the weight of a column of fluid the area of which is equal to that of the area on the side of the vessel, and the height of which is equal to the depth of the area from the surface of the water. If a hole were made in the side of the vessel, the fluid would escape as a jet; and if arrangements had been made for maintaining the height of the fluid in the vessel, the rapidity of the outflow (into vacuum) would be that gained by a body falling from the level of the surface of the fluid to the level of the aperture; that is, the rapidity of the outflow in unit of time would be as the square root of twice the height of the fall multiplied by gravity, $v^2=2gs$, or the square root of the height of the pressure. The rate of efflux from the aperture, or the rate at which the fluid flows out, depends on the velocity of the fluid and the size of the aperture. If k be the area of the aperture and v the velocity, then, in a unit of time, a portion of liquid will have passed through the aperture equal to a length, v, of a cylinder of which k is the base, therefore vk is the quantity which flows out in a unit of time, or vk is the rate of efflux. This is strictly true when the fluid issues from a tube of some length, so that no contracted vein is formed. If there is no pipe, but only a hole in the side of the vessel, then there will be such a vein, and k must be taken as its section. Suppose, however, that a tube were fixed horizontally into the hole in the side of the vessel, a part of the pressure would be used in overcoming the frictional resistance of the fluid in the tube, and consequently the rapidity of outflow would be diminished, and the longer the pipe the greater would be the diminution. When a fluid passes along a tube, the layer next the wall of the tube may be regarded as immovable, so the friction which the pressure has to overcome is not that of the fluid on the wall of the tube but the cohesion of the central core of fluid to the thin skin of fluid next the wall of the tube. Again, we may consider the fluid in a tube as consisting of several layers, one next the wall of the tube practically immovable, another nearer the centre moving with a certain velocity, a third still nearer the centre moving more rapidly, until we reach the central stream where the velocity is greatest.

The movements of fluids in rigid tubes may be experimentally studied by connecting together pieces of glass tubing, of equal calibre, having vertical tubes (*piezometers*) from 2 to 4 metres high, of the form of an inverted T, thus ⊥, inserted at various distances in the course of the horizontal tube. To one end of the long horizontal tube is connected by india-rubber tubing a pressure-bottle full of water, which may be raised to any required height so as to graduate the pressure.

When a clip is taken off the india-rubber tubing, between the pressure-bottle and the horizontal tube, the rise of water in the piezometers indicates the amount of pressure at the position of each piezometer. It will be seen that the side pressure in the horizontal tube is highest nearest the pressure-bottle, that it is less and less as we recede from the source of pressure, and that it reaches zero at the far end of the horizontal tube, from which the fluid is flowing. Thus it also appears that in tubes of equal calibre the resistance due to internal friction is proportional to the length of the tube. The rapidity of outflow from tubes is directly proportional to the cross-sectional-area (d, diameter; circumference $= 3{\cdot}14\, d$, and cross-sectional-area, or *lumen* $= \frac{3{\cdot}14}{4} . d^2$), and inversely proportional to the length of the tube. In a tube of uniform calibre, fluid will flow through each cross-sectional-area with a certain velocity, which will diminish in proportion to the length of the tube and the amount of friction.

The *mean rapidity* may be regarded as equal in all parts of the tube, and it varies: (*a*) with the *calibre* of the tube, increasing as the calibre becomes greater; (*b*) with the *length* of the tube, the shorter the tube, the greater the rapidity; (*c*) with the *pressure*, the rapidity increasing as the square root of the pressure, except in capillary tubes, when it is directly as the pressure; (*d*) with the *nature of the fluid*, thus water will flow in a tube with twice the velocity of serum and four times the velocity of blood, viscous fluids moving more slowly than limpid fluids; (*e*) with the *temperature* of the fluid, increasing as the temperature rises with a given fluid; and (*f*) with the degree of *friction* in the tube, being slower where the friction is great, and faster where it is small. The *volumes* of the fluids discharged are proportional to the squares of the diameters of the discharging tubes, except in capillary tubes, when they are proportional to the fourth power of the diameters. In tubes of unequal calibre, at different parts of their course, the *velocity* of the current varies—it is slower in the wide part of the tube and more rapid in the narrow parts. In tubes of unequal calibre, the *pressure* does not diminish uniformly from point to point of tho tube: in the wide part of the tube the pressure is greater, but in the narrow portions it is less, than the sum of the resistances to be overcome. When a fluid passes from a wider to a narrower tube there is a sudden increase, and when from a narrower to a wider tube, a sudden diminution, of pressure; the pressure rises in front of a narrowing in the calibre of the tube and it falls before widening.

Twistings and bendings of tubes increase the *resistance*, as the fluid presses more on the convex than on the concave side of the bend, thus increasing the resistance on the convex side. Division of a tube into two or more branches increases the resistance and diminishes the propelling power. If we have to deal with a system of tubes instead of with one tube, the same amount of fluid passes through any given cross-sectional-area of the system, and therefore the rapidity of the stream is inversely proportional to the cross-sectional-area, diminishing as the cross-sectional-area increases.

As we pass from the arteries to the capillaries, the area of the system of smaller vessels is always greater than the area of the parent vessel from which they spring, the only exception being that the area of the abdominal aorta is greater than that of the two common iliac arteries. In the circulation, instead of a pressure derived from a head of water, such as we have considered in the experiment with piezometers, we have that exerted by the pulsations of the heart. The heart, however, does not exert pressure constantly but intermittently, and we have also to deal in the arteries not with rigid but with elastic tubes. If we pump water intermittently through a rigid tube it will issue from the tube in a series of spurts or jets, each corresponding with a stroke of the pump, but if we pump the water into an elastic tube of sufficient length, it will issue as a continuous stream. This is the condition of the flow of blood in the capillaries, in which there is a continuous stream, although it is forced onward by the intermittent action of the heart, and it leads us to the consideration of the flow of fluids in elastic tubes.

When a stream of water is transmitted intermittently by a series of strokes of a pump, through a long elastic tube, formed, say of india-rubber, the fluid does not issue from the other end in a series of jets, which would be the case if the tube were rigid, but it flows continuously, as in the pause between the successive strokes of the pump, the outflow still continues. Consequently a continuous flow occurs in elastic tubes when the time between two strokes of the pump is shorter than the duration of the outflow after the first stroke. If the finger be placed on any part of such a tube, and more especially near the pump, an expansion and relaxation will be felt with each stroke. Further, if the right fore-finger be placed over the tube near the pump, and the left fore-finger over a more distant portion, a stronger impulse will be felt with the right than with the left. There is thus the transmission of a *wave* along the tube, the wave diminishing in *amplitude* as the distance from the pump increases. One must distinguish between the transmission of this wave (an oscillatory movement or change of form in the column of fluid) and the transmission of the current, that is the translation of a mass of fluid along the tube. Thus, in elastic tubes, the current is much slower than the transmission of the wave. The progress of the wave of oscillation requires careful study, as it has an important bearing on the phenomenon of the pulse.

The wave may be traced graphically by an apparatus devised by Marey, a portion of which is shown in Fig. 133. It consists of a rectangular wooden box, open at both ends, having in its interior a tambour which is carefully adjusted over the elastic tube. The slightest expansion of the tube acts on the tambour and is conveyed by the tube in connection with the registering tambour. By placing a series of these box-tambours at regular intervals along an elastic tube, shut at one end, and connecting each with a registering tambour as seen in Fig. 134, the various

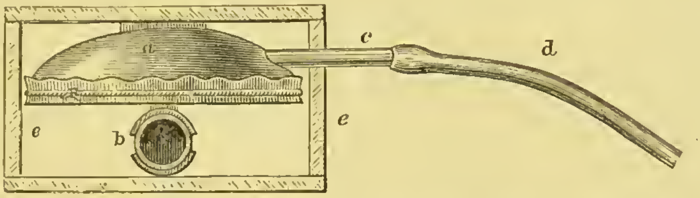

FIG. 133.—Section of an apparatus for transmitting the movement of an elastic tube to a recording tambour; *a*, tambour, placed in a wooden box, *e*, *e*, having the membranous surface adjusted over the tube *b*; *c*, tube passing from tambour and attached to the recording tambour by the india-rubber tube *d*. (Marey.)

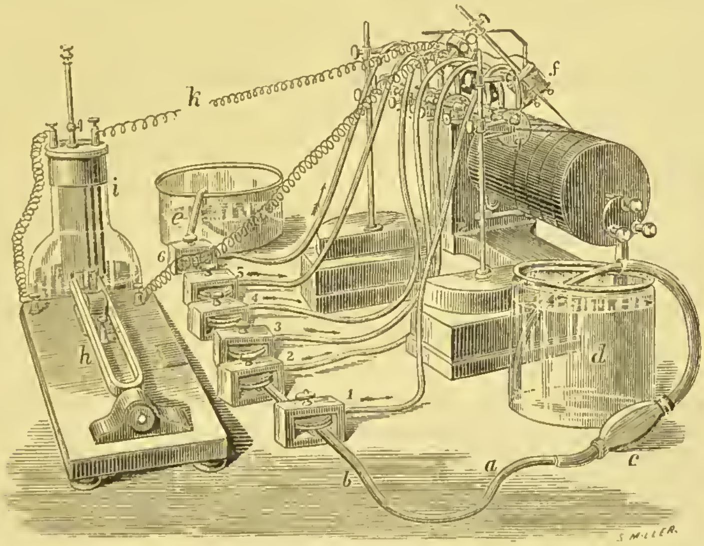

FIG. 134.—Arrangement of apparatus in the experiment for registering the movement of a wave along an elastic tube; *a*, *b*, long elastic tube of india-rubber, passing from the vessel *d* under the tambours, 1, 2, 3, 4, 5, and 6, to the vessel, *e*. Force-pump, or syringe, seen at *c*. Each receiving tambour is connected with a recording tambour and all are adjusted to the cylinder as at *g*; *f* is the chronograph, worked by the current from the battery, *i*, interrupted by the tuning fork, *h*. The small arrows indicate the direction of the impulse from the receiving to the recording tambour.

phenomena may be recorded with precision. The experiment is conducted as follows: after adjusting all the tambours and the chronograph so that they can be

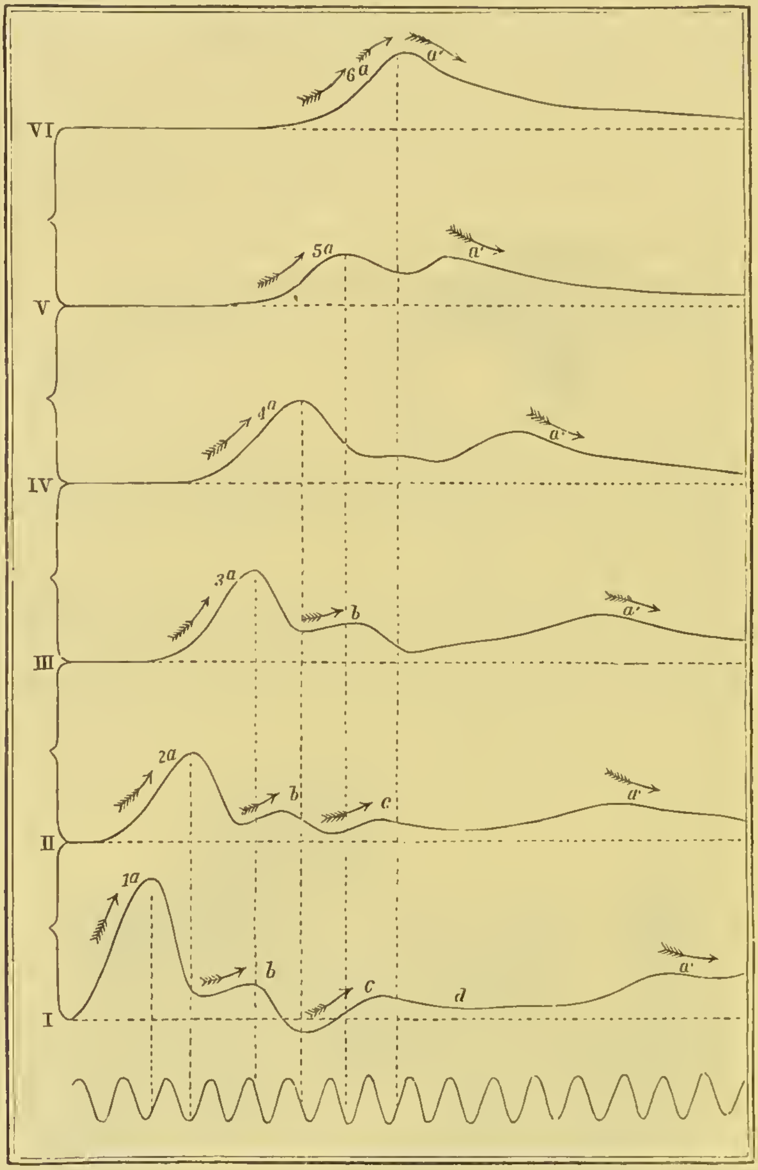

Fig. 135.—Tracings of the movements of a wave in a shut elastic tube. The length of the horizontal dotted lines i to vi represents time, as registered by the chronograph = 50 vibrations per second. The tambours were placed at distances of 20 centimetres along the elastic tube, so that from i to ii, from ii to iii, from iii to iv, from iv to v, and from v to vi the distance is 20 centimetres. The letters *a*, *b*, *c*, *a'*, in the six superposed tracings, mark each the summit of the same wave, and thus its progress may be followed. Thus 1*a*, 2*a*, 3*a*, 4*a*, 5*a*, and 6*a* indicate the progress of the wave *a*, and the arrows indicate the direction in which it is propagated. When the positive wave reaches the shut end of the tube, it is reflected, and the course of the reflected wave is indicated by the letters *a'* 6, *a'* 5, *a'* 4, *a'* 3, *a'* 2, and *a'* 1. The secondary waves are indicated by the letters *b*, *c*, *d*; thus *b* is the second wave, *c* the third, *d* the fourth. It will be observed that these waves are much less marked; *b* does not pass beyond the third tambour, that is to say, it traverses only a distance of 40 centimetres; while *c* does not pass beyond 20 centimetres. The arrows on the right, above *a'*, should be reversed. (Marey.)

brought into contact with the cylinder when it has attained its maximum velocity, a sudden impulse is given to the force-pump, *c*, so as to send a wave along the elastic tube, and at the same moment the recording tambours and chronograph are brought into contact with the cylinder. The tambour 1 acts first, then 2, 3, and so on, each inscribing its curve on the cylinder, and time is registered by the chronograph (Fig. 134). This tracing shows: (1) the *rapidity* of the propagation of the wave; (2) the *movement of the reflected wave;* (3) the changes in *height* of the wave at different parts of its course; (4) the successive changes of *form* of the wave; and (5) the formation of *secondary waves* from a single impulse. The *rapidity* of the wave may be ascertained by measuring the time which ensues between the instant of its appearance under the first tambour, and the moment it appears under the second. Thus if we draw a line from the summit of each wave down to the chronographic tracing (see Fig. 135), the rapidity may be measured with ease, and it will be found that in this experiment the wave travels 20 cm. in $\frac{1}{50}$ sec.—that is, the wave has a velocity of about 10 metres per second. The chief point to notice with regard to the *reflected* wave is that it almost blends with the advancing wave near the shut end of the tube (see line vi, 6 *a* and *a'* in Fig. 135), and that it is further and further distant from the advancing wave as we pass in the direction of the force-pump. It will also be seen that the wave has two maxima, as regards amplitude, one at each end of the tube, and that the minimum is in the middle of the tube. After an exhaustive research conducted in this manner by Marey, he arrives at the following amongst other conclusions, all of which have an important bearing on the hydraulics of the circulation, and on a correct explanation of the pulse:[1] (1) When a fluid enters intermittently and rapidly an elastic conduit, it forms a series of *positive* waves, which are transmitted with a velocity independent of the movement of translation of the fluid; (2) The *rapidity* of the transmission is proportional to the elastic force of the tube; it varies in inverse ratio with the density of the fluid employed; it diminishes gradually in the progress of the wave; and it increases with the rapidity of the impulsion of the fluid; (3) The *amplitude* of the wave is proportional to the quantity of fluid entering the tube, and to the suddenness of its entrance; it diminishes gradually during the course of the wave; (4) When the afflux of fluid in the tube is short and energetic, it may also form, with a single impulse, a series of *secondary waves*, according to the laws of vibratory movement; (5) When fluid enters the tube in great quantity, and for a sufficiently long time, its prolonged afflux is opposed by a retrograde oscillation which gives origin to secondary waves; (6) When fluid is propelled into two branched tubes, of similar calibres and thicknesses of walls, a very complicated mixture of waves passes from the one tube into the other. But, in the conditions of the circulation of the blood, the aorta does not permit the passage of waves from one artery into another. The aorta has its proper waves, which it transmits into all the arteries, to be there transformed, more or less; but, on the other hand, the aorta acts as an elastic reservoir for all waves passing backwards from the arteries, absorbing them completely, so that the waves of each artery are peculiar to itself, and are never transmitted into any other artery or arteries; (7) When a fluid is intermittently propelled through two tubes of equal lengths, the one rigid and

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[1] Marey, "Mouvement des Ondes Liquides." *Physiologie Experimentale*, 1875, p. 87.

the other elastic, more fluid will be discharged in a given time by the elastic than by the rigid tube. If an elastic tube become suddenly narrowed, or if the amount of fluid in a given length of tube be suddenly increased or diminished, as by pressing or sucking, a *negative* wave will be formed. It is important to notice the distinction between the rapidity of the progression of the wave in the wall of the tube and the rapidity of the flow of fluid in the tube.

E. H. Weber gives the velocity of waves in an elastic tube of 35·5 mm. in diameter and 4 mm. in thickness of wall at 11·5 metres per second, and Donders states it at 11-13 metres per second (34-44 feet). Increase of pressure in the tube lessens the velocity of the wave. The specific gravity of the liquid also affects the velocity. Thus the wave is propagated four times more slowly in mercury than in water. Moens has formulated the following laws as to the *velocity* of propagation of waves in elastic tubes:—(1) It is inversely proportional to the square root of the specific gravity of the fluid; (2) it is as the square root of the thickness of the wall, the lateral pressure being the same; (3) it is inversely as the square root of the diameter of the tube, the lateral pressure being the same; (4) it is as the square root of the elastic co-efficient of the wall of the tube, the lateral pressure being the same.

The application of these facts to the phenomena of the circulation will be seen in discussing the circulation in the arteries.

CHAP. II.—THE STRUCTURE AND PROPERTIES OF THE BLOOD-VESSELS.

The blood-vessels consist of the *arteries* carrying the blood from the heart and terminating in the *capillaries*, in which the blood is brought into intimate relation to the tissues; these again empty into the *veins*, which convey the blood back to the heart.

An **Artery** has three coats: (1) *tunica intima*, (2) *tunica media*, and (3) *tunica adventitia*. The *tunica media* shows a transverse, while the other two show a longitudinal, disposition of their structural elements. The structure and thickness of the coats vary according to the size of the artery, and therefore we may divide arteries into small, medium-sized, and large arteries. By a *small* artery, or *arteriole*, we understand the arteries shortly before their transition into capillaries. The inner coat of such vessels (*tunica intima*) consists of elongated spindle-shaped endothelial cells and of a structureless elastic membrane, often perforated with holes, and hence (especially in arteries of larger size) termed the *fenestrated membrane of Henle*. The middle coat (*tunica media*) consists of a single layer of smooth muscular fibres arranged spirally or circularly round the tube. In arteries somewhat larger than arterioles this layer is more complicated. The outer layer (*tunica adventitia*) is formed of bundles of connective tissue fibres, mingled with elastic fibres. Next, we have arteries of *medium* size (Fig. 138), and under this name we may include all the arteries of the body except the aorta and the pulmonary artery. In these the *tunica intima* has become thicker, owing to the development of a network of elastic fibres and of connective tissue (enclosing flattened cells) being interposed between the endothelial layer and the fenestrated membrane. The *tunica media* contains not only several layers of involuntary muscle, but also widely-meshed networks of fine elastic fibres. The *tunica adventitia* is also thick. A layer of strong elastic fibres exists at the boundary with the *tunica media*; this layer has been termed the *elastic layer of the tunica adventitia* (Fig. 138, A, *e*). Involuntary muscular fibres, in small longitudinal bundles, also occur in the *tunica adventitia* of medium-sized vessels.

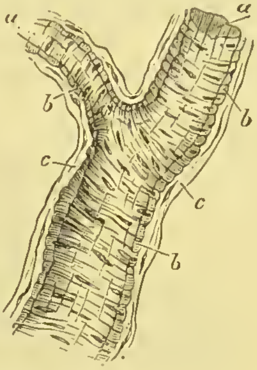


FIG. 136.—An artery of intermediate size: *a*, *a*, openings of branches and positions of lining of vessel; *b*, *b*, *b*, muscular coat showing transverse nuclei; *c*, *c*, coat of areolar tissue.

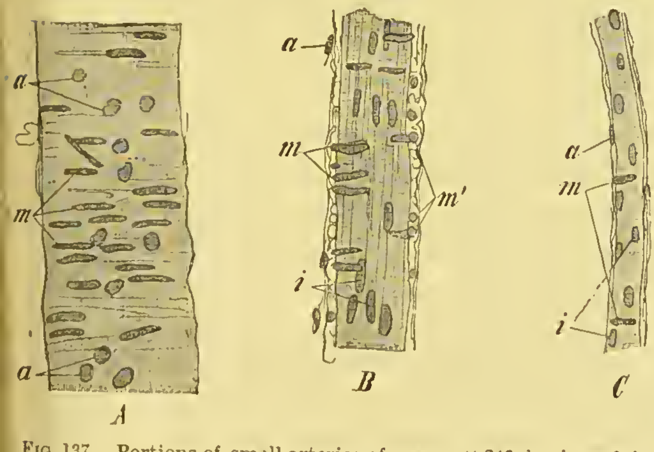


FIG. 137.—Portions of small arteries of man. × 240 d. *i*, nuclei of *tunica intima*, the contours of the cells not being seen; *m*, *tunica media*, showing the nuclei of the transverse layer of smooth muscle; *a*, nuclei of *tunica adventitia*; *A*, artery, outer surface; *B*, artery, view of inner surface. At *m'* observe section of nuclei of muscular layer. *C*, arteriole before transition into capillary. The *tunica media* consists here of isolated cells of involuntary muscle. (Method No. 57, Appendix.)

FIG. 138.—Portion of a transverse section of the brachial artery of man. × 50 d. *J*, *tunica intima*; the winding line is the elastic internal sheath. *M*, *tunica media*; observe the small rod-shaped nuclei of the muscular layer; *A*, *tunica adventitia*; containing *vasa vasorum*; *e*, elastic layer. At × we see a transverse section of a few muscular fibres. (Method No. 58, Appendix.)

In the case of *large* arteries (aorta and pulmonary), the *tunica intima* shows endothelial cells of a polygonal form. The layers of connective tissue below these cells are denser than in the medium sized arteries, and they are mixed with a considerable amount of elastic tissue and connective tissue cells. These layers also form networks, the meshes of which become denser as we approach the *tunica media*, and finally they pass over into a fenestrated membrane which is the representative of the elastic layer in the *tunica intima* of small and medium sized arteries. The *tunica media* of large arteries contains a vast amount of elastic tissue, far surpassing the muscular elements. In place of thin networks, there are dense masses of strong elastic tissue alternating with layers of smooth muscle. These elastic layers are also well developed in the carotid arteries. Both the elastic and the muscular layers are arranged circularly round the tube, and layers of muscle also run obliquely through the layers of elastic tissue. The *tunica adventitia* of the large arteries is similar to that on medium sized ones, with the exception that it has no special elastic layer. As a general rule, the coats of the smaller arteries show a considerable development of the muscular coat, whilst in the larger it is the elastic coat that attains the preponderance. In many of the larger arteries there are longitudinal muscular fibres at the boundary of the middle and inner coat. Such are met with in the aorta, iliac, superior mesenteric, splenic, renal, external to the middle coat, and in the umbilical arteries, there is a longitudinal layer internal, and another external to the circular layer. (Schäfer.) Whilst the circular fibres, on contracting, must narrow the calibre of the artery, the longitudinal may tend to keep the vessel open. In the external coat of the larger arteries, minute vessels, *vasa vasorum*, exist for the nourishment of the tissue elements of the arterial wall.

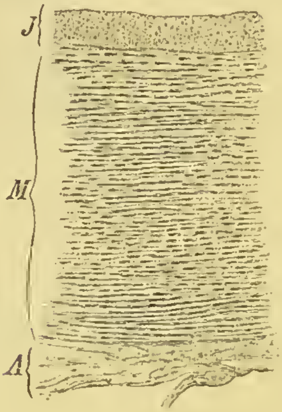


FIG. 139.—Portion of a transverse section of the thoracic aorta of man. × 50 d. *J*, *tunica intima*; *M*, *tunica media*, the clear lines or bands represent elastic elements; *A*, *tunica adventitia*. (Method No. 59, Appendix.)

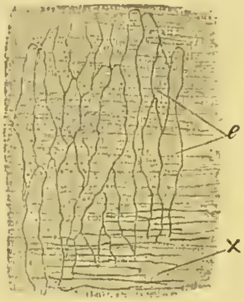


FIG. 140.—Endothelium of the artery of a kitten *in situ*. × 240 d. At × the cement substance binding together the muscular fibres in the *tunica media* is seen. (Method No. 60, Appendix.)

The **Veins** show the same coats as an artery, with differences in detail. The elastic layer is less developed in the internal coat; the middle coat is much thinner and has less elastic tissue, but more connective tissue. The *tunica intima* is lined by a single layer of elongated or (in the great veins) more polygonal endothelial cells. Many veins have semilunar folds of the internal coat strengthened with fibrous tissue, forming *valves*. In some veins (iliac, femoral, umbilical), longitudinal muscular fibres are found in the inner part of the middle coat; in the inferior vena cava, hepatic veins, and portal veins, these longitudinal fibres are external to the circular coat; in the superior vena cava and upper part of the inferior vena cava the circular coat is wanting; and the veins of the *pia mater*, brain and spinal cord, retina, bones, and the venous sinuses of the *dura mater* and placenta have no muscular tissue. (Schäfer.) The portal and renal veins have a layer of considerable thickness of longitudinally dispersed muscular fibres (Fig. 141). Valves exist in the larger veins only, especially in those of the limbs; they are not found in the veins of the viscera, of the cranium and vertebral canal, of the bones, nor in the umbilical vein. The epithelial cells on the side of the valve over which the blood passes are more elongated than on the cardiac side, where the long axes of the cells are placed transversely. This arrangement diminishes friction.

FIG. 141.—Transverse section of the wall of the renal vein of man. × 50 d. *J*, *tunica intima*; *M*, very thin *tunica media*; *A*, *tunica adventitia*, showing bundles of involuntary muscle cut across. (Method No. 61, Appendix.)

The ultimate or most minute **Capillaries** present the simplest type of structure, consisting of tubes formed of a single layer of transparent, thin, nucleated, endothelial cells, joined by their margins (Fig. 142). A perfectly fresh capillary does not show the edges of the cells, owing to the uniform refractive property of the wall of the tube. The nuclei show an internuclear plexus of fibrils. The cement substance uniting the cells is stained black by a ·25 per cent. solution of nitrate of silver (Fig. 143). Here and there minute dots or slits may be seen, which have been supposed by some to be openings (*stomata* or *stigmata*). As an artery passes into a capillary, the coats become simpler in structure. The circular muscle fibres of the *tunica media* become fewer in number and wider apart until they disappear. The *tunica adventitia* also gradually vanishes. The ultimate capillaries divide and subdivide without becoming much reduced in calibre, while they form networks, the size of the mesh of which varies in different organs. The narrowest meshes occur in the lungs and liver, and the wider in muscle, under serous membranes, and in the organs of sense. The widest capillaries occur in the liver, and the narrowest in the retina and in muscle

Fig. 142.—Capillaries of various size ; *a*, capillary much magnified and acted on by nitrate of silver, so as to show that it is composed of flattened cells ; *b*, a smaller vessel showing the same ; *c*, a small artery or vein showing transverse or longitudinal nuclei ; *d*, ultimate capillary from *pia mater* of sheep's brain.

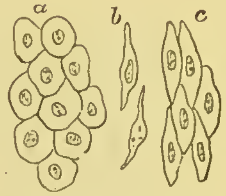


Fig. 143.—Varieties of endothelium ; *a*, from pleura ; *c*, from vessels ; *b*, two detached cells.

(Fig. 61, p. 110). In the transparent parts of animals, such as the web of the frog's foot, the mesentery and lung of the frog, and the tail of a fish, the blood may be seen flowing through the capillary network from the arteries into the veins. The current is rapid in the small arteries, less rapid in the veins, and slow in the capillaries. It is also fastest in the centre of the vessel and slowest near the wall. The colourless corpuscles of the blood may be seen to pass from the centre of the stream to the margins, to adhere to the inner surface of the blood-vessel, and occasionally to pass through the coats of the more minute vessels, appearing in the surrounding tissues as migratory cells Fig. 89), p. 166).

All medium-sized and large blood-vessels have minute blood-vessels in their walls, *vasa vasorum*, and exclusively in the *tunica adventitia.* The *tunica intima* has no vessels. Blood-vessels are supplied with *nerves* forming a plexus of delicate fibres. These are distributed to the plain muscular fibres. Many blood-vessels are surrounded by lymphatics, which are sometimes so wide as to form sheaths, termed *perivascular canals* or *spaces.*

Even in the smallest vessels the following differences may be observed between arterioles and venules : "The veins are larger than the corresponding arteries ; they branch at less acute angles ; their muscular cells are fewer, and their epithelium cells less elongated ; the elastic layer of the inner coat is always less marked, and sooner disappears." (Schäfer.)

The *Cavernous spaces*, as existing in erectile tissues (*corpus cavernosum* of the penis), consist of the anastomoses of large veins of unequal calibre. The walls and partitions have numerous perforations, threads of delicate tissue, covered with epithelium, pass through the cavities, and the walls are strengthened by connective tissue.

The *cohesion* of vessels is great and their elasticity is small and perfect. The walls of blood-vessels have the property of *contractility*, by which alterations take place in the calibre of the vessel, and consequently in the amount of blood supplied to a part.

CHAP. III.—THE ARTERIAL CIRCULATION.

The arterial walls are at the same time muscular and elastic; the muscular coat, as already stated, predominating in the smaller, whilst the elastic coat is strong in the greater arteries. The chief action of the elasticity of the greater vessels is to transmute the unequal movement of the blood in the large arteries, caused by the intermittent action of the ventricle, into a uniform flow in the capillaries. Thus, when the ventricle contracts, it propels a certain amount of blood into the elastic aorta which expands in all directions. On the commencement of the diastole of the ventricle, the *vis a tergo* is removed, the aorta recoils by its elasticity so as to close, on the one hand, the semilunar valves, and on the other, to force part of its contents into the vessels farther onwards. These, in turn, as they already contain a quantity of blood, expand, recover by an elastic recoil, and transmit the movements with diminished intensity. Thus the blood is driven along the vessels by the action (1) of the ventricular systole, and (2) of the elastic recoil of the walls of the vessels occurring during the intervals between the ventricular systoles. As the sum of the diameters of the branches of an artery is always greater than the diameter of the artery from which they sprung, and as the arteries divide and sub-divide very quickly as they advance to the periphery, the total capacity of the smaller arteries is very much greater than that of the large ones. Each systole of the ventricle, however, throws into the vessels the same amount of blood, so the distension of the large arteries will be greater than the distension of the small ones, or, in other words, the size of the wave will gradually diminish as we pass from the large arteries to the smaller ones, and the smaller will be both the distension and the elastic recoil. Then the wave will frequently suffer a reflexion at points where an artery divides into two branches, and finally the frictional resistance will be increased as the lumen of the individual branches diminishes. Thus the wave set up by the ventricular systole is gradually weakened, and it ceases when it reaches the capillaries. The effect is, as already stated, that the blood flows in the capillaries in a continuous stream. By these actions a series of movements, consisting of expansions and relaxations, gradually diminishing in amplitude, pass along the arterial system, from the greater to the smaller vessels, the latter becoming, as already pointed out, less and less elastic. These expansions and relaxations of the arterial wall, passing along like a wave, constitute the pulse.

The pulse then represents the transmission of an undulating movement, not the progression of the fluid, the blood, in the vessels. The undulations of the pulse travel with a rapidity of 8·6 metres per sec., about 30 times faster than the rapidity of the movement of the blood, which, in the carotid artery of the horse, has been estimated to be 300 mm. per sec.

E. H. Weber showed that the velocity of the pulse wave from the heart to the capillaries is about 8·6 metres per sec. The time required by a wave to advance its own length is that of the duration of the cause of the wave, and as in this case the cause, the ventricular systole, lasts ·3 sec., then 8·6 × ·3=2·6 metres, the length of the pulse wave. As the distance to be travelled is less than 2·6 metres, it follows that a complete wave never at one time exists in the arteries. In the dog, the pulse wave travels 4·75 metres per sec., and taking the pulse beat at 90 per minute, the length of the pulse wave in this animal will be 1·3 metre.

THE PULSE.

(*a*) The movements of the arteries, termed the pulse, are registered graphically by means of instruments termed *sphygmographs*. In 1829, Poiseuille invented a *pulse-measurer* consisting of an oblong box filled with a fluid and placed around an exposed artery. A vertical tube communicated with the interior of the box and the column of fluid rose in this tube and oscillated with each pulse beat. About 1850, Hérisson and Chelius used a glass tube having a funnel-shaped end over which a membrane was tightly stretched. The tube and funnel-end were filled with mercury, and when the membrane was placed over a pulsating artery the mercury moved with each beat. This was called a tubular *sphygmometer*. About the same period, Upham and Kemp constructed a *sphygmophone* consisting of a funnel-shaped tube at each end of a long thick-walled elastic tube filled with fluid. The end of each funnel was covered by a membrane. One membrane was placed over the pulse, the pulse-beat caused an oscillation in the fluid in the tube, raising the membrane at the other end of the tube, and thus affecting a continuous current of electricity so as to ring an electric bell with each pulse beat. In 1855, Vierordt constructed the first *sphygmograph*, substituting for a column of fluid a lever placed on the pulse, communicating with a system of levers and thus amplifying the movement. This instrument, although clumsy, is the parent of all sphygmographs, of which there are now many modifications. The best form is that of Marey, devised in 1861 (Figs 144 and 145). It consists essentially of a long lever which is moved near the fulcrum by a screw acting on a small horizontal wheel, from whose axle projects the long, light, wooden lever. The point of the screw rests on a flat disk of steel or ivory at the end of an elastic spring which presses the ivory disk or pad on the artery. The lever inscribes the movements on a blackened surface, usually a strip of paper smoked in the flame of a lamp burning turpentine, carried in front of the point of the lever by clockwork. In the instrument, as modified by Mahomed, Byrom Bramwell (Fig. 146), and others, there is an arrangement for adjusting the amount of pressure made on the artery by the ivory pad, so that tracings may be taken at different times from the same artery with different or with the same pressures (Fig. 147.) The tracings are "fixed" by passing them through shellac or photographic varnish. Various other forms of sphygmographs have been devised by Pond, Mach, Brondgeest, Dudgeon, Landois, and Fleming. Landois, Klemensiewicz, and Mayer have also used gas *sphygmoscopes* consisting of a small casket the bottom of which is formed of membrane. The casket is provided with an inlet and outlet tube for the

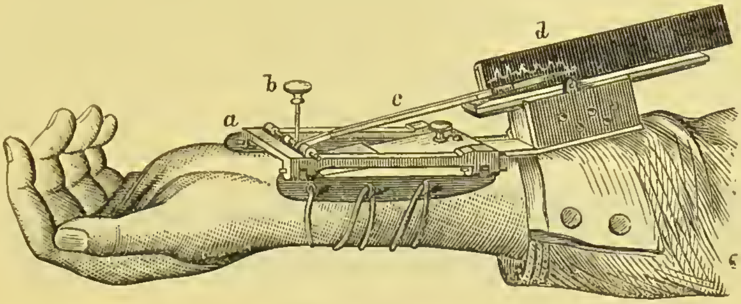


FIG. 144.—Marey's sphygmograph in position. *a*, Framework bound to the arm; *b*, screw for adjusting pressure to the vessel; *c*, lever, writing on smoked paper *d*. (Marey.)

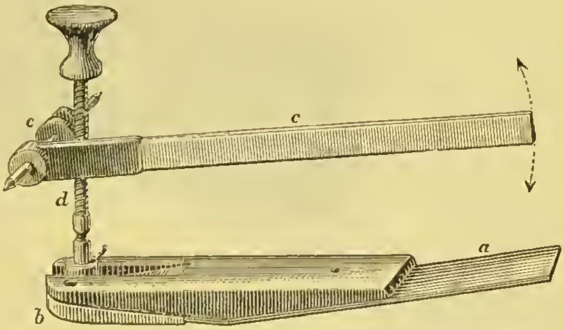
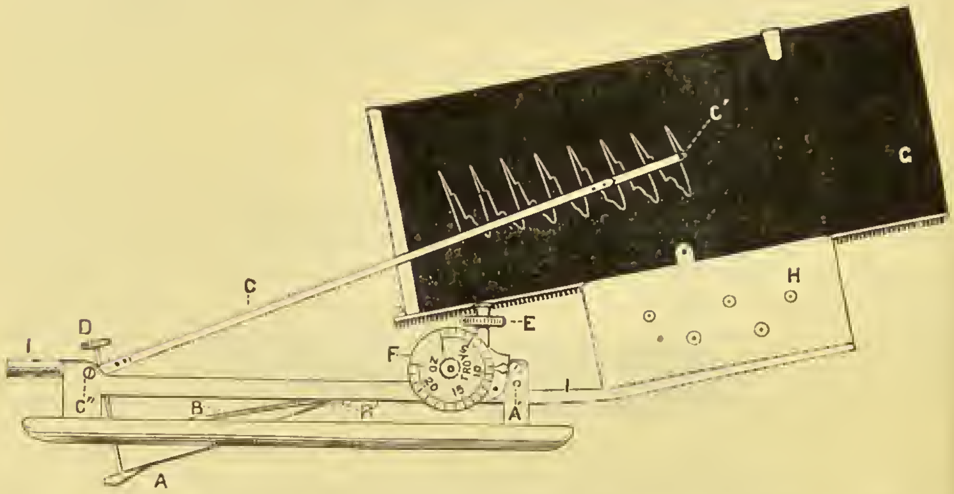


FIG. 145.—Transmitting portion of Marey's sphygmograph. *b*, ivory plate applied to the artery; *a*, steel spring; *d*, fine screw working on the wheel, *c*, on the axle of which the lever is fixed. The arrows represent the direction of the movements of the end of the lever, and it will be seen that this arrangement increases greatly the amplitude of the movements over the pulse. (Marey.)

conveyance of gas. The inlet tube being connected with an ordinary gas tap and the outlet with a small gas burner, the flame is lit, and the membrane is placed over the pulse. Each pulse-beat, by varying the pressure in the casket, affects the flame which beats synchronously with the pulse-beat. Czermak placed a small bit of silvered glass on the pulse, and from it reflected a beam of light on a moving photographic surface, and thus obtained a picture of the pulse curve. Stein, Landois, and Richardson have caused the pulse to act on a microphone and telephone. Waldenburg has registered the tension, the diameter of the artery, and the volume of the pulse on a dial slowly moved by clockwork (the *angiometer*, or pulse-clock). Finally, to get rid of the effects of friction of even the most delicate apparatus, Landois has allowed the stream of blood issuing from a large artery to strike against a piece of paper drawn in front of it, and has thus obtained a *hæmautographic curve* closely resembling the curve traced by sphygmographs.



IG. 146.—Sphygmograph of Mahomed and Byrom Bramwell showing arrangement for graduating pressure on artery.

(*b*) *Characters of a Pulse-tracing or Sphygmogram.*—The following changes take place in an artery when it pulsates :—(1) it dilates and at the same time lengthens to a small extent ; (2) the pressure of the blood increases in the artery, and this increase is indicated by the feeling of hardness and resistance which is experienced when the artery is compressed with the finger. These facts are illustrated in a sphygmographic curve, which is shown diagrammatically in Fig. 147. The ascending line, *ab* (line of ascent, up-stroke, or percussion stroke), corresponds to the distension of the artery produced by the systole of the left

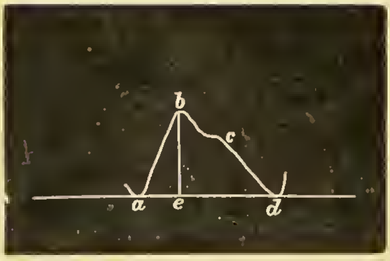


Fig. 147.—Diagram of a sphygmographic tracing.

ventricle, and the descending line, *b*, *c*, *d*, to its elastic recoil; the length of the line, *ad*, represents the total duration of the movement, which is divided into two portions by the perpendicular line, *be*. The distance, *ae*, then measures the duration of the time of the distension of the artery, and *ed* the time of its elastic recoil. When a continuous tracing is obtained, as in Fig. 148, it is seen that the durations of the individual pulsations are equal, and that this duration is in the inverse ratio to the number of pulsations in a unit of time. In a normal pulse the distension and elastic recoil of the vessel succeed each other without interruption, so that there is no period of repose of the artery. When, however, the pressure of blood in the artery falls below a certain point, these characters disappear or are modified. On examining Fig. 147, it will be observed that the duration of the distension of the artery is only about two-fifths of that of its relaxation. The rapidity and slowness of the pulse depend on the ratio of the duration of these periods. The pulse is quick when the duration of the arterial distension diminishes, and slow when this duration increases. As the line, *ab*, Fig. 149, becomes less oblique and more nearly vertical, it indicates that the time of the distension is short, quick, and nearly instantaneous. The rapidity of the pulse is increased by quick action of the heart, considerable power of yielding in the arterial walls, easy afflux of blood owing to dilatation of smaller vessels, and nearness to the heart. The term *quickness* has reference to a single pulse-beat, and *frequency* to the number of beats in a given time, say one minute. The line, *bcd*, is always more oblique than *ab*, and it presents in carefully taken tracings several elevations or notches, as seen in Fig. 149. If we refer the different portions of the curve to their origin the result is as follows:—(1) the upstroke corresponds to the systole of the left ventricle, opening the aortic valves, pouring the blood into the arteries, and distending them; (2) the downstroke represents the time when the blood is flowing out of the arteries at their periphery into the capillaries; (3) the larger wave in

FIG. 148.—Normal tracing from radial artery.

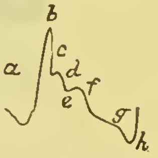


FIG. 149.—Sphygmogram of radial artery; pressure 2 oz. Each part of the curve between the base of one up-stroke and the base of the next up-stroke corresponds to a beat of the heart. *ab*, the ascent; *b*, the apex of the up-stroke; and *b* to *h*, the descent, with an elevation, *d*, called the *first tidal* or *predicrotic* wave; *e*, an angle or notch, the *aortic notch*; *f*, a second elevation, called the *dicrotic* wave; *g*, a slight curve, sometimes called the *second tidal* wave. The descent is continued to *h* where the ascent of the next heart-beat begins. (Landois.)

the descent, called the *dicrotic wave*, the *recoil wave*, or the *aortic systolic wave*, represents the time of the closure of the aortic valves; (4) the *predicrotic wave* or *first tidal wave*, or *second ventricular systolic wave*, occurs after the first systolic wave (forming the apex *b* in Fig. 149) and during the ventricular contraction. In many pulse-tracings there are still smaller *secondary waves*, which are due to elastic vibrations of the wall of the vessel. Various forms of pulse-tracings are shown in Figs. 150, 151, and 152.

FIG. 150.—Tracing from radial artery of a healthy man. The elevation in the descending portion of the curve is scarcely observable, indicating a state of high arterial tension.

FIG. 151.—Tracing from radial artery, showing irregularity in the downstroke, indicating by these secondary curves, and by the great amplitude of the chief curve, a state of low arterial tension

Considerable discussion has taken place as to the cause of the dicrotic or recoil wave, but there can be no doubt that it is a secondary wave reflected from the closed aortic valves. As already explained, when the ventricle contracts, a positive wave is transmitted from the aorta throughout the arterial system to the smallest arterioles, where it is extinguished. The elastic recoil of the aortic wall closes the aortic valves by propelling a portion of the blood backwards; from these closed valves a wave is reflected, which is also propagated to the periphery, and in some cases a second reflected wave may be observed in the carotid arteries and in the arteries of the upper extremity, but not in those of the lower extremity, on account of their length. It is the first reflected wave that causes the distension of the wall of the vessel, producing in the sphygmogram the dicrotic elevation. The following facts support this view:—(1) just as the true pulse-wave is later in the more distant arteries than in those near the heart, so the dicrotic wave occurs later in the descending part of the curve the further the tracing is taken from the heart. The apex of the dicrotic wave occurs in the carotid ·35 to ·37 sec. after the pulse; in the upper extremity, it is ·36 to ·38 sec., in the lower extremity, *i.e.*, farthest from heart, it is ·45 to ·59 sec. after pulse-beat; (2) the farther the wave has to travel the less distinct it will be, and thus the dicrotic wave is smaller as we recede from the heart; (3) the stronger and quicker the action of the ventricular systole, the more pronounced is the primary pulse-wave and also the dicrotic wave; (4) the lower the degree of tension of the arterioles all the greater is the dicrotic wave (Fig. 151), as the wall of the vessel yields more readily. Again, if a blood-vessel, say the radial artery, be so full as to approach complete distension (high tension), and if more blood be then forced into it, the wall of the vessel will yield only a little more, and the tracing obtained will be similar to that in Fig. 150. On the other hand, if the vessel be only partially full (low tension), it is evident that when more blood is propelled into it distension will take place to a considerable extent, and there will be an oscillation (producing the dicrotic wave and also possibly the secondary waves) of the wall of the vessel at that point. In these circumstances the pulse will be soft and compressible and the tracing will resemble those in Figs. 151 and 152, 1. The three factors causing an arterial pulsation are : (1) the more or less energetic contraction of the ventricle ; (2) the quantity and pressure of the blood, and (3) the elastic and contractile properties of the arterial wall. If these factors be in any way modified there will be a corresponding modification in the physical characters of the pulse.

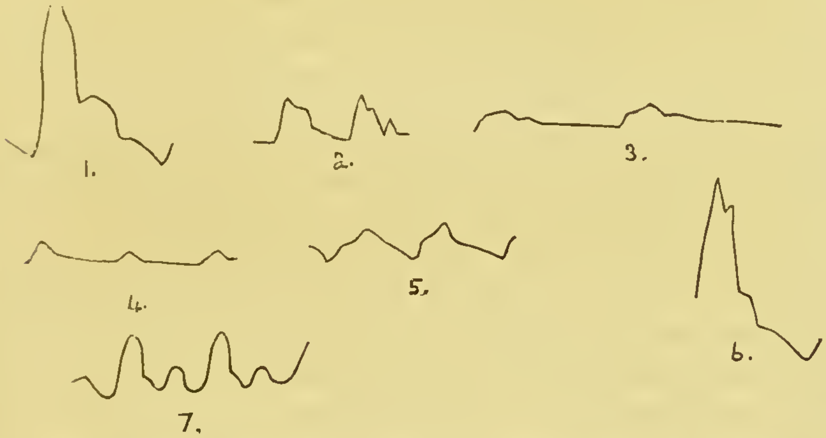


FIG. 152.—Sphygmographic characters of various forms of the pulse. 1. *Aortic insufficiency*, showing low tension and the arterial expansion strong and rapid. 2. *Mitral insufficiency*, showing arterial expansion to be small, a part of the blood returning from left ventricle to left auricle. 3. *Contraction of aortic orifice.* Line of ascension oblique. Blood passes through aortic orifice with difficulty. Tension great so that the artery slowly returns to its original calibre, and the pulse curve is prolonged. 4. *Contraction of mitral orifice.* Pulse very small, as only a small amount of blood enters aorta with each stroke. 5. *Atheromatous arteries.* Ascending line undulating as arterial wall does not readily yield. 6. *Aortic insufficiency* showing a "bounding" pulse, or the pulse of Corrigan. 7. Dicrotic pulse, showing the double beat. Low tension.

(c) *Physiological Characters of the Pulse.*—The normal pulse-rate in man is about 72 per minute, in the female about 80 per minute; but it is to be noted that in some individuals a state of health is consistent with a pulse-rate as rapid as 100 or as slow as 50 beats per minute. The pulse-rate is influenced:—(1) *By age:* newly-born child, 130 to 140 beats per minute; 1 year, 120 to 130; 2 years, 105; 3 years, 100; 4 years, 97; 5 years, 94 to 90; 10 years, about 90; 10 to 15 years, 78; 15 to 50 years, 70; 60 years, 74; 80 years, 79; 80 to 90 years, over 80. (2) *Length of Body:* As the height increases the pulse slows. (3) *Bodily states*, such as active muscular exercise, increased blood-pressure, active digestion, pain, nervous excitement, extreme debility, quicken the pulse. (4) *Temperature:* increase of temperature quickens the pulse. An increase of 1° Fahr. above 98° Fahr. is associated with an increase of 10 beats per minute. (5) *Posture:* it is less frequent sitting than when standing, and still slower on lying down. (6) *Sensory impressions:* music quickens the pulse. (7) *Pressure:* increased barometric pressure slows the pulse. (8) *Diurnal rhythm:* 3 to 6 A.M., 61 beats; 8 to 11.30 A.M., 74; falls towards 2 P.M.; towards 3 (at dinner-time) another rise, which goes on until 6 to 8 P.M., when it may be 70; falls towards midnight, 54; rises again towards 2 A.M., when it soon falls again, and afterwards rises, as before, towards 3 to 6 A.M.

(*d*) *The Pulse-rate in Animals.*—Colin gives the following figures:—Elephant, 25 to 28 beats per minute; camel, 28 to 32; giraffe, 66; horse, 36 to 40; ox, 45 to 50; tapir, 44; ass, 46 to 50; pig, 70 to 80; lion, 40; lioness, 68; tiger, 74; sheep, 70 to 80; goat, 70 to 80; leopard, 60; wolf (female), 96; hyæna, 55; dog, 90 to 100; cat, 120 to 140; rabbit, 120 to 150; mouse, 120; goose, 110; pigeon, 136; hen, 140; snake, 24; carp, 20; frog, 80; salamander, 77.

(*e*) *Velocity of the Pulse-wave.*—The pulse becomes later in time as we recede from the heart. Thus Czermak estimated the delay as follows:—Carotid pulse, after the cardiac beat, ·087 seconds; radial, ·159 seconds; posterior tibial, ·193 seconds. By placing delicate tambours, or electro-magnetic sphygmographs, at different points of the circulation and recording the movements on a rapidly-moving surface, it is not difficult to determine the velocity of the pulse-wave. By such methods E. H. Weber gives it at 8·6 metres per sec.; Garrod at 9-10·8 metres; and Moens at 8·3 metres. In the arteries of the upper limb it is stated to be 9·43 metres, and in those of the lower limb 9·40 metres per second.

(*f*) *Other Pulse-like Movements.*—It is well known that the beating of the heart and great vessels may communicate vibrations to the whole body. If we place a person in the erect attitude in the scale pan of a large balance, it will be found that the index oscillates synchronously with the beats of the heart. Movements synchronous with the pulse may be seen when one sits in a chair with one leg crossed over the other. The supported leg is raised with each pulse-beat. Again, if the incisor teeth of the lower jaw be allowed to touch the upper incisors lightly, a beat may be felt, owing to the pulse-beat in the external maxillary artery. Pulse-beats may also be observed affecting the air in the nose, mouth, and tympanum, and even, after violent exercise, in the retinal vessels, causing entoptical phenomena. The large arteries at the base of the brain communicate movements to the brain, visible in the pulsating fontanelles in the heads of infants. Aneurisms or tumours pulsate, slowing the velocity of the pulse-wave, so that the pulse beyond the aneurism is a little later than on the sound side.

(*g*) *Influence of Respiratory Movements on the Pulse.*—As already pointed out, inspiration favours the flow of blood into the veins and retards the flow in the arteries, whilst expiration has the reverse effect. The tension of the arteries during inspiration is therefore less than in expiration, and this affects the form of the pulse-curve. During expiration the pulse-curve (not the individual pulsations) rises higher, and the dicrotic wave becomes less, owing to increased pressure.

Contractility of the Arteries.

Non-striated muscle, as has been already stated, exists to a considerable amount in the walls of the smaller arteries, and the calibre of these vessels may consequently be changed by the activity of the contractile coat. The contractility of vessels may appear under two forms:—(1) *Rhythmical Contractions*, as have been seen in the vessels of a rabbit's ear, or in a bat's wing, which are independent both of the pulse and of respiratory movements; and (2) *Persistent Contractions*, under the influence of the nervous system, which play an important part in the distribution of the blood. The amount of contraction of an artery will affect the pressure of the blood in its interior, it will accelerate or retard the rapidity of the blood current, and it will regulate the supply of blood to the capillary area to which the vessel is distributed. By such arrangements, also, the distribution of blood to various organs is regulated, thus establishing what has been termed a *balance of local circulations*. For example, if the vessels in one organ remain permanently contracted, whilst those in a neighbouring organ are dilated, more blood will pass to the latter than to the former, and thus some end of physiological importance may be served. Thus physiological correlations may be established between the cerebral and thyroid circulations, the gastro-hepatic and the splenic circulations, and the distribution of blood in the lower extremities as related to the abdominal organs.

ARTERIAL SOUNDS.

If a stethoscope be placed over a large artery, a murmur, sound, or bruit will be heard, caused by the blood rushing through the vessel narrowed by the pressure of the instrument. The fluid escapes into a wider portion of the vessel beyond the point of pressure, and the sound is caused by the particles of fluid being there thrown into rapid vibrations. It is not caused by vibrations of the wall of the vessel. Such sounds are favoured by a certain degree of elasticity of the walls of the vessel, by diminished peripheral resistance allowing the blood to flow away freely, and by a considerable difference of the pressure in the narrow and wide parts of the tube. They are always heard over an aneurism, when the arterial tube is dilated and when pressure is made on a large vessel. The placental souffle or *bruit* heard during pregnancy is a sound of this kind, arising from pressure on the widely dilated uterine arteries.

CHAP. IV.—THE CAPILLARY CIRCULATION.

The circulation in the capillaries may be readily studied by placing under the microscope any transparent membrane containing vessels, such as the web of a frog's foot, the mesentery of a frog, the lung of a toad or frog, the tail of a fish, the wing of a bat, the tail of a tadpole, the tongue of a frog, the mucous membrane of the inner surface of the human lip, and the conjunctiva of the eyeballs and eyelids. When seen under favourable conditions, the following phenomena may be noticed:—(1) the diameter of the finest capillaries is such as to permit only the passage of corpuscles in single file, and it may vary from 5 μ to 20 μ; (2) the average length is about 5 mm.; (3) the number varies according to the degree of activity of the tissue, being large where nutritive processes are active, as in the liver and muscles; (4) they form networks or anastomoses, the form and arrangement of which is determined by the tissue elements; (5) in the smaller arterioles and venules, and in the capillaries, the current is continuous, and there is no pulse. By the elasticity of the larger vessels, the intermittent movement of the blood, caused by each ventricular contraction, has been transformed into a continuous flow. (6) In some of the larger vessels, the current is more rapid than in others of equal calibre, that is to say, the current is more rapid in small arteries than in small veins; (7) in the ultimate capillaries the current appears to have a uniform velocity in all capillaries of the same size; (8) sometimes a slight acceleration of the rapidity, even in the smallest vessels, may be observed to follow each cardiac beat; (9) in a vessel larger than an ultimate capillary, so large as to permit the passage of several coloured corpuscles abreast, the coloured corpuscles may be seen travelling with great apparent velocity in the centre of the stream (the most rapid part of the current), whilst the colourless move more slowly and with a rolling motion next the walls of the tube in a layer of plasma called *Poiseuille's space.* It will also be observed that the coloured corpuscles remain separate, and do not exhibit any tendency to stick together, or to adhere to the walls of the vessels, whereas the colourless corpuscles do both, more especially after the membrane has been exposed for some time to the air, so as to excite the early stages of inflammation. D. J. Hamilton has shown that the nearer a suspended body approaches the specific gravity of the liquid in which it is immersed, the more it tends to keep in the centre of the stream, and he states that the reason why the coloured corpuscles keep the centre and the colourless the sides of the stream is that the specific gravity of the former is the same or slightly greater than the blood plasma whilst the specific gravity of the colourless corpuscles is less. (10) If the calibre of an ultimate capillary be marked at the beginning of an observation, and again some time afterwards, it will frequently be noticed that it has become narrower or wider, indicating that contractility is one of the properties of capillaries; (11) the velocity is greater in the pulmonary than in the systemic capillaries; (12) the phenomenon known as *diapedesis*, or migration of the white blood corpuscles, first described by Waller in 1846, is seen readily in the mesentery of the frog after inflammation has been excited by exposure to the air for one or two hours (Fig. 89, p. 166). It consists of the adhesion to the wall of the vessel of the colourless corpuscles and their protrusion through the wall into the surrounding tissues. Hering is of opinion that it is due partly to the filtration of the colloidal matter of the cell under blood-pressure. Diapedesis is of importance as constituting a part of the inflammatory process. The colourless cells become pus corpuscles. (13) If a vascular membrane be gently irritated whilst under the microscope, the capillaries become first slightly narrowed, then dilated and crowded with corpuscles, whilst the blood stream becomes slower. By and by the stream oscillates and then altogether stops. This constitutes *stasis*, a part of the inflammatory process, and is followed by exudation of the plasma of the blood, along with colourless corpuscles, and more rarely coloured corpuscles.

Vital Properties of Capillaries.—The most important vital property is, as already mentioned, *contractility*, by which the calibre of the capillary may be modified. The protoplasm forming their walls contracts when stimulated. Some have supposed the nuclei to be active agents in contraction, but more likely the cell substance is the seat of change. Oxygen causes the nuclei to swell whilst carbonic acid has the opposite effect. Roy and Graham Brown attach much importance to the active contractility of the capillaries as regulating the distribution of blood, now contracting, now relaxing, according to the needs of the tissues in their vicinity. Elasticity is also a characteristic of the capillary walls.

The arrangement of the capillaries in an organ or tissue is adapted to the functional activity of that organ or tissue. Where there is great functional activity there is a rich plexus of capillaries, and the converse is also true. Contrast, for example, the capillary supply in connective tissue with that of muscle, or in the grey matter of the nerve centres with that of the white matter. But, in addition, the distribution of capillaries always corresponds to the intimate structural arrangements of the tissue or organ. So precisely is this the case that a good histologist is able to identify the organ from an injected preparation showing the vessels, although none of the ultimate histological elements of the organ or tissue is to be seen. In muscle, for example, the capillaries exist in the form of elongated meshes; in connective tissue, such as is found beneath the skin, in an irregular network; in the papillæ of the skin, in loops; and in close reticulations to form the glomeruli of the kidney.

The *movement* in the capillaries is due to the force of the heart, as modified by the vessels (*vis a tergo*). Some have supposed that it is supplemented by an attractive influence exerted by the tissues (*vis a fronte*), and the statement is supported by the observation that when there is an increased demand for blood owing to active nutritional changes, there is an increase in the amount of blood flowing to the part, such as occurs, for example, in the mammary gland during lactation, and in the growth of the stag's horn. Such an attractive influence on the part of the tissues is quite conceivable as a force assisting in the onward flow of blood, acting along with capillarity, but its amount is infinitesimally small in comparison with the force exerted by the heart. The force of the heart is sufficient to drive the blood through the capillaries into the veins.

When capillaries are examined in a transparent membrane of a living animal no pulse-like movement is visible. By the elasticity of the vessels the pulse-wave has been almost, if not quite, extinguished, and what might have remained of it is destroyed by the great resistance offered by the numerous capillaries. If, however, the capillaries and the arterioles be widely dilated, a pulse may appear in the veins, as occurs when the vaso-dilator fibres of the *chorda tympani* nerve are stimulated, causing a pulse-like movement in the veins of the submaxillary gland (p. 59). By increasing extra-vascular pressure pulsations may occur in the capillaries. The well-known throbbing in the finger when constricted by an india-rubber band, and the throbbing in inflammatory swellings are examples of pulsation in capillaries.

CHAP. V.—THE VENOUS CIRCULATION.

The walls of the veins are thinner, less elastic, and more distensible than the walls of the arteries. They contain both elastic and contractile tissue, though to a smaller extent than the arteries. Numerous anastomoses exist between veins and even between superficial and deep veins, so that if the flow of blood be obstructed in one direction it readily finds a passage in another. The circulation in the veins depends on: (1) inequality of blood-pressure—the pressure being much less in the veins than in the arteries; (2) on muscular action compressing the veins, and thus, in consequence of the valves (found in many veins) opening towards the heart, so acting on the blood as to force it onward in the direction of that organ; (3) on the movements of respiration—inspiration, as already seen, favouring the flow of blood in the great veins towards the heart; and (4) the suction-like action of the right, and in the case of the lungs, that of the left, auricle, drawing the blood towards the heart. During venesection, muscular action is seen to increase the flow of blood from the divided vein. Hence the use of the barber's pole which was grasped by the patient during bleeding by the barber-surgeon of old. The flow of blood in veins is continuous, or nearly so, so that, when a vein is cut, it does not "spurt" as an artery does, but it "wells out" in a stream.

The influence of gravity on the movement of the blood in the veins is very marked. If the hand is allowed to hang down for a few minutes, the skin becomes bluish red and the veins swell, showing engorgement, but if the hand is then held above the head, the veins quickly empty and the hand becomes pale. To prevent these engorgements the pressure of the muscles comes into play, the blood being forced onwards towards the heart, the valves preventing a backward flow. It is just where no external pressure can be brought to bear on the veins, that the latter have no valves, as in the sinuses of the brain, in the bones, and the veins forming the portal system. Valves, however, do more than merely prevent the blood flowing downwards, as in the extremities, owing to gravity, as we find them in the veins of some animals where the position is always horizontal. They come into play, as already said, when pressure is made upon the mass of blood in their cavities. By this pressure, the blood is forced onwards, as it cannot go back because the valves shut the lumen of the vein, while they cannot be folded back towards the periphery. In some rare instances, the blood-pressure still acting through the capillaries, the pressure of the muscles and the aspiration of the chest are unable apparently to carry on the circulation, and there we find portions of the veins pulsating, constituting accessory hearts, as in the caudal vein of the eel, and in the veins in the wing of the bat.

There is normally no pulse in veins, but sometimes a pulse may be observed in the veins of the neck, isochronous with the auricular systole, when there is an obstruction to the passage of blood from the right auricle into the right ventricle. Pulse-tracings taken in these circumstances are very similar to those of the cardiac impulse. During the systole of the right ventricle, the tricuspid valve closes, and if it be insufficient, that is, if it does not close properly, a positive wave is transmitted along the superior vena cava to the jugular. Then during the diastole of the right auricle and ventricle, the blood flows to the heart and the curve descends. A pulse in the jugular vein does not necessarily mean insufficiency of the tricuspid valve but a weakened condition of the valve in the jugular vein itself, as the pulse will not be propagated into the jugular, even in cases of insufficiency of the tricuspid valve, if the jugular valve be perfect. In great obstruction at the mitral orifice, a venous pulse may also be observed, which is associated with engorgement of the right auricle. Sometimes a pulse in the vein occurs when there is such rigidity from atheroma in the walls of the great vessels as to destroy the elastic influence of these parts, and at the same time such a degree of dilatation of the arterioles and capillaries, as to admit of the onward propulsion of the movement caused by the heart's contraction. Lastly, it may occur when the blood-pressure rises and falls suddenly, as in insufficiency of the aortic valves, and when the arterioles are much dilated. Towards the close of life, when the heart is feeble, and effusion may be taking place into the pericardium, a venous pulse may be observed.

If a stethoscope be placed at the root of the neck above the collar bones, and on the right side in particular, a whistling, rushing, or blowing sound will be heard. This is the *bruit de diable*, familiar to physicians. If heard without pressure being made by the stethoscope it is abnormal, as it occurs in conditions of anæmia from almost any cause; but it may be heard in a healthy person when pressure is made and when the head is turned to the opposite side. It is held to be due to the vibration of the blood in rushing from the contracted portion of the common jugular vein into the more dilated part of this vessel. During the auricular diastole and during inspiration it is more marked, as the blood flows then more rapidly in the veins towards the heart. Bruits of another kind may be heard in the jugular vein when the valve of that vein is incompetent, even during expiration, and in the crural vein after a sudden effort.

C.—The Circulation as a Whole.

Having described the structure and functions of the organs concerned in the circulation, namely, heart, arteries, capillaries, and veins, we are in a position to study the phenomena of the circulation as a whole. Consider the organs of the circulation as a closed system of tubes, over filled with blood: when the tubes are in a state of rest, it is evident that if the blood be uniformally diffused and under the same pressure, it will remain motionless and in equilibrium. When the pressure is changed at any point, as occurs when the left ventricle contracts and throws blood into the arterial system, the blood will move from the part where the pressure is higher to where it is lower, or, in other words, there will be a circulation as a consequence of a difference of pressure. When the heart stops beating, the blood continues to flow more and more slowly until the difference of pressure is equalized, and then there is no circulation. It is also clear that the greatest pressure will be at the commencement of the arterial system, that it will become less and less towards the arterioles, that it will be small in the capillaries, still less in the veins, and least of all where the veins enter the right side of the heart. Hence the blood flows from arteries through capillaries into veins. Each stroke of the heart throws as much blood into the arteries as flows into the heart from the veins, the orifices of the veins at the heart are more distensible than the beginnings of the arteries, and consequently the arterial pressure rises more rapidly

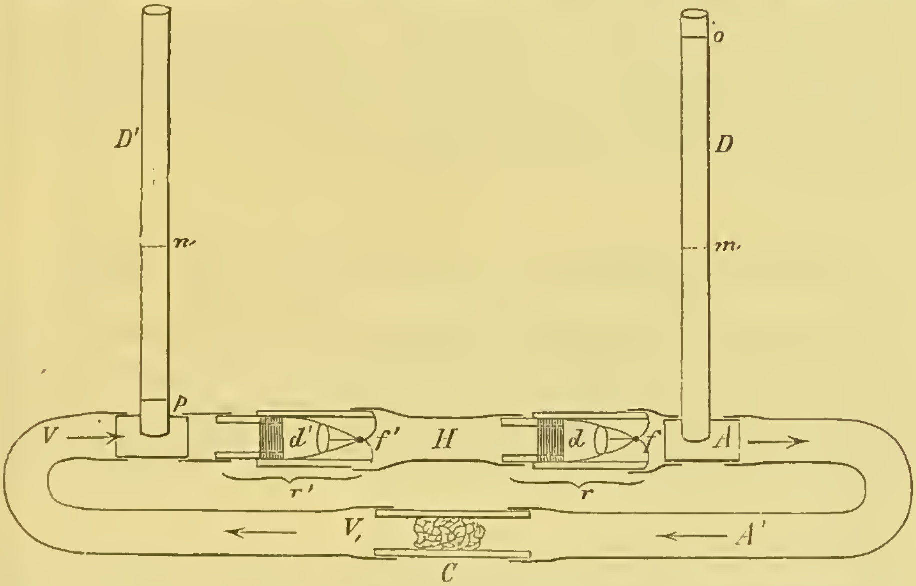


FIG. 153.—Weber's schema of the circulation. *H*, elastic bag; *d*, *f*, valve opening towards *A*, beginning of arteries; *A A'*, arterial system; *C*, tube containing sponge, which may be more or less compressed, representing capillary system; *V' V*, venous system; *d' f'*, valve opening towards *H* and closing when *H* is compressed; *D*, manometer showing pressure at beginning of arterial system; *D'*, manometer showing pressure in venous system; *m*, *n*, pressure in arterial and venous system when there is no circulation. When pressure in arterial, *D*, is at *o*, and in venous, *D'*, at *p*, then the current will flow in the direction of the arrows. (Rollet.)

than the venous pressure diminishes, and thus the beating of the heart raises the mean pressure throughout the arterial system. It was a consideration of these facts that led E. H. Weber, in 1851, to construct an apparatus, termed by him a *schema* of the circulation which illustrates the phenomena in a very striking manner (Fig. 153). A convenient form has been devised by Hering in which a pump, representing the heart, is intercalated between the arterial and venous portions of the apparatus at H. Rutherford has also constructed an excellent schema, formed of india-rubber tubing, having manometers placed at suitable points.

With Weber's apparatus many instructive experiments may be made. (1) If the arterial and venous pressure be equal, there is no circulation ; (2) if by rapidly working the pump (representing the heart) the arterial pressure is made greater than the venous, the fluid flows from the point of greater to the point of less pressure ; (3) the arterial pressure may be increased by (*a*) working the pump faster and faster (heart beating quickly), other things remaining constant ; (*b*) working the pump slowly but so as to throw a large volume of fluid with each stroke (heart beating strongly and throwing out a large amount of blood) ; and (c) diminishing the rate of flow through the capillaries by compressing the sponge in C, thus increasing peripheral resistance. It can thus be shown that the circulation is influenced by two factors : (1) the *heart* as regards number, strength, and volume of beats ; and (2) the amount of resistance in the *arterioles*. Modifications of these influence the pressure and the velocity of the blood.

CHAP. I.—THE PRESSURE OF THE BLOOD IN THE VESSELS.

As the blood is circulating through vessels, under the influence of the action of the heart, it exerts a certain pressure or tension, the existence of which is shown by the jet of blood which is thrown out on puncturing an artery, and the amount of which is indicated by the height to which the jet is propelled.

The first attempt to measure the pressure in the vessels was made, in 1727, by Rev. Stephen Hales, D.D., who connected a long vertical tube one-fourth inch in diameter and 9 feet long, provided with a stopcock, as seen in Fig. 154, with the crural artery of a horse, turned the stopcock, or untied a ligature previously passed around the vessel, so as to admit the blood of the animal into the vertical tube, and observed the height of the column of blood and the oscillations to which it was subjected with each beat of the heart. It is evident that by such an arrangement the pressure exerted on the vessels might be measured by the height of the column of blood, and that the variations in pressure would be indicated by the oscillations of the column. It was not until 1828, that Poiseuille bent the tube into the form of the letter U, and placed in the bend some mercury which was at the

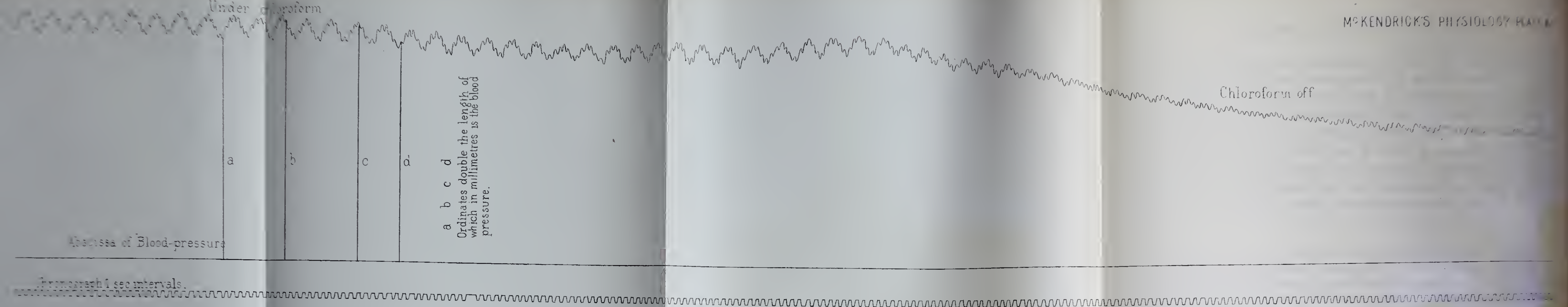


Fig. 1.

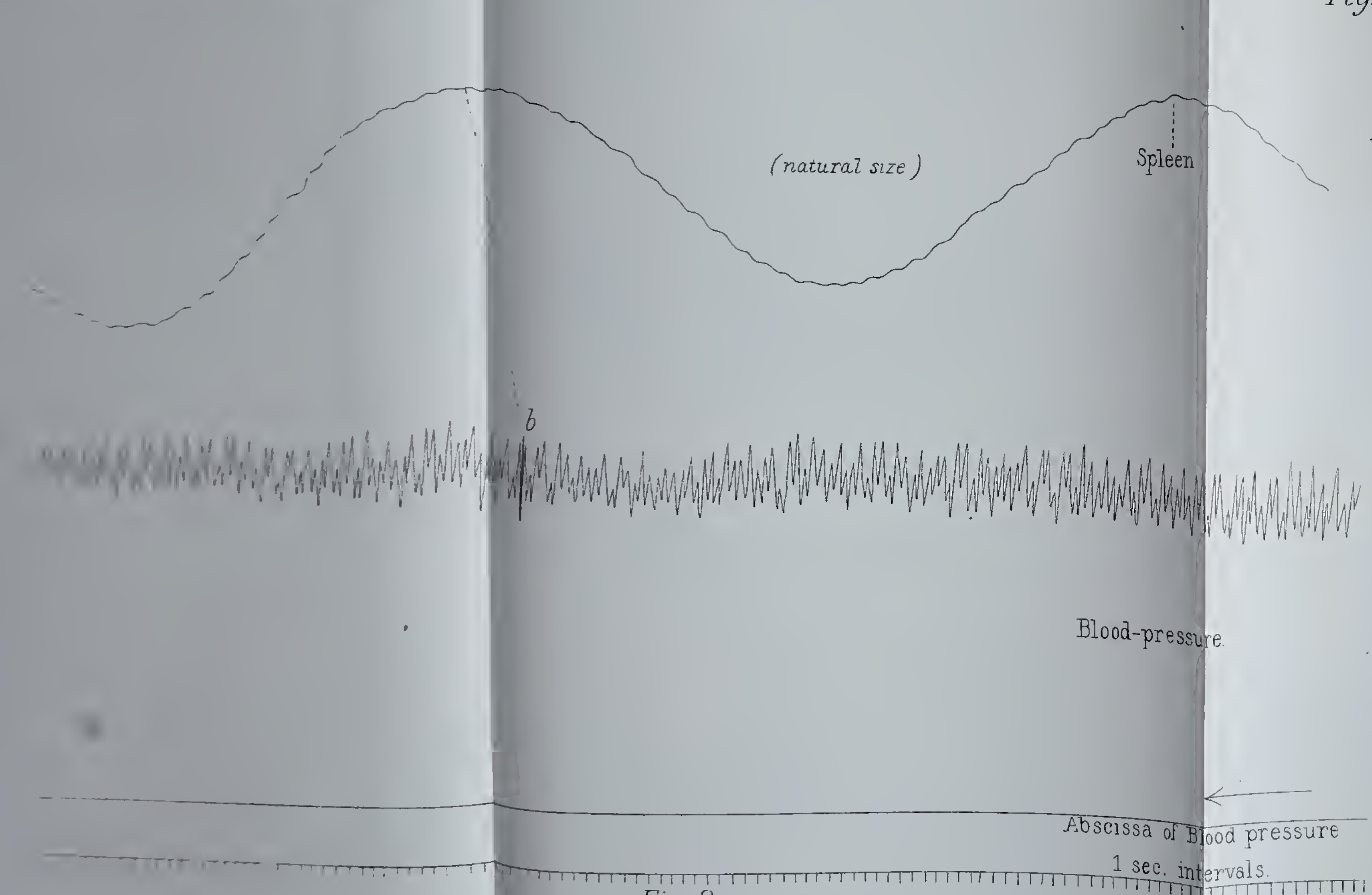


Fig 2

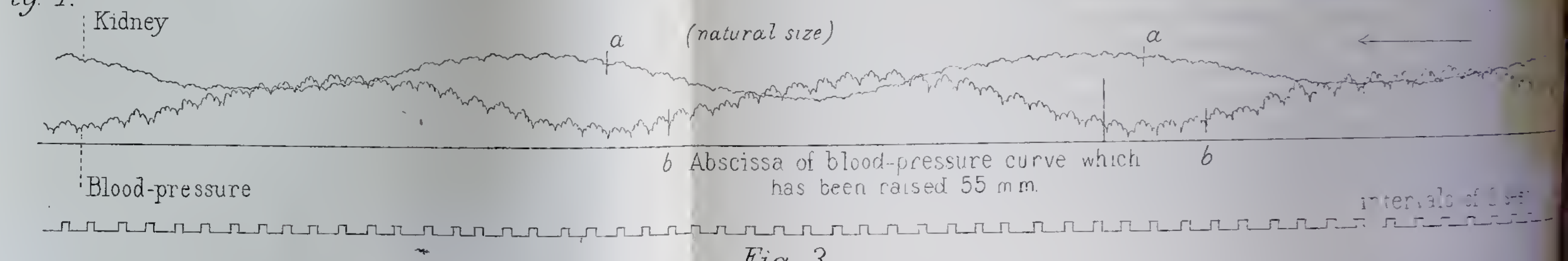


Fig. 3.

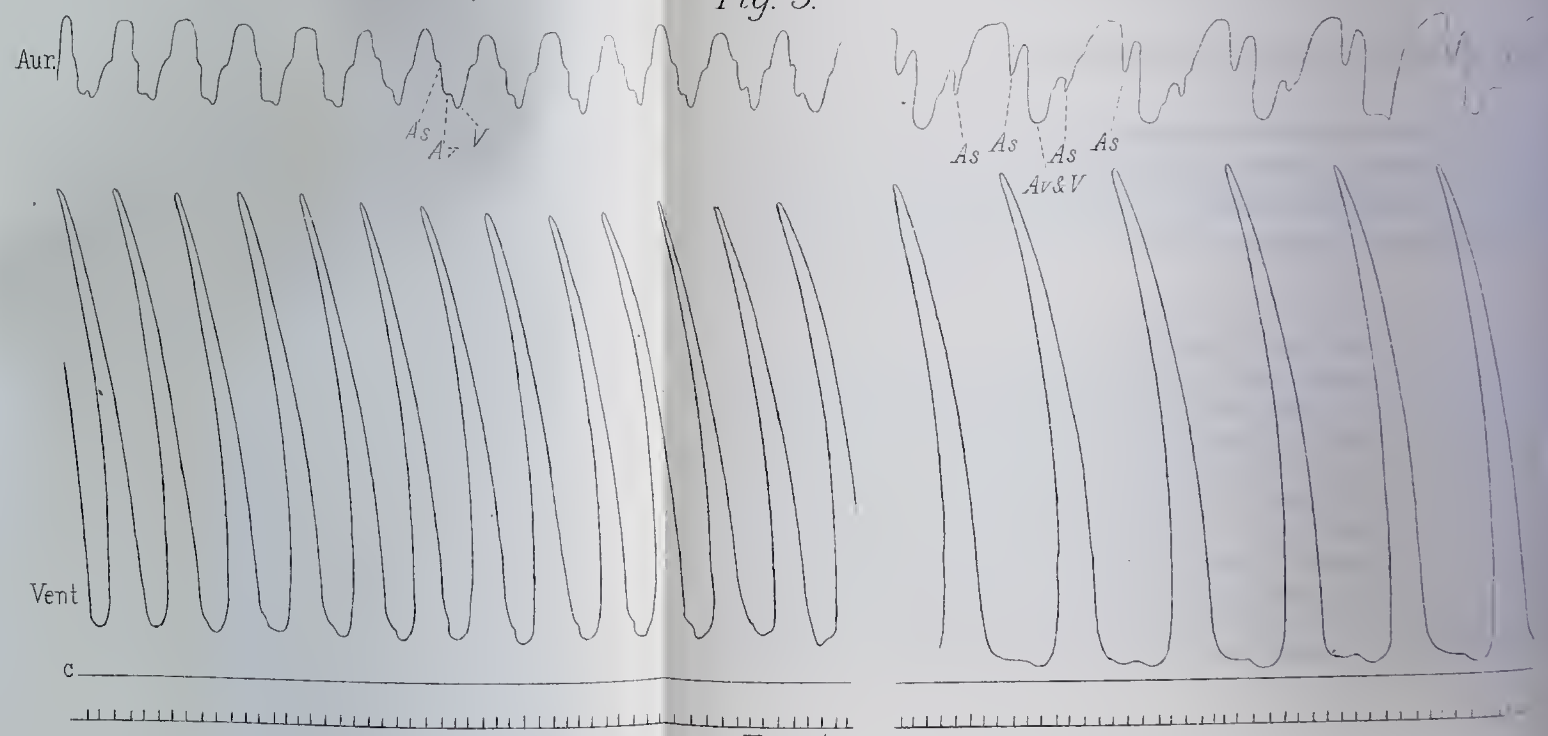


Fig. 4.

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DESCRIPTION OF PLATE A.

Fig. 1.—Tracing of *blood pressure* in the carotid artery of a dog, taken with the mercurial kymograph, showing the gradual fall of pressure under the influence of chloroform. The small teeth represent individual heart beats, and the larger undulations are caused by respiration, p. 273.

Fig. 2.—Tracing, showing the *movements of the spleen* of a dog, and at the same time the blood pressure in the carotid artery. The movements of the spleen were registered by Roy's oncograph, and the blood pressure by the mercurial kymograph. It will be observed that the amount of blood pressure varies only slightly, and that it is not increased during the enlargement of the spleen nor diminished when that organ contracts, p. 174.—Roy.

Fig. 3.—Tracing, showing the *movements of the kidney* of a cat and at the same time the blood pressure in the carotid artery. The movements of the kidney were registered by Roy's oncograph and the blood pressure by the mercurial kymograph. Observe that the kidney attains its maximal volume nearly at the time when the blood pressure is least. Both curves show the individual heart beats and also the variations due to respiration, p. 429.—Roy.

Fig. 4.—Tracings taken from *heart of tortoise* to illustrate a method of producing a block of nervous impulses. One auricle was cut away, the sinus venosus being left in connection with the ventricle by the remaining auricle. The beats of the auricle and ventricle were recorded by being attached by threads to delicate levers. Normally, the ventricle contracted in sequence with the auricle because a wave of contraction passed along the auricular muscle, and induced a ventricular contraction when it reached the auriculo-ventricular groove. In the experiment the auricle was slit up, so as to be almost divided into two parts, and the portion connected with the sinus was called the "sinus auricle," or As, and the part connected with the ventricle, the "ventricle-auricle," or Av. *Curve on the left.*—Each auricular beat is here composed of three parts:—1st, contraction of sinus auricle, As; 2nd, contraction of ventricle-auricle, Av, and then the ventricular contraction, V. Here we see a ventricular with each auricular beat. *Curve on the right.*—The auricle was now slit up further, with the result that the pause between the contractions of As and Av was increased, and every second contraction of the sinus auricle, As, was unable to pass the block, and therefore no contraction of Av or V followed. Time marker, every two seconds, p. 230.—Gaskell.

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same time more mobile and much heavier per volume than the blood. This instrument, modified to the form seen in Fig. 154, was termed a *hæmadynamometer*. By attaching opposite each column of mercury a graduated scale, and connecting the shorter limb of the tube with the interior of the vessel, arterial pressure was thus communicated to the mercury, the amount of which was indicated by a depression of the metal in *k*, and an elevation in *h* (Fig. 154). Vierordt took the important step of introducing a solution of carbonate of soda between the blood and the mercury (first using a long straight tube like that of Hales) thus preventing the coagulation of the blood. The next great improvement in the apparatus was made by Ludwig, who made arrangements for communicating to a moving surface the oscillations of the column of mercury. This he accomplished by placing on the surface of the mercury in the longer limb a little float, carrying a marker (Fig. 155, *e*), which recorded on a moving surface any oscillations of the mercury. Such an apparatus, termed by Volkmann a *Kymograph*, or wave-writer, seen in Fig. 156, is one of the most valuable instruments in a physiological laboratory. The expedient of communicating variations in pressure to a moving surface is generally supposed to have originated with James Watt, who contrived, by this method, to record the movements of a pressure gauge attached to a steam engine; but it must be remembered that recording instruments on this principle were constructed for meteorological purposes by Ons-en-Bray in 1734, by Changeux in 1785, and by Rutherford in 1794.

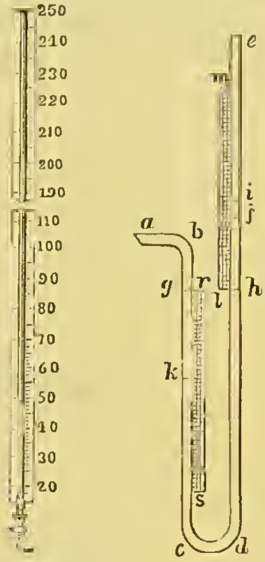


FIG. 154.—To the left the tube used by Hales, which may be graduated into fractions of an inch, or millimetres, provided at the end with a copper tube and stopcock. (Pitot's tube.) To the right the bent tube of Poiseuille: *a*, connected with the vessel, communicating pressure to mercury in bent tube, *b*, *g*, *k*, *c*, *d*, *h*: *r*, *s*, and *l*, *m*, graduated scales.

The apparatus of Ludwig from the inertia of the mass of mercury can only register mean blood-pressure, and the more delicate variations escape notice. Fick, in 1864, attempted to register these smaller fluctuations by means of a *curved spring-kymograph*, a form of which, as improved by Hering, is depicted in Fig. 157. It has the advantage of facility of adjustment and of recording with accuracy a single oscillation of the spring, caused by a single slight variation in blood-pressure, which cannot be readily done with a mercurial manometer, in consequence of successive oscillations occurring after each impulse, especially if the impulse be sudden and strong. Fick has more recently constructed a *flat spring kymograph* in which the column of blood in the vessel communicates the pressure through a layer of carbonate of soda solution to a membrane at the end of the tube. This membrane, by a point attached to it, presses on a straight spring. To estimate absolute pressure, both of Fick's instruments must be graduated with a mercurial manometer. Many modifications of recording instruments suitable for taking long continuous kymographic tracings are now in use. An instrument for measuring the external pressure of an artery, devised by Von Basch, is termed a *sphygmomanometer*. Small portions of tracings taken with the mercurial manometric kymograph and with the curved spring kymograph are shown in Figs. 158 and 159. (See also Plate A, Figs. 1, 2, and 3, and Plate B, Figs. 5, 9, 14, and 15, for examples of mercurial kymographic tracings, and Plate B, Figs. 11 and 12, for spring kymographic tracings.) From Fig. 158 it will be observed that there is (1) an increase and diminution of blood-pressure with each cardiac beat, as seen in the smaller curves; and (2) an increase and diminution produced by respiratory movements, the increase occurring chiefly during inspiration, and the decrease chiefly during expiration, as indicated by the larger waves. It is evident also that all the lesser curves have the same general character, and that they show little or nothing as regards any variation in pressure during individual beats. To show such variations, Fick's kymograph must be used, when a tracing will be obtained (Fig. 159) in which slight oscillations of pressure in the down stroke of each separate beat may be observed. (For examples of tracings taken with these instruments, see also Plates A and B. In Fig. 1, Plate A, we see a tracing taken with the mercurial kymograph from the carotid of a dog, and in Fig. 11, Plate B, a tracing with Fick's kymograph also from the carotid of a dog.)

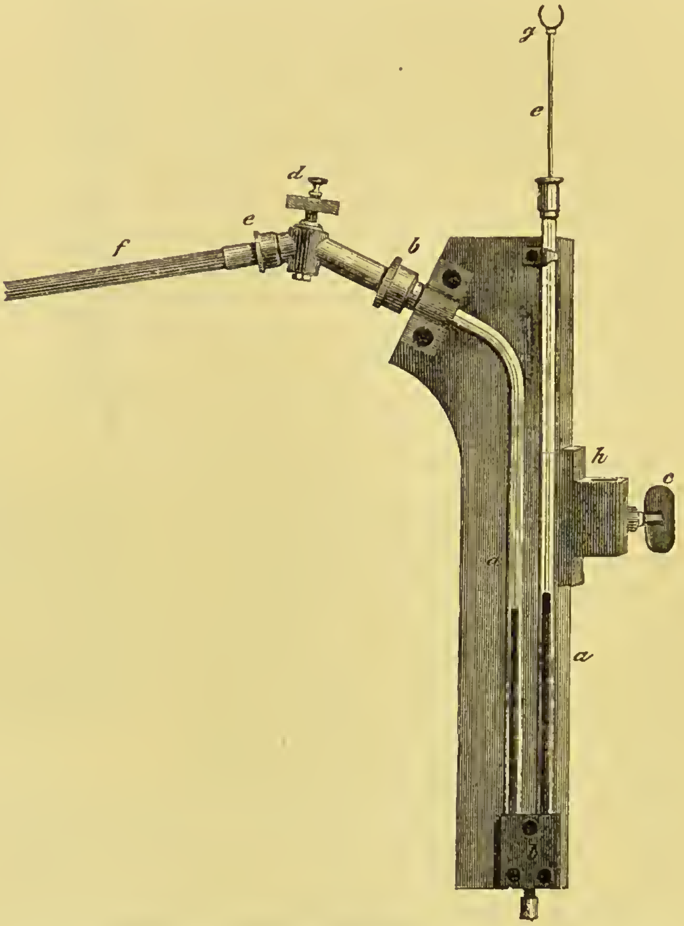


FIG. 155.—Ludwig's recording manometer. *e*, marker, with long slender rod having a bulb at the lower end floating on mercury in limb of tube *a*.

The method of obtaining a blood-pressure tracing is to expose the artery in an animal deeply under the influence of chloral and morphia and to isolate a portion by two ligatures tied with a slip knot. A V-shaped incision is made into the artery between the ligatures and a canula (Fig. 160) is inserted into it with the apex towards the heart. The canula is then filled with a saturated solution of sodium carbonate, and, by a flexible bit of india-rubber tubing, the canula is connected with a leaden

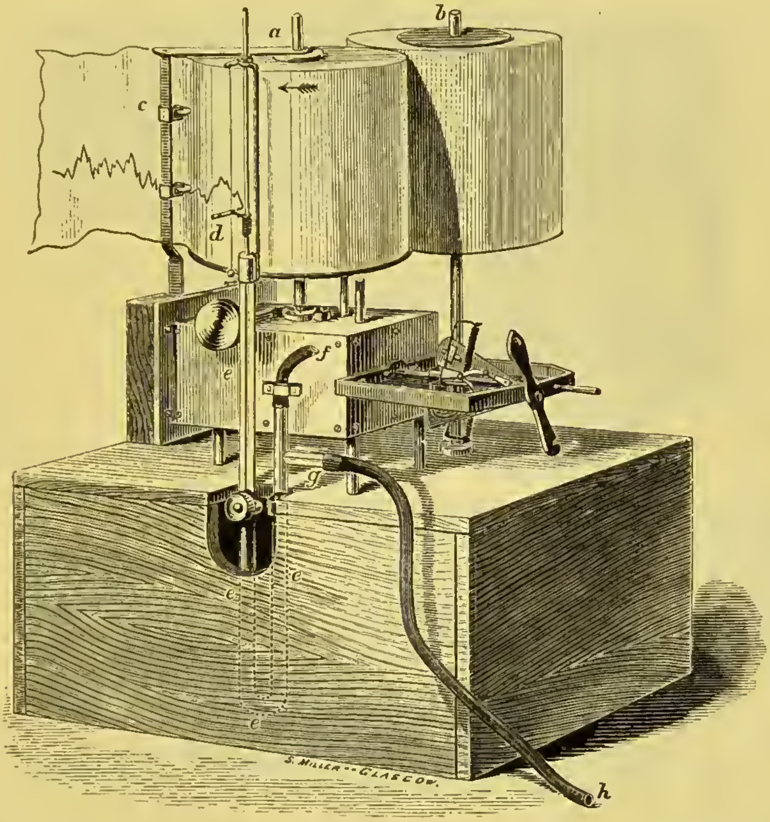


FIG. 156.—Mercurial kymograph for recording mean blood-pressure and its variations. *a*, band of paper rolling off, in the direction of the arrow, from the cylinder *b*; *e*, *e*, *e*, U-tube, or manometer, containing mercury, bearing on the surface of the mercury in one limb a float, to which is attached the marker *d*, inscribing the curve seen on the paper; *f*, tube for connection with a bottle of carbonate of soda, elevated above the apparatus so as to exert sufficient pressure to prevent the blood from entering, except to a very slight extent, the canula inserted into a vessel, say the carotid, and communicating with the tube *h*, *g*. (Burdon-Sanderson.)

tube leading to the shorter limb of the manometer. By means of a pressure bottle containing a solution of carbonate of soda, and suspended at any required height, or by means of a syringe filled with same solution screwed on to the top of the short limb of the manometer and connected also with the leaden pipe, the communication being guarded by a three-wayed stopcock, the leaden pipe is filled with the soda solution and sufficient pressure is made to keep the blood from ascending in the leaden pipe. The ligature on the cardiac side is then removed, the blood-pressure acts on the column of soda solution and through it on the mercury in the manometer, the float ascends and then begins to oscillate and write its movements on the recording surface.

The pressure is ascertained by measuring the height of any ordinate dropped from the curve to the abscissa and doubling the number of millimetres,—as it is evident that if, from the point of no pressure when the mercury stands at the same height in both limbs of the manometer, the mercury be raised by pressure say 10 mm. in one limb it will be depressed 10 mm. in the other. The work done by the blood-pressure may be estimated by the formula $h = 2n\left(1 - \frac{1}{2q}\right)$ in which h = work, n the height of the co-ordinate, and $1q$ the ratio of the specific weight of the carbonate of soda solution to that of the mercury employed.

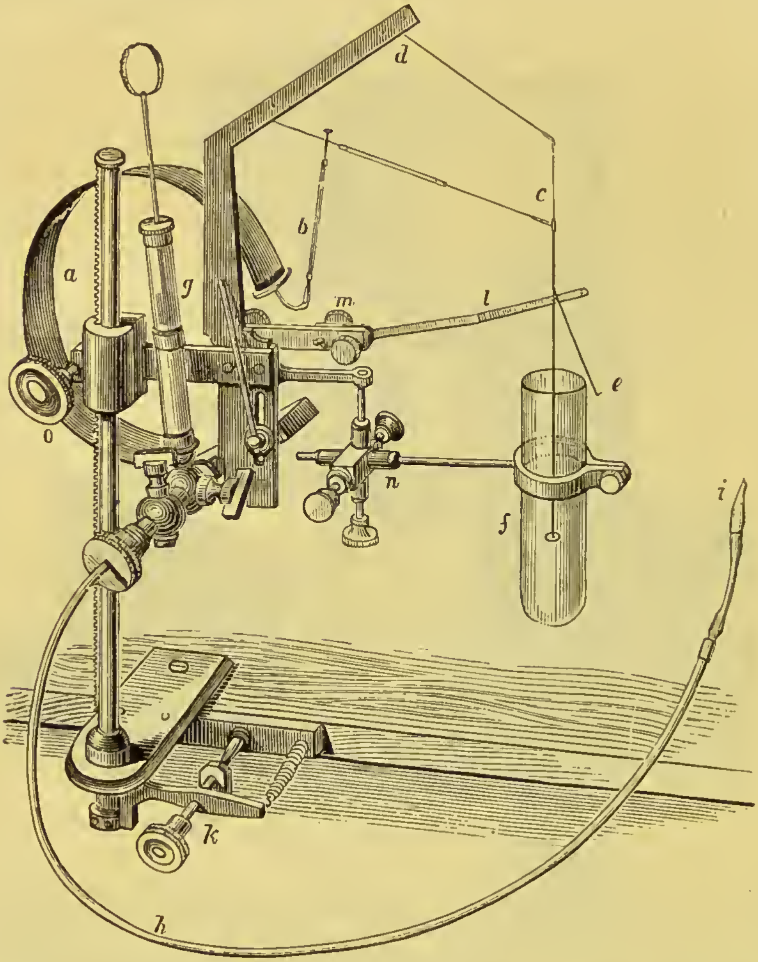


FIG. 157.—Fick's kymograph as modified by Hering. *a*, Hollow spring filled with alcohol, bearing lever arrangement *b*, *d*, *c*, to which is attached the marker *e*; the rod *c* passes downward into the tube *f*, containing oil or glycerine, which offers resistance to the oscillations of *c*; *g*, syringe for filling the leaden tube *h* with a solution of sodium carbonate, and to exert a certain pressure so as to prevent the blood from passing into the tube *h* at *i*, the canula inserted into the vessel; *l*, abscissa marker, which can be applied to the moving surface by turning the screw *m*; *k*, screw for adjusting the whole apparatus to the moving surface; *o*, screw for elevating or depressing by a rack and pinion movement, the kymograph; *n*, screw for adjusting the position of the tube *f*.

By such methods the following conclusions have been arrived at:

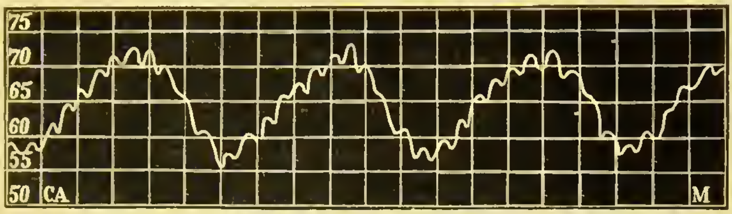


FIG. 158.—Mercurial kymographic tracing from carotid of a dog showing the form of the curve on a large scale. The figures on the left represent mm. of mercury. (Marey.)

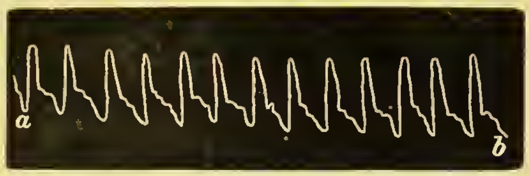


FIG. 159.—Curved spring kymographic tracings from carotid of dog. (Burdon-Sanderson.)

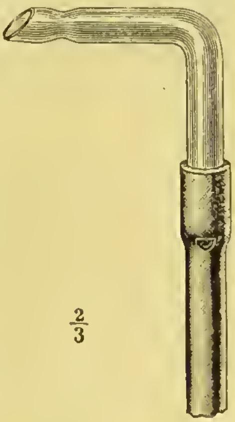


FIG. 160.—Canula, suitable for introduction into the vessels of animals.

(*a*) *Arterial Pressure.*—(1) The pressure diminishes from the heart to the capillaries; (2) it attains its maximum in the ventricle at the moment of systole, and its minimum in the auricle at the moment of diastole, at which time also the pressure in the auricles and in the great veins may be negative, that is, below atmospheric pressure; (3) in the carotid of the horse, the pressure is from 210 to 320 mm. of mercury; in dogs, from 100 to 170 mm.; in the sheep, about 170 mm.; in the cat, 150 mm.; and in the rabbit, 90 to 110 mm. Large animals have a higher pressure than smaller ones, but the increase is not in direct proportion to size. In man, the aortic pressure is probably about 250 mm. As examples of other animals, we have the pressure in the gill artery of a pike, stated at 35 to 84 mm.; in the aorta of the frog, 22 to 29 mm.; in the carotid of a goose, 162 mm. The pressure in the brachial artery of man during an operation was 110 to 120 mm., and in the anterior tibial artery of a boy, 100 to 160 mm. (4) The arterial pressure at any given point undergoes periodic variations, increasing at the instant of ventricular systole, and diminishing during diastole,—variations which are most marked in arteries near the heart; (5) these periodic variations may be observed in the intermittent jetting of an artery when it is punctured; (6) it is necessary to distinguish between the *mean arterial pressure* at any point of an artery and the *mean pressure of the blood in the whole arterial system*, which can only be obtained by taking the mean of the pressures in many different arteries at various distances from the heart; (7) the mean arterial pressure depends directly on the quantity of blood in the arterial system, and consequently on the total calibre of the system, so that any diminution of calibre, produced mechanically, or by nervous influences, will increase the mean arterial pressure; (8) the mean arterial pressure increases with the energy of the beats of the heart; (9) the blood-pressure becomes greater with increased and accelerated action of the heart, sometimes with plethora, and after an increase in the amount of blood, as occurs after a full meal, or transfusion of blood, whilst it becomes smaller during diminished or enfeebled action of the heart, in anæmia, and after hæmorrhage and excretion from the blood by the skin, kidneys, or bowels; (10) the pressure is affected by the degree of contraction or of dilatation of the blood-vessels, as influenced by the nervous system; (11) the pressure is increased in cases of sclerosis of the arterial walls, in lead poisoning, after injection of ergotin (which contracts the small arterioles) or of digitalis (which acts on the heart), where there is granular or contracted kidney, and in cardiac hypertrophy with dilatation; (12) the pressure is diminished in fever, in chlorotic anæmia, in phthisis, and by severe hæmorrhage; (13) any circumstance causing contraction of the muscular coat of any particular artery, so as to diminish the calibre, increases the pressure in that artery,—thus, by a slight contraction, the pressure in the femoral may become greater than in the carotid.

(*b*) *Venous Pressure.*—It has been ascertained (1) that in the veins near the heart the pressure is only $\frac{1}{20}$th to $\frac{1}{10}$th of that in the corresponding arteries; (2) during auricular diastole the pressure in the veins near the heart may become negative (–0·1 to –·6 mm. of mercury); (3) there are no periodic variations of pressure in the veins as in the arteries, except in the great venous trunks in the neck and near the heart, where there is a diminution of pressure during auricular diastole and an increase during auricular systole; (4) great activity of the heart diminishes venous pressure; (5) the pressure in the veins increases in veins farther and farther from the heart—thus, in the external facial vein of the sheep, it was found to be ·3 mm., in the brachial, 4·1 mm., in branches of the brachial, 9 mm., in the facial vein, ·3 mm., and in the crural vein, 11·4 mm.; (6) plethora increases venous pressure whilst anæmia diminishes it; (7) inspiration causes in the great veins near the heart an increase in pressure whilst expiration diminishes it, but the respiratory movements have no effect on pressure in peripheral veins; (8) changes in the position of the limbs affect venous pressure hydrostatically; thus elevation of the extremities favours the flow of blood towards the heart, whilst if the head hangs downwards the face becomes turgid as the outflow by the veins is retarded; (9) gravity favours the emptying of descending, and hinders the emptying of ascending, veins, so that the pressure becomes less in the former and greater in the latter; (10) muscular movement, by compression of the veins, and aided by the mechanism of the valves, favours the flow of blood towards the heart, and thus increases the pressure in these vessels.

(*c*) *Capillary Pressure.*—Du Bois Reymond states that the pressure in the middle of a capillary area is about *one half that in the large arteries;* but for obvious reasons capillary pressure has not been directly measured. Von Kries has measured the amount of pressure necessary to occlude the capillaries in an area abounding in these vessels, such as the skin at the root of the nail, on the terminal phalanx, or on the ear in man, and in the mucous membrane of the gum in rabbits, and he found the pressure in the capillaries of the hand, when the hand is raised, to be 24 mm. of mercury; when it hangs down, 54 mm.; in the ear, 20 mm.; and in the gum, 32 mm. (that is, from $\frac{1}{7}$th to $\frac{1}{12}$th of that in the aorta). Roy and Grahame Brown also measured the pressure necessary to close the capillaries in the web of the frog's foot, in the tongue and mesentery of the frog, and in the tails of newts and small fishes. It is evident that any condition favouring the afflux of blood to a capillary area will increase the pressure in the capillaries. Thus dilation of the small arterioles conveying blood to an area of capillaries, contraction of the venules carrying off the blood from it, any increase of pressure in the arterioles or in the venules, will increase the pressure in the capillaries of that area. The opposite conditions will have a reverse effect. The arrangement and position of the capillary network must affect the pressure. Finally, any change in the degree of contraction of the wall of the capillary itself will affect the pressure.

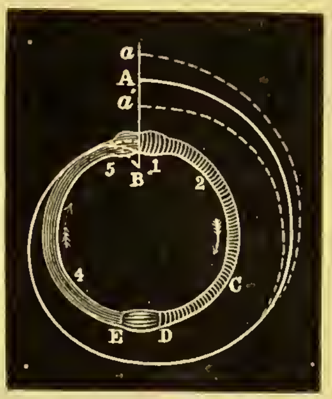


Fig. 161.—Diagram showing the pressure in the vascular system. 1, ventricle; 2, arteries; E, D, capillaries; 4, veins; 5, auricle. From A to C the line of pressure in the great arteries; C to D, in the small arteries; D to E, in the capillaries; E to B, in the veins. The dotted lines *a* C and *a'* C indicate the pressure during ventricular systole (*a* C) and during diastole (*a'* C). Beyond C the blood-pressure is uniform on to the auricle B 5, where it is negative during auricular diastole (Beaunis.)

The general facts regarding pressure in arteries, capillaries, and veins are well illustrated by the diagram (Fig. 161).

The pressure in the left ventricle of a dog (or, as it may be termed, the *intracardiac* pressure) was found to be from 8 to 14 mm. higher than that in the aorta.

In the carotid of a dog, Ludwig found a systolic increase of pressure of 10 mm. of mercury, or an increase of $\frac{1}{10}$th. During diastole, on the other hand, there must be a sucking of the blood into the heart cavities, thus producing a negative pressure in the veins. This sucking power for the left ventricle of the dog has been found to be – 7 to – 13·5 mm. of mercury, and for the right ventricle from ·5 to 1·5 mm.

When the heart stops beating, the pressure in the arteries falls enormously, but there is always a residual positive arterial pressure even in these circumstances, amounting in the dog to 10 or 15 mm. of mercury, showing that in the normal state, and even when the walls of the vessels are quiescent, the vascular system is over full. In a short time, however, the residual pressure in the arteries forces the blood into the veins, and the arteries are found empty after death.

It is remarkable that no less than $\frac{1}{3}$rd of the blood may be removed from the body without any change being produced on the blood-pressure; it only begins to fall when $\frac{2}{5}$ths of the blood have been removed, and it falls considerably when $\frac{1}{2}$ of the blood has been shed. If $\frac{2}{3}$rds or $\frac{3}{4}$ths are taken away, the pressure falls more and more, until the heart stops beating. After great hæmorrhage, life may be saved not only by the transfusion of fresh blood, but, as shown by Kronecker, the transfusion of even a ·75 per cent. solution of common salt will save life, raising the blood-pressure and stimulating the heart. According to Von Ott, it is less dangerous, in such circumstances, to transfuse a solution of salt than of defibrinated blood.

CHAP. II.—THE VELOCITY OF THE BLOOD.

1. Various attempts have been made by Volkmann, Vierordt, Ludwig and Dogiel, Hering, Chauveau and Lortet to measure the velocity of the

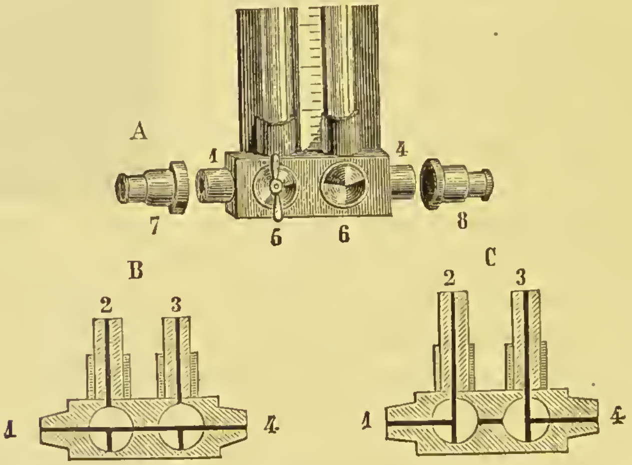


FIG. 162.—Volkmann's hæmadromometer. B, arrangement of stopcocks so as to allow blood to flow directly through without passing through the glass tube; C, position of stopcocks to allow blood to flow through the glass tube; 1-4, canulæ for cut ends of artery; A, end of instrument; 7, canula inserted into cardiac end of artery; 8, canula inserted into distal end of artery; 5, 6, stopcocks. The upper end of the U-shaped glass tube is not shown.

circulation, and special instruments have been invented for that purpose.

In 1850, Volkmann constructed an instrument termed the *hæmadromometer*, consisting of a U-shaped glass tube 60 to 130 c.c. long by 2 to 3 mm. in diameter, attached to a metal plate having suitable stopcocks as shown in Fig. 162. The blood is allowed to flow through the tube at a given moment, the time to make the circuit is noted, and as the length of the tube is known, the velocity of the circulation can be ascertained. It is evident that the velocity of the blood current will be soon retarded in the narrow glass tube. Vierordt, in 1858, attacked the problem by means of an apparatus called by him a *hæmatachometer*, consisting of a small metal box (Fig. 163) with parallel glass sides having a canula at each end, for insertion into the ends of the divided artery. A small pendulum is suspended in the box, whose vibrations along a curved scale may be read off. In the complete instrument, there is a rack and pinion arrangement of levers bearing a marker (moved by the hand whilst the eye follows the movements of the pendulum), for the registration of the movements on a drum. Here again the conditions are abnormal, and the apparatus is almost unworkable.

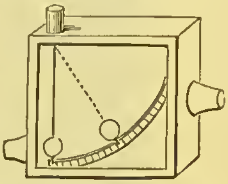


FIG. 163.—Vierordt's hæmatachometer.

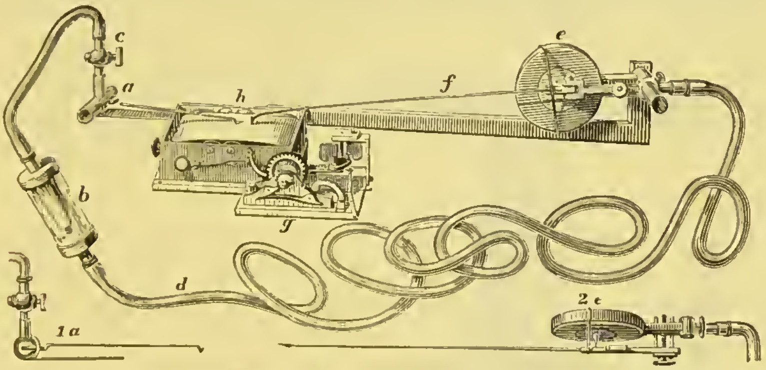


FIG. 164.—Hæmadromograph of Chauveau and Lortet. 1 *a*, section of tube *a*, showing oar-like end of lever in blood current. See text.

In 1860, Chauveau and Lortet (1867) constructed a *hæmadromograph* which gave better results. It consists of a copper tube, *a b* (Fig. 165), about 8 centimetres in length, which is introduced between the ends of the cut vessel; in the middle of the wall of this tube there is a slit closed by an india-rubber membrane, which is traversed as seen in 1 *a* (Fig. 164) by a light ivory needle, one end of which, somewhat flattened, like an oar, floats in the blood passing through the copper tube, whilst the other inscribes the movements on the paper *h*, moved by the clockwork *g*; the blood current, passing through the tube *a*, moves the needle, and the movement is registered on the paper. From *a* there also passes a tube *c*, communicating with a sphygmoscope of Marey. An improved form of the hæmadro-

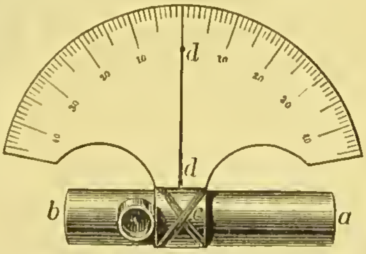


FIG. 165.—Simple form of hæmadromograph. *d*, index attached to float in tube, *b a*, through which blood flows.

mograph is shown in Fig. 166. The tube T T is inserted into the vessel. In this tube is a float attached to a rod which works on the tambour by which movement is transmitted. At S is a *sphygmoscope.* The *sphygmoscope* consists of a small glass cylinder, *b* (Fig. 164), in the interior of which is an elongated india-rubber bag communicating with the tube, *c*; the sphygmoscope transmits its movements by the india-rubber tube, *d*, to a registering tambour, *e*, the lever of which, *f*, writes the variations of pressure in the tube, *a*, alongside of the curve showing the velocity. Suppose the tube, *a*, fixed in the carotid artery of a horse,

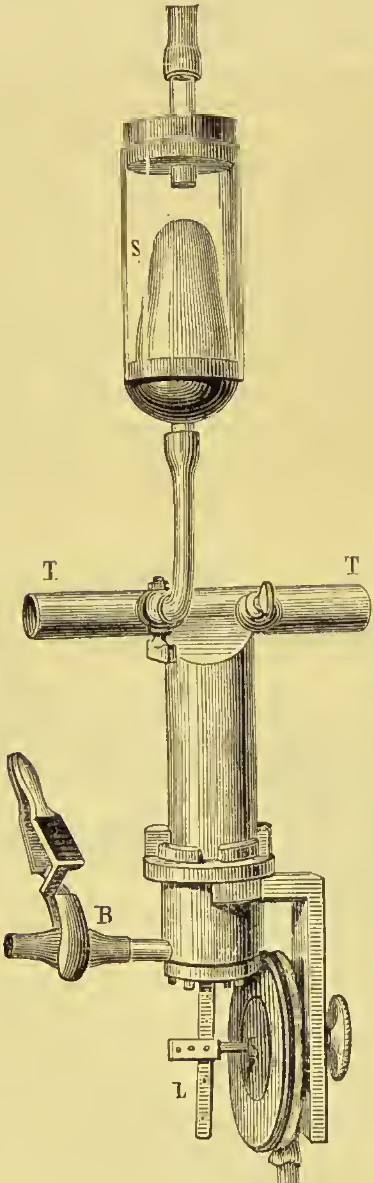


FIG. 166.—Improved form of the hæmadromograph of Chauveau and Lortet. S, sphygmoscope; T T, tube introduced into artery; B, exit tube of cylinder guarded by clip; L, end of float in T T, arranged to act on transmitting tambour.

controlled by a ligature placed above and below the apparatus. On removing the ligatures, the current flows onwards, moves the needle in the direction of the current, and this movement, assisted by the elasticity of the india-rubber membrane through which the needle passes, is registered on the paper. A specimen of the curve is shown in Fig. 167.

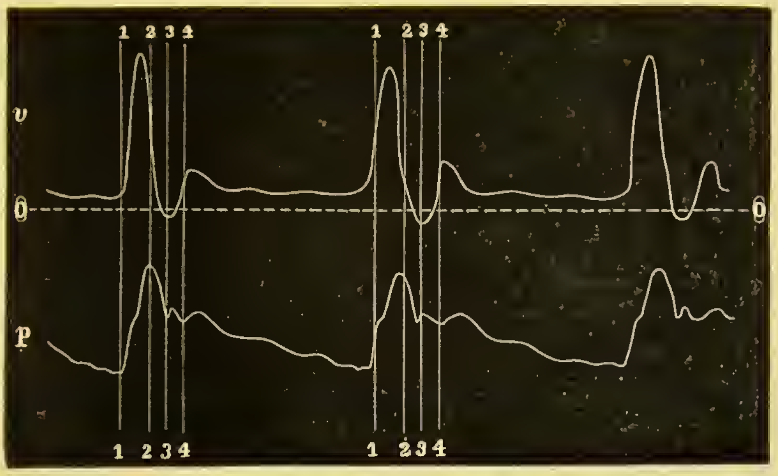


Fig. 167—Tracings of variations of rapidity and of pressure of the blood in the carotid of a horse, obtained by the hæmadromograph of Chauveau and Lortet. The line, *v*, represents the curve of the velocity of the blood, and *p* the curve of arterial pressure. The figures and vertical lines represent corresponding parts of the tracings, and a comparison of the tracings shows that there are oscillations in the velocity corresponding to those of the blood-pressure. (Lortet.)

Lastly, in 1867, Ludwig and Dogiel invented an instrument on another principle named a *stromuhr* (current clock) or *rheometer*. This instrument measures the amount of blood which passes through an artery in a given time. It consists of two glass bulbs (Fig. 168), *K* and *K'* of equal capacity communicating by a tube *O*; at the other end there are two tubes m and m', bearing canulæ *H* and *C*, which are inserted into the ends of the divided artery. The bulbs are supported by a metal disk *p*, *p'*, which turns on a lower disk *s*, *s'*, so that each of the bulbs may be successively put into communication with the tube *m* and with the tube *m'*. Before the experiment, having filled the bulb *K* with defibrinated blood, and bulb *K'* with oil, the tube *C* is put into connection with the central end of the artery, and the tube *H* with the distal end (as shown in Fig. 168). The blood pours through *C* into the bulb *K'* and displaces the oil in bulb *K'* into the bulb *K*, forcing the defibrinated blood in bulb *K* into the distal portion of the artery. The time from the instant the blood reaches the apparatus to the time when the oil fills the bulb *K* is noted. This is evidently the time in which a quantity of blood equal to the capacity of the bulb *K'* passes through the artery, and it is easy to deduce from this the velocity of the current. The experiment is then repeated by turning the disk *p*, *p'*, so that the bulb *K*, full of oil, communicates again with *Q* and with the cardiac end of the vessel, and the bulb *K'*, full of blood, with the distal end. Thus the experiment may be made many times in succession, and the mean of the observations will approach exactitude. The calculation is then made thus: Suppose that the quantity held by the bulb *K'* when filled is 5 c.c., and that from the moment of allowing the first 5 c.c. of blood to begin to enter the tube to the moment when the escape of the last 5 c.c. from the artery into the tube was complete, 100 seconds had elapsed, during which time 5 c.c. had been received 10 times into the tube from the artery (all but the last 5 c.c. being returned into the distal portion of the artery), obviously ·5 c.c. of blood had flowed from the proximal section of the artery in 1 second. Hence, supposing that the diameter of the canula (and of the artery, they being the same) were 2 mm. with a sectional area therefore of 3·14 square millimetres, an outflow through the section of ·5 c.c. or 500 c. mm. $(\cdot 5 \times 10^3)$ in a second would give $\left(\frac{500}{3\cdot 14}\right)$, a velocity of about 159 mm. in a second.

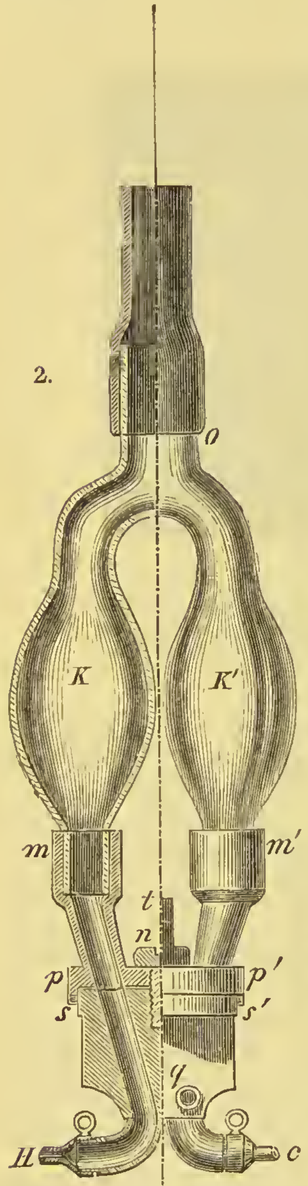


FIG. 168.—Ludwig and Dogiel's stromuhr for measuring the velocity of the blood.

By the use of such methods and instruments important results have been obtained. The following figures give, in mm. per sec., the velocities of the blood in different arteries:—Carotid of dog, 205 to 357 mm.; carotid of horse, 306 mm.; maxillary of horse, 232; metatarsal of horse, 56 mm. (Volkmann); mean velocity in carotid of dog, 261 mm.; in carotid of dog at end of diastole, 215 mm.; at end of systole, 297 mm.; in crural artery of dog at end of diastole 140 mm.; at end of systole, 239 mm. (Vierordt). With the hæmadromograph, Chauveau found in the great arteries near the heart during systole a velocity of 520 mm. per sec., at the beginning of diastole 220 mm., and during the pause 150 mm. Dogiel, with the stromuhr, gives the following:—In carotid of rabbits, from 94 to 226 mm.; in carotid of dog, weighing 23·28 kilos., poisoned with morphia, from 349 to 733 mm.; in carotid of another dog, weighing 12·13 kilos., from 243 to 520 mm. The velocity in the *capillaries* cannot be directly measured. E. H. Weber gives it at ·8 mm. per second in capillaries of mammals and ·510 mm. in those of the frog. Vierordt gives the velocity in man as ·6 to ·9 mm. per second. Volkmann states that the flow of blood in mammalian capillaries is 600 times slower than the blood in the aorta, and about twice as fast as that in the *vena cava*. Donders asserts that the velocity of the current in the smaller arterioles is 10 times faster than in the capillaries. When the current reaches the *veins* it is accelerated in consequence of diminished resistance, but even in the larger venous trunks it is ·5 to ·75 times less than in the corresponding arteries. The rapidity in the jugular vein of a horse was found by Volkmann to be 225 mm. per sec., while in the carotid of the same animal it was 300 to 400 mm. per sec. The following general conclusions may be drawn:—(1) The velocity of the blood is in the inverse ratio with the total calibre of the vessels; rapid in the aorta it diminishes as we recede from it; (2) each systole is followed by an increase in the velocity of the blood in the larger vessels; (3) in the smaller arteries, capillaries, and smaller veins, the velocity is uniform and constant; (4) the velocity increases in the venous system as we approach the heart; (5) in the large arteries the movements of inspiration retard the velocity, whilst those of expiration increase it; (6) in the large veins the movement of respiration and also the suction action of the auricle during diastole causes a rhythmic increase and diminution of the velocity. The explanation of these variations in velocity is obvious. As the arteries pass outwards they give off branches, the united calibre of which is, with rare exceptions, greater than that of the parent vessel. Thus, as Küss expresses it, the arterial system may be regarded as a cone, the base of which ends in the capillaries whilst the summit is at the aorta; on the other hand, the venous system is a second cone, the base being also at the capillaries and the apex at the right auricle. Vierordt states that the sectional area of the capillaries is to that of the aorta as 800 to 1, but as the sectional area of the venous orifices at the heart is greater than that of the arterial orifices, the ratio of the sectional area of the capillaries to that of the veins at the heart has been stated as 400 to 1. The increased cross-sectional area retards the velocity, and the velocity of the blood-current in sections of the vessels at various points is inversely as their calibre. The blood travels at the slowest rate in the capillaries where the cross-sectional area is greatest, and it increases in the veins as, from their confluence, the cross-sectional area again diminishes. The veins, however, having a greater capacity than the ventricles, the rapidity of flow in the arteries is always much the greater. The velocity of the blood does not depend on the mean blood-pressure, and, as pointed out by Ludwig and Dogiel, the velocity in any section of a vessel depends on (1) the *vis a tergo* (*i.e.*, action of the heart), and (2) on the amount of resistance at the periphery.

Chap. III.—THE DURATION OF THE CIRCULATION.

It is important to distinguish between the rapidity of the blood current and the time occupied by a blood corpuscle in making a complete circuit through the heart and vessels, say from the left ventricle to the left ventricle again. Attempts have been made to measure the time, starting from the jugular vein. Thus, about 1838, Hering injected into the jugular vein a few drops of a 2 per cent. solution of ferrocyanide of potassium, and he examined the blood of the opposite jugular every five seconds by testing with perchloride of iron—the formation of Prussian blue indicating the moment when the ferrocyanide made its appearance in the blood of the jugular after having made a tour of the circulation. Vierordt so modified the method as to examine the blood received from the jugular each half second. The duration of the circulation as thus determined for various animals is thus stated: horse, 31·5 seconds; dog, 16·7; rabbit, 7·79; hedgehog, 7·61; cat, 6·69; goose, 10·86; duck, 10·64; buzzard, 6·73; and common fowl, 5·17 seconds. In considering the striking variations in these numbers, Vierordt also made the discovery that in most animals the duration of the circulation is equal to the time in which the heart makes about twenty-seven beats. These facts are illustrated by the following table:—

Name of animal.	Weight of the body in grammes.	Pulse beats per minute.	Number of pulsations in the duration of the circulation.
Guinea-pig,	222	320	23·7
Cat,	1,312	240	26·8
Hedgehog,	911	189	23·8
Rabbit,	1,434	220	28·5
Dog,	9,200	96	26·7
Horse,	380,000	55	28·8
Fowl,	1,332	354	30·5
Buzzard,	693	282	31·6
Duck,	1,324	163	28·9
Goose,	2,822	144	26·0

It may also be shown by another method that a volume of blood equal to that in the whole body passes through the heart in about thirty pulsations. Taking the quantity of blood in the body as one-twelfth of the total weight, a man weighing 140lbs. contains about 11lbs., or 5632 grammes of blood. These represent in capacity 5322 cubic centimetres. Each beat of the heart throws 172 cubic centimetres into the aorta : 5322 ÷ 172 = about 30. Taking the pulse beat at 72 per minute, it follows that in from 27 to 30 heart-beats, occupying about 32·2 seconds, a volume equal to the total blood of the body will pass through the heart, or, in other words, about 32 seconds is the duration of the circulation. Munk makes the statement thus : An amount of blood equal to that in the body, passes through the heart of the horse in $\frac{5}{8}$; in the ox, in $\frac{2}{3}$; in the man, in $\frac{3}{7}$; in the dog, in $\frac{1}{3}$; and in the rabbit, in $\frac{1}{5}$ of a minute.

Chap. IV.—CHANGES IN THE VOLUME OF ORGANS.

It has been satisfactorily proved by Mosso, Basch, Dogiel, and François-Franck that there is a slight change in the volume of any distensible organ with each beat of the heart. Mosso devised an instrument known as the *plethysmograph*, a form of which, as used by Franck, is shown in Fig. 169. The following results have been obtained : (1) the volume of an organ is not fixed, but varies according to the amount of blood contained in it ; (2) its volume changes with each cardiac pulsation, increasing when blood is forced into it, and diminishing by emptying of the capillaries into the veins ; (3) variations in the volume of one or more organs, say by compression, or by the application of cold, or by the internal administration of substances which affect the calibre of blood-vessels, such as ergot, will cause corresponding variations in the volume of the organs ; (4) the pulsatile variations are very similar to the pulse-curve, and there are respiratory undulations corresponding to similar variations in blood-pressure tracings ; (5) movements of the limb cause diminution in volume in consequence of acceleration of the venous current ; (6) mental exercise and sleep cause a diminution in volume of the limb ; (7) so delicately attuned is the organism that

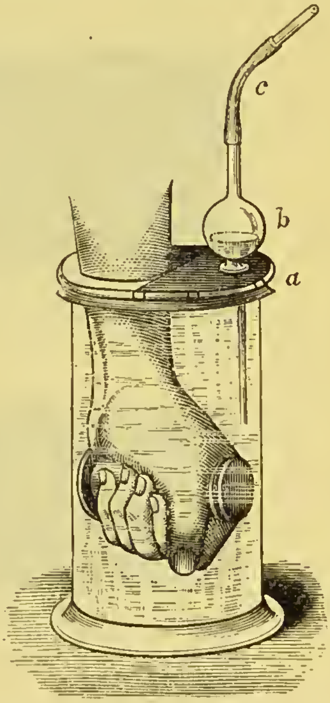


Fig. 169.—Apparatus for showing changes of volume of the hand. The india-rubber membrane, through which the forearm is passed, is kept immobile by a metallic plate *a* ; a tube, blown into a bulb at *b*, is connected with a registering tambour by the tube *c*. The glass vessel is filled with water, the hand is inserted, and, to aid in giving steadiness, the transverse bar is firmly grasped. (Franck.)

music has been observed to cause a rise and fall in the tracings. (See tracings, with descriptions, in Figs. 170, 171, 172, and 173.)

FIG. 170.—The upper line shows cardiac tracings, and the lower line shows tracings from change of volume of the hand. The two tracings were taken simultaneously. The dotted vertical lines show corresponding times.

FIG. 171.—Reduced tracing given by Franck, showing change of volume of the hand and suppression of the pulsations by compression of the brachial artery, at the time indicated by *b*. Observe the fall indicating diminution of volume and the absence of pulsations in *b*, *c*, *d*; soon after *d* compression was removed, the curve mounted to *e*, and oscillations recommenced.

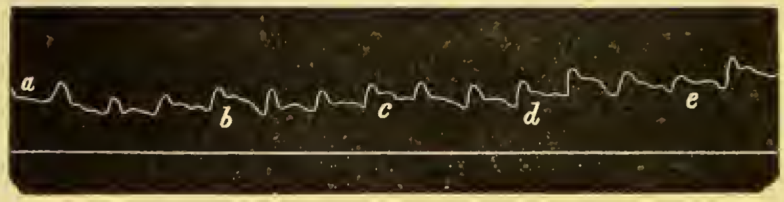


FIG. 172.—Reduced tracing given by Franck, showing the effect of compression of the two femoral arteries on the volume of the hand. On compressing at *b*, shortly after *c*, the volume of the hand increased, as shown by the ascent of the curve towards *e*.

The Distribution of Blood.

The blood is distributed throughout the body in varying proportions, according to the requirement of any set of organs at a particular time. When any tissue or organ is active, there is a determination of blood towards it—the amount being increased from 30 to 50 per cent. Thus, during digestion the mucous membrane of the stomach and intestinal organs is richly supplied with blood, and increased muscular activity is

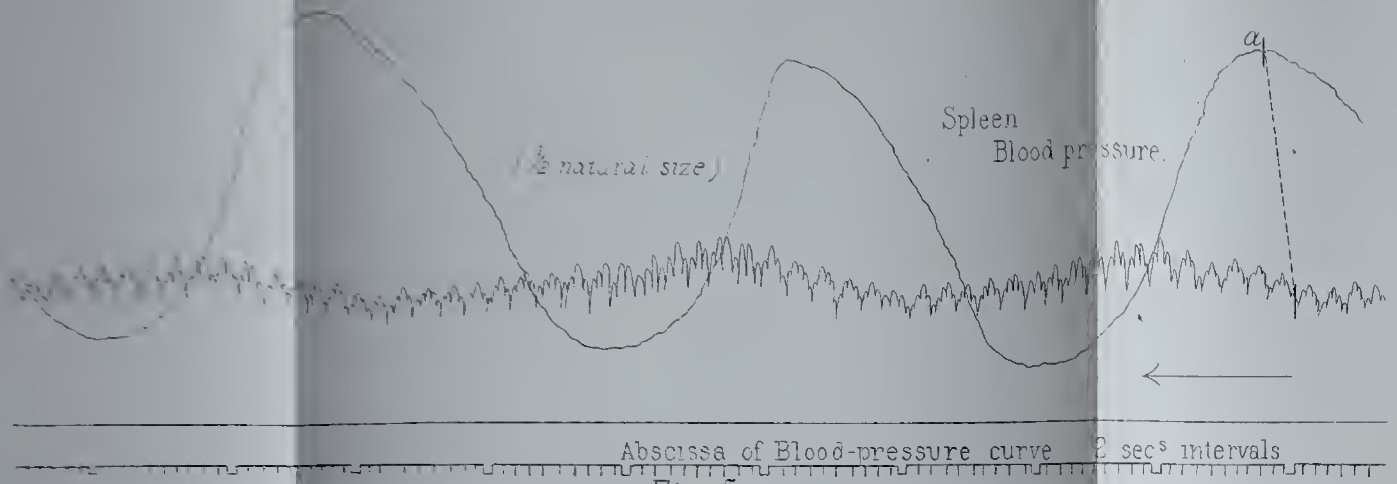


Fig 5

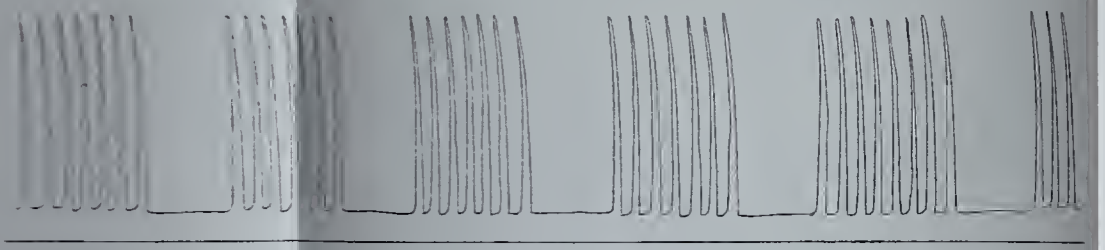


Fig. 6.

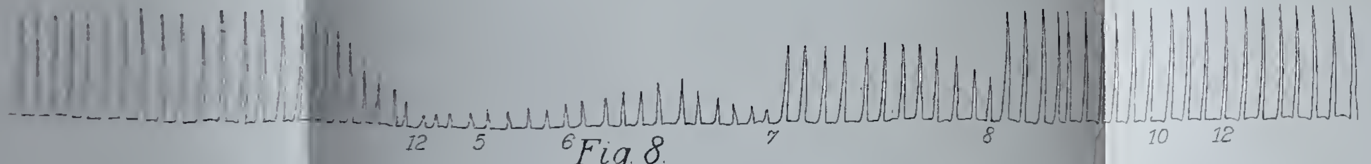


Fig 8.

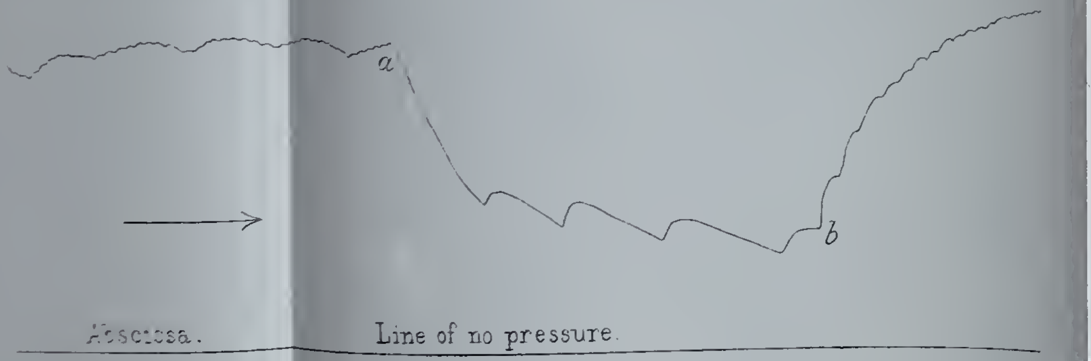


Fig. 9.

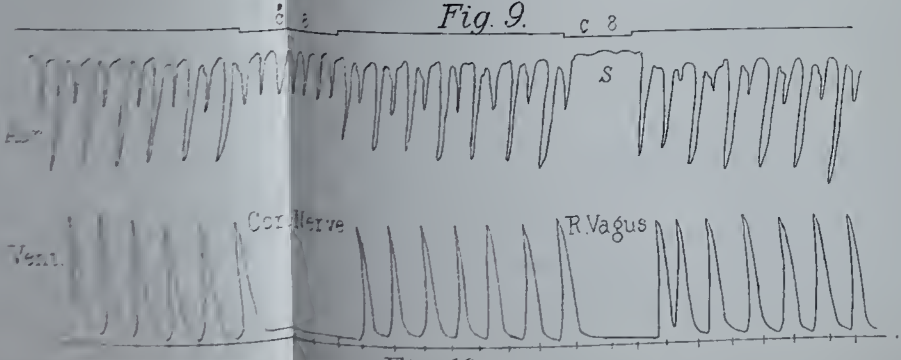


Fig. 10.

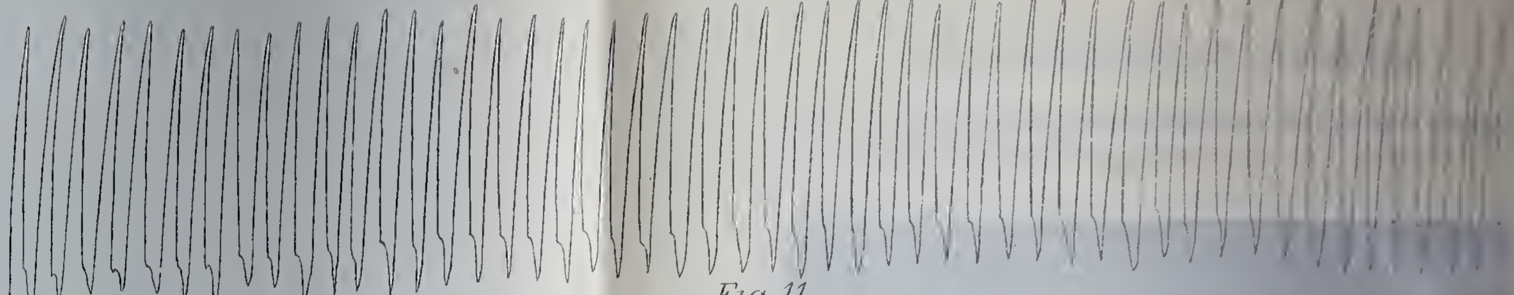


Fig. 11.

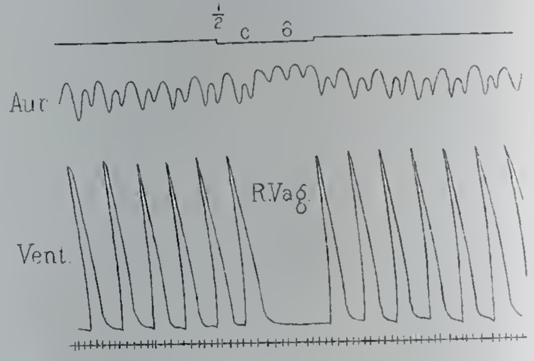


Fig. 7.

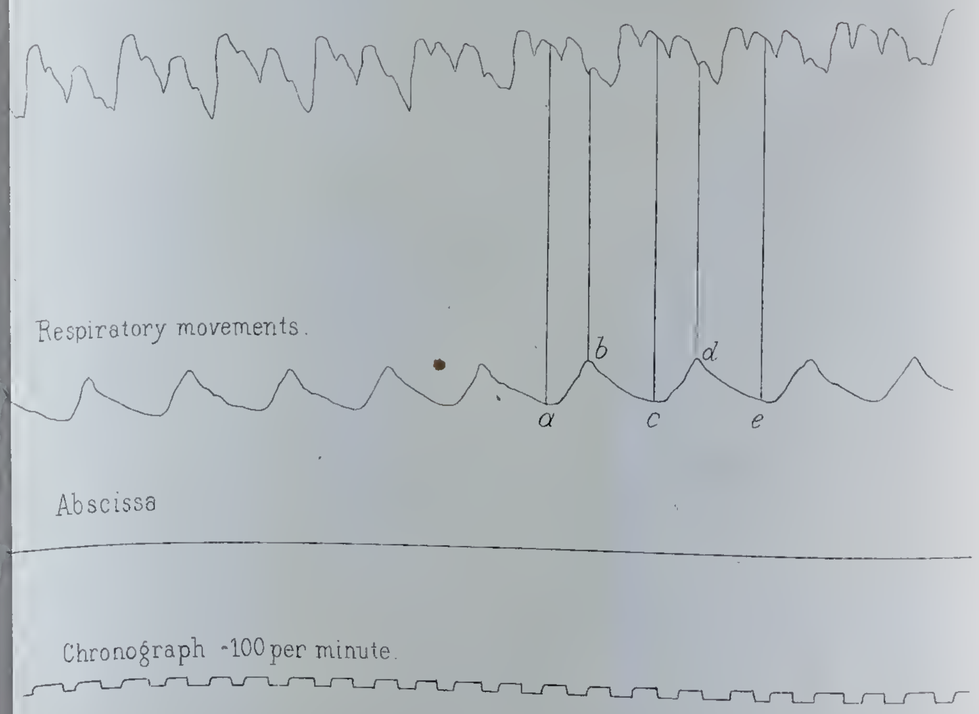
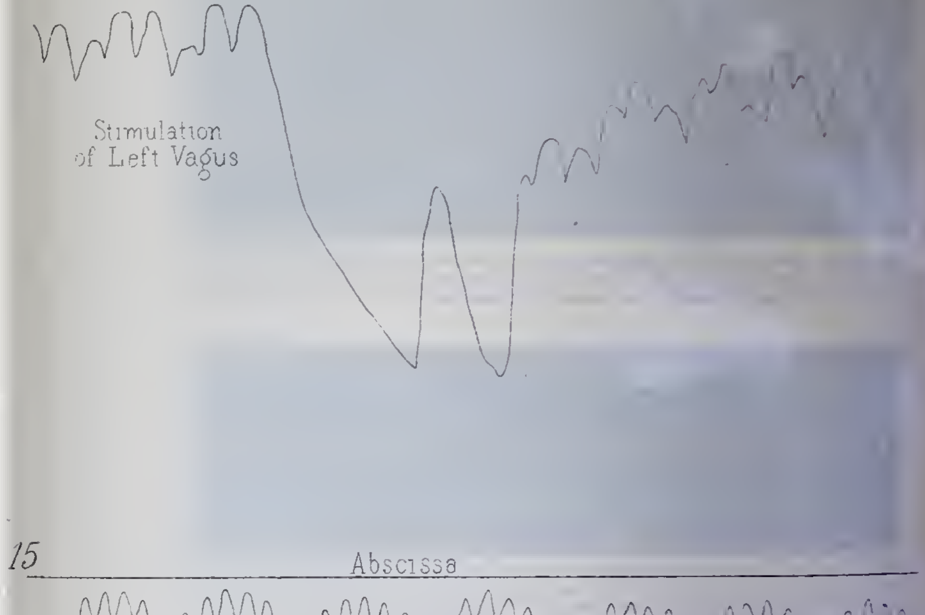


Fig. 13.

Fig 15



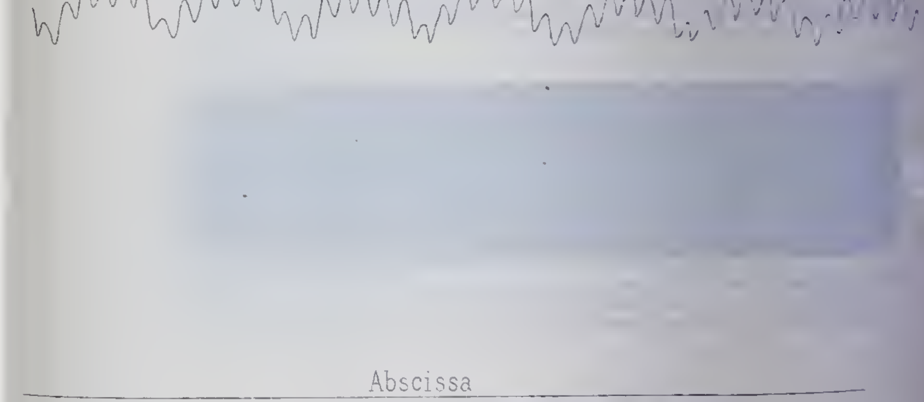


Fig 14.

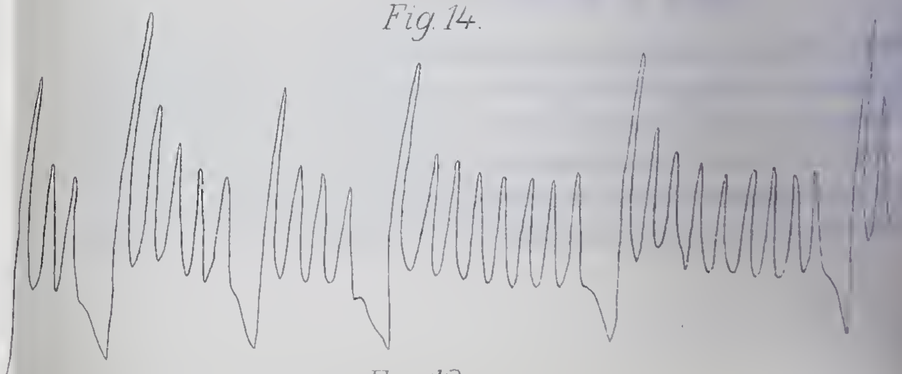


Fig. 12.

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DESCRIPTION OF PLATE B.

Fig. 5.—Tracing showing the *movements of the spleen* of a cat, and at the same time the blood pressure in the carotid artery. The movements of the spleen were recorded by Roy's oncograph, and the blood pressure by the mercurial kymograph. It will be noticed that there is no correspondence between the variations of blood pressure and the enlarging and diminishing in volume of the spleen, p. 174.—Roy.

Fig. 6.—Tracing of the pulsations of the *ventricle of a frog's heart*, taken with Roy's tonometer, showing the groups of pulsations described by Luciani. The groups are five in number, the first four being made up of seven contractions, and the last of eight. Here the contractions are of the same height, because the pressure against which the ventricle contracted (25 c.cm. of water) "was one against which it was able to empty itself completely at each beat." When the pressure is greater, the individual contractions diminish in each group—the first being greater than the second, the second than the third, and so on, p. 224.—Roy.

Fig. 7.—Tracing from *heart of tortoise*, studied according to the method described in Fig. 4, Plate A. The aorta was held and the auricle slit up. The stimulus applied was from an induction apparatus with the secondary coil 6 cm. from the primary. Time marker, 2 seconds. On stimulating the right vagus, indicated by c 6, a partial block occurred, and the ventricle missed two beats, p. 230.—Gaskell.

Fig. 8.—Tracing of the pulsations of the *auricle of a frog's heart*, taken with Roy's tonometer, showing the effects of stimulation. The figures 12, 10, 8, 7, etc., on the abscissa, give the strength of the current employed to stimulate the auricle, the zero indicating that the secondary coil was pushed as far as it would go over the primary. The tracing shows the rhythm unchanged, but the force of the contractions was modified by the strength of the stimulus. With the secondary 12 cm. from the primary there was no effect; at 10 cm. the effect was slight; at 8 cm. the contractions were at first weakened, but they soon became more powerful; at 7 cm. the weakening was at first more marked; at 6 cm. and 5 cm. it was still more evident, and at 12 cm. they again became stronger, and attained the same height as at the beginning of the experiment, p. 233.—Roy.

Fig. 9.—Tracing of the *blood pressure* in the carotid of a rabbit, taken with the mercurial kymograph. At *a*, the *depressor nerve* was irritated, and the irritation ceased at *b*. Observe the great fall in pressure, p. 293.

Fig. 10.—Tracing from *heart of tortoise*, studied according to the method described in Fig. 4, Plate A. The aorta was held, the auricle slit up, and the coronary nerve was stimulated with the secondary coil at 8 cm. from the primary. Time marker every eight seconds. Observe, a partial block was produced by stimulating the coronary nerve, *e* 8, and by stimulating the right vagus, the ventricle missing several beats, p. 230.—Gaskell.

Fig. 11.—Tracing of *blood pressure* in the carotid of a dog, taken with Fick's spring-kymograph, p. 276.

Fig. 12.—Tracing of *blood pressure* in the carotid of a dog, taken with Fick's spring-kymograph, whilst the animal was very deeply under the influence of chloroform. Observe the occasional failure in the heart's action, the heart missing a beat; then followed by a strong contraction. The phenomenon was not unlike the grouping of beats of Luciani, see Fig. 6, p. 276.

Fig. 13.—Tracing of the *blood pressure* in the carotid of a dog, whilst deeply under chloroform, taken with the mercurial kymograph. The respiratory movements were simultaneously recorded by Marey's pneumograph connected with the thorax. *a, b*, inspiration; *b, e*, expiration, p. 294.

Fig. 14.—Tracing of the *blood pressure* in the carotid of a dog, deeply under the influence of ether. Taken with mercurial kymograph. Observe that there is no fall of blood pressure, such as is seen in Fig. 1, Plate A, while the animal was under the influence of chloroform, p. 235.

Fig. 15.—Tracing of the *blood pressure* in the carotid of a dog, showing the sudden fall of pressure caused by stimulation of the left vagus. The tracing is to be read from left to right. Taken with mercurial kymograph, p. 225.

always accompanied by increased vascularity. Whilst this is the rule, there are organs, such as the heart, the muscles of respiration, and nervous centres like those in the *medulla oblongata*, in which there is a condition of continuous activity, and in which there is a uniform vascularity. Seeing that the activity of certain organs varies at different times, it follows that whilst some organs are congested others are at rest. In the child there appears to be a different distribution of blood from what obtains in the adult. The heart of a child is relatively small up to puberty, while the vessels are relatively large; after puberty the reverse is the case. Arterial pressure is less in the child than in the adult, whilst the pressure in the pulmonary circulation is larger in the child than in the adult. Attempts have been made to estimate the distribution of blood after death. Thus Ranke states that $\frac{1}{4}$ of the total blood remains in the muscles, $\frac{1}{4}$ in the liver, $\frac{1}{4}$ in the heart and vessels, and the remaining $\frac{1}{4}$ in the rest of the organs.

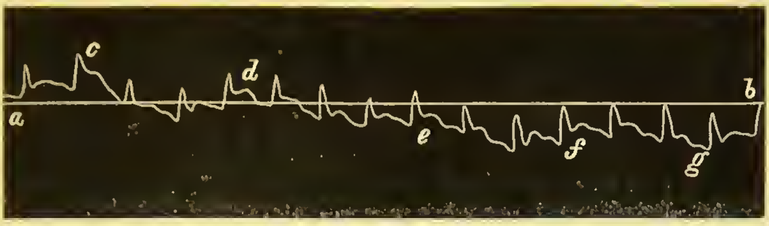

Fig. 173.—Reduced tracing by Franck, showing a diminution in the volume of the hand, produced by placing a lump of ice on the skin of the shoulder at the time indicated by *d*. Observe the falling of the curve toward *e*, *f*, *g*, showing diminution of the volume of the hand.

Chap. V.—SPECIAL FORMS OF CIRCULATION.

1. **The Hepatic or Portal.**—The peculiarity of the portal circulation is that the blood passes through two sets of capillaries. Arterial blood is conveyed to the stomach, spleen, pancreas, and intestines by branches of the abdominal aorta. These branches divide and subdivide, terminating in a capillary plexus in the various organs above enumerated. From this plexus the radicles of the various veins spring, unite with each other so as to form larger and larger trunks, until, by the confluence of the mesenteric veins with the splenic vein, the portal vein is formed. The portal vein conveys the blood to the liver, dividing in that organ into smaller and smaller branches until a plexus is formed in the lobules of the liver. From this plexus spring the roots of the hepatic vein which unite again and again to form the hepatic vein. Finally this vessel conveys the blood from the liver to the inferior vena cava. There are thus in the portal circulation two sets of capillaries—one in the abdominal viscera, and the other in the liver. Ligature of the portal vein causes distension of all the abdominal vessels and a highly congested state of the abdominal viscera, whilst the blood-pressure quickly falls, and the animal dies. So distensible are the abdominal vessels that they can

contain nearly all the blood in the body. The ventricular systole may send a pulse down the valveless inferior vena cava and cause a pulse in the liver. The liver swells with each systole and relaxes with each diastole of the heart.

2. **The Pulmonary.**—The pulmonary artery, carrying venous blood, divides and subdivides, and the smallest branches end in a plexus of capillaries on the walls of the air-cells of the lung. From this plexus the radicles of the pulmonary veins originate, and finally the four pulmonary veins, two from each lung, carry the arterialized blood to the left auricle. Considering the apparently small extent of the pulmonary as compared with the systemic circulation, and the fact that the two ventricles, of about equal capacity, empty themselves simultaneously, it is clear that the pulmonary circulation presents many points of interest. In the first place the pressure in the pulmonary artery is much less than that of the aorta. In 1850, it was determined by Ludwig and Beutner to be in the dog 29·6 mm., in the cat 17·6 mm., and in the rabbit 12 mm., or about 3 times less in the dog, 4 times less in the rabbit, and 5 times less in the cat than the pressure in the aorta. Hering passed simultaneously a tube through the muscular walls of each ventricle of a calf, and the blood rose in the tube in the right ventricle 325 mm., and in the left ventricle 835 mm., that is, in the ratio of 1:2·5. Fick and Badoud found a pressure of 90 mm. in the pulmonary artery of the dog, whilst the carotid pressure at the same time was 111 mm. The ratio of pulmonary to aortic pressure has been stated as 1 to 3, or as 2 to 5.

Next, it is important to note the peculiar physical conditions in the chest during respiration. As already shown, p. 218, the lungs are distended, in consequence of the positive pressure on their inner surfaces being greater than the negative pressure on their outer pleural surfaces. But when the lungs are distended by a *full* inspiration there is an elastic force exerted by them (termed elastic recoil, or "elastic traction"), amounting to about 30 mm. of mercury. Outside the lungs, in the cavity of the chest, the surfaces of the heart and vessels are subjected to a pressure which is the difference between atmospheric pressure (760 mm.) and the "elastic traction" (30 mm.) or 730 mm. It is clear that the more the lungs are distended the greater will be the elastic traction, and consequently the less will be the pressure on the outer surface of the vessels. The thin-walled pulmonary veins will yield more during a deep inspiration, thus diminishing pressure, than the thicker-walled pulmonary artery, and thus the flow of blood from the capillaries of the lung by the pulmonary veins to the left auricle will be favoured. On the other hand, expiration by increasing the pressure will tend to retard the flow of blood. Further, the velocity of the stream of blood is accelerated in the pulmonary vessels by inspiration and retarded by expiration. As regards the influence of the movements of the lung on the calibre of the pulmonary capillaries and smaller vessels, experiment has shown that the blood-vessels of the lungs containing air and distended are wider than those of collapsed lungs. Suppose an elastic bag having minute tubes in its walls. If such a bag is dilated in a free space the lumen of these tubes is diminished, but if it be placed in a closed space, as in a wide glass bottle, and if the pressure on its outer surface be diminished by removing air from the space between the bag and the side of the bottle, the bag will distend and the lumen of the tubes will also be increased. Thus it is evident that inspiration, by increasing the calibre of the pulmonary vessels, draws blood towards the lungs, and the movements of he lungs become an effective force in carrying on the pulmonary circulation.

The velocity of the blood is greater in the pulmonary than in the systemic capillaries, and the velocity is greater in the pulmonary veins than in the pulmonary arteries. The great degree of distensibility of the pulmonary vessels allows of frequent adjustments being made, so that, within limits, as much blood in a given time will pass through the pulmonary as through the systemic circulation. This adjustment, however, may be readily disturbed. For example, violent muscular exertion hurries the blood along the veins to the right side of the heart, and by the right ventricle the blood is discharged into the pulmonary circulation. If more arrives than can be transmitted to the left auricle by the pulmonary veins in a given time, the pulmonary capillaries become engorged, breathing becomes quick and possibly irregular, the right side of the heart becomes engorged, signs of venous congestion appear in the flushed face and turgid veins, and perhaps pulmonary capillaries may rupture, causing hæmorrhage from the lung. The weaker the muscular structure of the heart the more likely is this to occur. Hence the breathlessness in many cardiac affections, aggravated by muscular exertion, more especially in ascending a stair or hill.

The special arrangements of the cranial circulation will be described in treating of the nervous system and of the fœtal circulation in discussing the subject of reproduction.

Chap. VI.—THE INNERVATION OF THE BLOOD-VESSELS.

If the sympathetic nerve is divided in the neck, there is a dilatation of the vessels and an increase of temperature on the same side; but irritation by weak induction-currents of the cephalic end causes the vessels to contract and the temperature to fall. In the sympathetic, therefore, there are nerve fibres which influence the contractile coats of the blood-vessels. These fibres, called *vaso-motor*, originate from a vaso-motor centre in the *medulla oblongata* between the point of the *calamus scriptorius* and the lower border of the *corpora quadrigemina*, in the floor of the fourth ventricle. From this chief vaso-motor centre, nervous influences emanate which tend to keep the smaller vessels in a more or less contracted condition. If it is injured, paralysed, or destroyed there is at once great dilatation of the vessels, more especially those in the abdominal cavity, and the blood collects in these dilated vessels. This of course diminishes the arterial pressure in the larger vessels. Consequently, by observations on blood-pressure, it has been found possible to study the conditions of vaso-motor action. By connecting a kymograph with a large vessel, say the carotid, observing for a time the mean blood-pressure, and afterwards injuring the supposed vaso-motor centre, Ludwig and Owsjannikow at once observed an enormous fall of blood-pressure, to be explained by the paralysis of the smaller, and a consequent emptying of the larger, vessels.

The vaso-motor nerves causing contraction of vessels have been called *vaso-constrictors;* but there are other nerve fibres possessing the property of causing a dilatation instead of a contraction. These have been called *vaso-dilators*. Excitation of the *chorda tympani nerve,* for example, causes the vessels of the submaxillary gland to dilate. Erection, as it occurs in the penis, has long been known to depend on dilatation of vessels and consequent increased afflux of blood. Stimulation of the nerves of the sacral plexus may cause erection. But how do such nerve fibres act? It cannot be that they directly cause relaxation of the muscular fibres in the walls of the vessels. These contain layers of involuntary muscular fibres in the transverse and longitudinal directions, and it is difficult to understand how any contraction of fibres in either of these directions could possibly cause dilatation of the vessel. Probably the effect is brought about by the action of some kind of inhibitory mechanism. Ganglia abound in the walls of the vessels. From these, fibres pass to and from the muscular elements of the vessel. Such ganglia, or local reflex centres, may be supposed to be under the influence of two sets of nerve fibres—(1) *accelerating* or strengthening, corresponding to the accelerating fibres that influence the heart; and (2) *inhibitory*, like the fibres of the vagus distributed to the heart, having the power of restraining the action of the local ganglia. According to this view, the fibres in the chorda which cause dilatation of the vessels of the submaxillary gland on stimulation are vaso-inhibitory nerves.

Dr. Gaskell is of opinion that with regard to the vessels, as with regard to the heart, the vaso-constrictor nerves may be concerned in katabolism, while the vaso-dilators or vaso-inhibitory nerves (like the cardiac fibres of the vagus) are anabolic in their action. This view has much in its favour.

Bearing in mind, then, the existence of a *vaso-motor centre* in the *medulla oblongata,* we have next to consider whether, and to what extent, it can be controlled by impressions coming from other organs or from the periphery.

In describing the innervation of the heart (p. 225), it was pointed out that stimulation of the pneumogastric nerve in the neck slows the rate of the heart-beats, and if the stimulation is strong, arrests the heart in a state of diastole. Suppose a kymograph to be connected with the carotid in the neck of a rabbit deeply under the influence of chloral so as to be quite unconscious of pain; if one of the vagi in the neck is stimulated, the blood-pressure curve at once falls as shown in Fig. 5, Plate B., and on removing the stimulation it rises to its former height by a few leaps and bounds. Whilst this occurs in the arteries the venous pressure rises in consequence of the flow of blood into the veins from the arteries. But the pressure may be influenced by another method. As pointed out by Ludwig and Owsjannikow, a centre exists in the *medulla oblongata* (*vaso-motor centre*) whence influences emanate that tend to keep the vessels in a more or less contracted condition. If this centre is injured, the smaller blood-vessels throughout the body dilate, or in short, they are paralysed; they receive more blood and consequently the pressure in the larger vessels at once falls. This vaso-motor centre, in turn, can be influenced by impressions reaching it from the periphery. This was clearly proved by Cyon in 1866, when he discovered the function of the *depressor* nerve, a small nerve (the *superior cardiac*) originating in the rabbit from the superior laryngeal and from the pneumogastric nerve (Fig. 174), but in many animals blended with the pneumogastric nerve. Stimulation of the distal end of this nerve produces no effect, but stimulation of the cephalic end causes a great fall of blood-pressure and a diminution in the frequency of the pulse (Plate B., Fig. 9). Such *depressor* filaments also exist in the trunk of the vagus below the origin of the superior cardiac nerve (depressor of Cyon), in the nerves coming from the lungs, in the great auricular nerve, in the tibial, and in all probability in all sensory nerves. The depressor nerve of Cyon and Ludwig appears to influence chiefly the vaso-motor arrangements of the abdomen and lower extremities. Thus, after section of the splanchnics, which control the vessels of the abdominal viscera, excitation of the depressor does not produce nearly the same diminution of pressure in the carotid vessels. By the influence of the depressor a balance is kept up between the central and the peripheral circulations. Imagine the heart to be pumping blood through the vessels. If from some cause the smaller vessels become constricted so as to offer greater resistance to the passage of the blood, the arterial pressure in the larger vessels is increased, and the heart has more work to do to

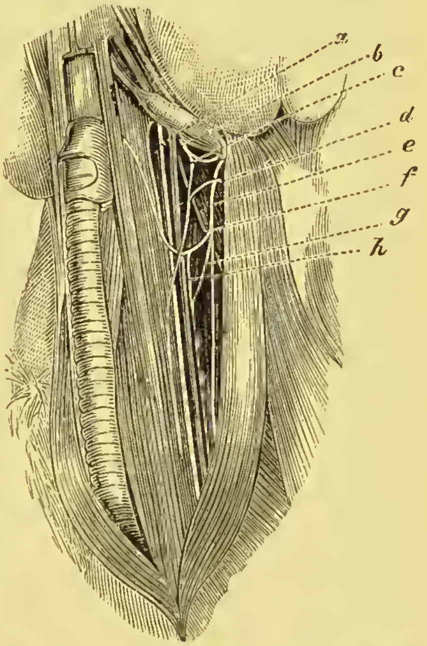

Fig. 174.—Nerves in the neck of a rabbit according to Ludwig and Cyon. *a*, sympathetic; *b*, hypoglossal; *c*, the descending branch of hypoglossal (*descendens noni*); *e*, vagus; *f*, superior laryngeal branch of vagus; *g* and *h*, roots of the depressor. (Cyon.)

overcome this resistance. When the resistance reaches a certain amount the heart will be in danger of exhaustion in endeavouring to overcome it. But by the depressor this danger is removed, as an influence may pass from the heart along the fibres of the depressor to the vaso-motor centre, the effect of which is to inhibit the activity of this centre, and thus allow the smaller vessels to dilate. When this occurs, either locally, as in the abdominal region, or generally (affecting the whole body), the result is a depletion of the larger vessels, a consequent fall of pressure in these, and therefore less resistance to the efforts of the heart. Thus it would appear that in the heart itself there is an arrangement by which, to a certain extent, it governs its own work, and there is an adjustment between the activity of the heart and the distribution of blood throughout the body. Further, it may be shown that it may be influenced by nerve fibres, the stimulation of which *excites* the centre, causing a rise in pressure (*pressor nerves*). Thus such filaments have been experimentally demonstrated to exist in the superior and inferior laryngeal nerves, in the *trigeminus,* and in the cervical sympathetic. The vaso-motor centre is thus under the influence of two antagonistic sets of impulses—one stimulating it, causing constriction of the smaller vessels, and thus a rise of arterial pressure; the other inhibiting it, causing dilatation of the smaller vessels, and thus a fall of pressure.

But this is not all. On examining a blood-pressure tracing (see Fig. 1, Plate A., or Fig. 158, p. 277), it is seen that the arterial pressure is influenced by the movements of respiration, the larger waves corresponding to these movements. (See also Fig. 13, Plate B.) To ascertain precisely how much of the wave corresponds to inspiration and how much to expiration, suppose a blood-pressure tracing is taken from the carotid artery, whilst, at the same time, arrangements are made for recording simultaneously the variations of intrathoracic pressure. Such a double tracing is seen in Fig. 175. In this curve, when expiration begins (*ex*), and the expiratory pressure rises,

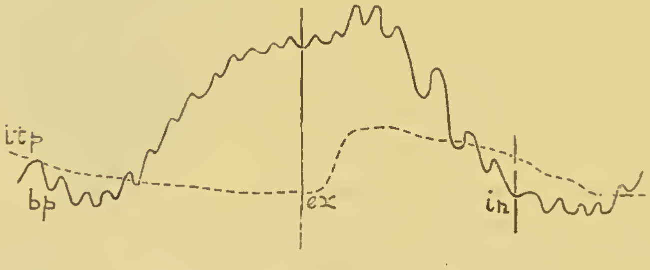

FIG. 175.—Mercurial kymographic blood-pressure tracing and respiration curve taken simultaneously. *ex*, expiration; *in*, inspiration; *itp*, internal thoracic pressure; *bp*, blood-pressure. (After Foster.)

the blood-pressure rises, while, when inspiration begins, (*in*) both fall. Inspiration removes pressure from the outer surface of the vessels, and thus allows the walls both of the great veins and of the aorta to distend; but the thin-walled veins yield to a greater extent than the thick-walled aorta. Consequently during inspiration the blood tends to accumulate in the great veins and in the right side of the heart and less escapes by the aorta, and thus during inspiration the blood-pressure in the aorta falls. On the other hand, during expiration the blood-pressure rises, owing to the opposite set of conditions. Roughly speaking, therefore, during inspiration blood-pressure falls, whilst during expiration it rises. But a careful examination of the curves shows that they do not exactly coincide as to their maxima and minima. Thus the blood-pressure rises before the rise of expiratory pressure, or, to put it in other words, during the first part of inspiration there is a fall of pressure and during the second part of it a rise. This cannot be explained by the mechanical movements of the chest wall, and it has been found to be caused partially, at all events, by the action of the vaso-motor centre. During the latter portion of the inspiratory period impulses pass from this centre, causing constriction of the smaller vessels, and consequently the rise of arterial pressure observed during this time. Again, an examination of a blood-pressure tracing shows that during the fall of the respiratory curve the smaller curves are larger and fewer in number than during the rise of the curve. After section of the vagi, this difference disappears, and it can only therefore be explained by stating that during the first portion of the time of inspiration, and during the fall of arterial pressure, the cardio-inhibitory centre also acts, slowing the beat of the heart. Another important fact, showing that the respiratory undulations cannot be accounted for by the mechanical movements of the chest wall, is that they continue in a blood-pressure tracing taken during artificial respiration. When a canula is inserted into the trachea and air is forced into the chest by a bellows, it is evident that the mechanical conditions are not those of ordinary respiration. When air is forced in, inflating the lungs, to correspond to inspiration, the intra-thoracic pressure is increased instead of diminished, as in ordinary respiration, and when the air is sucked out, to correspond to expiration, the intra-thoracic pressure is diminished instead of being increased as in ordinary expiration. And still the respiratory curves remain. If artificial respiration is suddenly stopped, the blood-pressure quickly rises, but this does not occur to nearly the same extent if the spinal cord is divided. In other words, the rise of blood-pressure when artificial respiration is arrested is due to stimulation of the vaso-motor centre in the *medulla* by the circulation through it of blood become too highly venous by stoppage of the circulation, as is proved by the fact that if the influence of the vaso-motor centre is removed, the rise of blood-pressure does not take place. Finally, if during artificial respiration both *vagi* are cut so as to remove the influence of the cardio-inhibitory centre, and artificial respiration is stopped, the pressure will rise as already described, and in a short time a series of undulations will appear in the blood-pressure tracing, known as the *Traube-Hering curves,* a rising and falling of blood-pressure not due to the action of the heart, as they continue even when a pump is substituted for that organ, nor to the movements of respiration, but to rhythmic variations of the activity of the vaso-motor centre itself, contracting and dilating the blood-vessels, and thus influencing the peripheral resistance.

To sum up, the circulation is affected by the nervous system—(1) by the inhibitory action of the *vagi* restraining the activity of the heart; (2) by the accelerating action of fibres in the *sympathetic* stimulating the activity of the heart; (3) by the action of the *intrinsic cardiac ganglia* affecting the heart directly; (4) by the action of the *vaso-motor centre* (*vaso-constrictor* nerves) in the *medulla* tending to keep up a greater or less degree of constriction of the vessels; (5) by the action of *vaso-dilator* nerves inhibiting the vessels, allowing them to dilate, in a manner similar to the cardio-inhibitory action of fibres in the vagi; (6) by the influence on the vaso-motor centre of impulses coming from the periphery: *pressor* fibres stimulating it, *depressor* fibres inhibiting it; (7) by the diffusion of impulses in the *medulla* from the respiratory centres; (8) by the interaction of the *vaso-motor*, *respiratory,* and *cardio-inhibitory* centres in the medulla; and (9) by rhythmic changes in the *vaso-motor centre* itself. Thus, in this remarkable mechanism, a series of adjustments is constantly taking place affecting the activity of the heart and the peripheral resistance, in accordance with the wants of the economy, and adapting it to the varying conditions of existence.

SECTION V.

RESPIRATION.

CHAP. I.—GENERAL STATEMENT.

The presence of oxygen is essential to the life of every tissue, and one of the products formed during vital activity is carbonic acid, a gas inimical to life. This is also true of the life even of simple organisms, such as the amœba and infusoria. Deprived of oxygen, or introduced into a medium containing an excess of carbonic acid, they die, so that it is essential to their existence that carbonic acid is removed and fresh oxygen is introduced. In all grades of animal life, an interchange between the gases of the organism and the gases of the medium in which it lives is constantly taking place, and this interchange is *respiration*. In a humble organism, small in bulk and simple in structure, no complicated mechanism is necessary, inasmuch as the body of the organism is either bathed directly by the fluid in which it lives, or there are canals, as in a sponge, passing through it in various directions, for the conveyance of the fluid, so as to bring it into intimate relation with the whole mass. When the organism increases in size and in complexity and when a nutrient fluid is required to circulate through it, arrangements are evolved by which gaseous interchanges take place between this fluid and the surrounding medium. Thus, by the water-vascular system of many of the lower forms of invertebrates, the air-tubes (tracheæ) distributed through the bodies of insects and spiders, and by the gills of many invertebrates and of fishes, the nutrient fluid is brought into close relation with the air, and interchanges take place which constitute respiration. Still higher in the scale, we find, as in reptiles, sac-like organs differentiated, communicating with the air by means of a tube, and on the walls of which the vessels containing the blood form a network, and thus again we have facilities for gaseous interchanges between the gases of the blood and of the air in the sacs. Such sacs are the simplest form of lungs. In higher animals, the bag or lung becomes more and more complicated until it forms a honeycomb structure, the cells of which contain air. On the walls of these minute cells capillary vessels ramify, and thus there is an enormous surface, having the blood of the organism on the one side, and the air in the lung-cells on the other, through which gases pass from the one medium to the other medium. On taking a comparative view of the process throughout the animal kingdom, it will also be observed that, in the simpler arrangements, no mechanism is necessary for facilitating the gaseous interchange. The amœba, for example, is surrounded by a fluid containing gases in solution; in higher forms, canals, along which air passes by diffusion, are necessary; in still higher forms, as in the fish, by the rhythmic movements of the gills, the water is permitted to bathe the respiratory apparatus on all sides; still higher, as in frogs, the air is forced into the air-bag by a process resembling that of deglutition; and lastly, in the highest forms, we find an automatic mechanism, involving many rhythmic nervous and muscular movements, by which the air is introduced into, and expelled from, the respiratory organ.

It will thus be seen that the lower organisms respire directly by exchanges between the body and the medium; whereas, in the higher organisms, respiration is a twofold process: (1) *internal respiration*, or the interchanges between the gases of the blood and the tissues; and (2) *external respiration*, or the interchanges between the gases of the blood and the gases in the air-cells of the lung. Even in the higher animals, however, interchanges may take place in other regions than in the lungs. Thus, there is a true *cutaneous respiration* in the skin, an *intestinal* respiration in the bowel, and probably interchanges take place in other organs.

CHAP. II.—STRUCTURE OF THE RESPIRATORY ORGANS.

We shall here shortly consider the structure of the larynx, trachea, bronchi, and lungs.

1. **The Larynx.**—The mucous membrane of this organ is a continuation of the mucous membrane of the pharynx, and it consists of epithelium resting on a *tunica propria*, beneath which is a submucous coat connecting it with underlying parts. The epithelium is almost everywhere a stratified ciliary epithelium, the cilia moving towards the throat. On the true vocal cords, on the anterior surface of the arytenoid cartilages, and on the posterior surface of the epiglottis the epithelium is of the stratified pavement variety. The *tunica propria* consists of fibres of elastic and of connective tissue, so condensed as to form a basement membrane. In it we usually find numerous leucocytes, and in the ventricles of Morgagni in the larynges of dogs and cats, we may find even nodules of adenoid tissue. In the situations where pavement epithelium is found, the mucous membrane shows papillæ. The *submucous coat* con-

tains small mucous glands from ·2 to 1 mm. in diameter. The *cartilages* of the larynx consist chiefly of hyaline cartilage, like that of the ribs. To this class belong the thyroid and cricoid cartilages, the greater part of the arytenoid cartilages, and the *cartilagines triticeæ*, in the lateral thyrohyoid ligaments. On the other hand, the epiglottis, the cartilages of Santorini and of Wrisberg, and the apices and *processus vocales* of the arytenoid cartilages are composed of reticulated yellow fibro-cartilage. The larynx is rich in blood-vessels and nerves. The vessels form a rich plexus in the submucous coat, from which numerous fine capillaries run below the epithelium. Two networks of lymphatics also exist—one, finely meshed, below the epithelium, and the other, wide meshed, below the capillary plexus. The nerves have minute ganglia in their course, and they terminate in end-bulbs, or in taste-bulbs.

2. **The Trachea.**—The ciliated mucous membrane of the trachea is like that of the larynx, except that the elastic fibres are more abundant and run largely longitudinally. The cartilages are also composed of the hyaline variety. The posterior wall of the trachea contains a large amount of involuntary muscle, and in the submucous tissue of this part, and often embedded among the muscular fibres, there are small mucous glands, 2 mm. in diameter.

3. **The Bronchi and the Lungs.**—The lungs are similar, in a sense, to racemose glands, and they may be primarily divided into efferent and respiratory portions. The *efferent* portions are represented by the larynx, trachea, and the bronchi. Each bronchus, on entering the lung, divides and sub-divides, each pair of branches coming off from the parent branch at an acute angle. Thus the calibre of the bronchi diminishes until we reach fine bronchi having a diameter of ·5 mm.

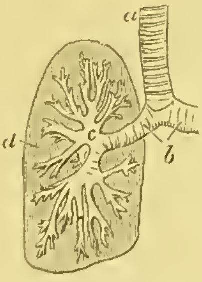

Fig. 176. — Diagram showing *a*, trachea ; *b*, division of trachea into two *bronchi* ; *c*, still smaller bronchi ; *d*, substance of the lung.

Fig. 177. – Ultimate group of lobules of the lung. *b*, bronchial tube, dividing and subdividing ; *c*, external view of group of air-cells ; *d*, internal view of the same.

(Figs. 176 and 177). Beyond this point, we have the proper respiratory portion of the lung. A minute bronchus shows near its termination minute swellings. These freely communicate to form alveolar passages, and at the end of each of these passages we find a swelling or dilatation of an oval form, termed the *infundibulum*, on the walls of which are numerous *alveoli*. The proper lung substance is divided by connective tissue into small *lobules*, from ·3 to 3 cm. in diameter, and here and there between the lobules there are interlobular masses of connective tissue. The structure of the larger bronchi is the same as that of the trachea, but as they become smaller, various modifications appear. The C-shaped rings of cartilage break up into small irregular plates found on all sides of the tube, and these also become smaller and finer until they are absent in bronchi of 1 mm. in diameter. A ring of involuntary muscle fibres surrounds the tube, and is situated nearer the mucous membrane than the cartilages. The thickness of the muscular layer diminishes with the diameter of the bronchus, but it does not entirely disappear, fine muscular fibres being seen on the walls of the alveoli, although they are absent from the infundibulum. The *mucous membrane*, lying in longitudinal folds, so that in cross section it gives the appearance of papillæ, consists of stratified ciliated epithelium cells, intermingled with a few goblet cells (like those on an intestinal villus), and of a *tunica propria* of connective tissue. The ciliated epithelium shades off into stratified epithelium in the finest bronchi. The *tunica propria* consists of a fine reticulum of connective tissue and elastic fibres, with many leucocytes intermingled. Here and there, beneath the *tunica propria*, small nodules of adenoid tissue may be found, from which leucocytes wander through the epithelial layer into the bronchus. Minute mucous glands are found below the muscular layer, as far along

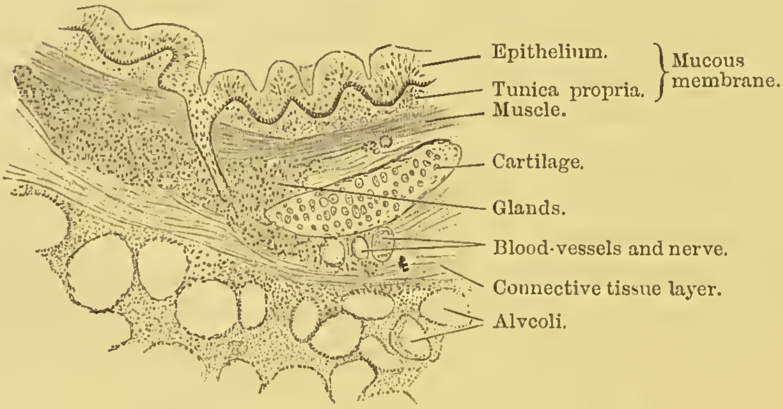

Fig. 178.—Transverse section of a bronchus, 2 mm. thick, from a child. × 50 d. The folds of mucous membrane are like papillæ. (Method No. 62, Appendix.)

the bronchi as cartilages are found, and they are absent in the fine respiratory bronchi. Outside the layer containing the cartilages, there is a layer of connective and elastic tissue surrounding the bronchus, and in this layer are found the vessels and nerves. The structure of the most minute bronchi is modified by the absence of cartilages and of glands.

The finest bronchi, which we may term *respiratory bronchi*, or *bronchioles*, have at their commencement a stratum of fine ciliated epithelium, but farther on the cilia disappear, the cells become cubical in shape, and between these cells we find cells in the form of large, thin plates, having no nuclei. These plates constitute *respiratory epithelium*. Still farther on, we observe a transition of the cubical epithelium into free respiratory epithelium—not an abrupt, but a very gradual transition—so that the cubical cells are seen on one side of the bronchiole and respiratory epithelium on the other, or we may find groups of cubical cells surrounded by respiratory epithelium. The respiratory epithelium cells become more and more abundant, and the cubical cells fewer in number, until the epithelium of the bronchiole merges into that of the alveolar passages. The epithelium of the alveolar passages and of the respiratory alveoli consists of large non-nucleated plates and of small polygonal cells, somewhat like the cubical cells of the bronchioles, arranged in groups. A study of the development of lung structures shows that the non-nucleated plates spring from cubical cells, and that they have become flattened out when the alveoli were distended in inspiration. Thus all the cells in the alveoli of the lungs of still-born children are cubical in form. The walls of the alveolar passages and of the alveoli contain a finely-striated basis of connective tissue, intermingled with

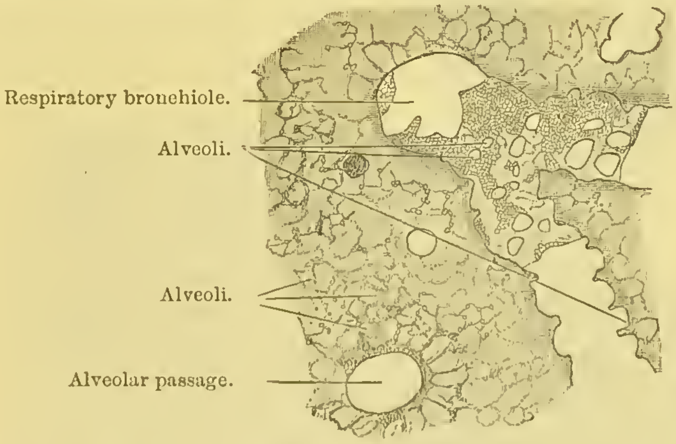

FIG. 179.—Section through lung of an adult man. × 50 d. The respiratory bronchiole divides towards the right. The lower wall has fallen out of the section. Observe, above, the alveoli communicating with it. In the lower branch the alveoli are seen from the side. (Method No. 63, Appendix.)

elastic fibres. The latter are arranged circularly round the alveolar passages, and at the points where the alveolar passage merges into alveoli there are fine elastic rings out of which fibres radiate over the wall of each alveolus. These elastic rings blend together to form the *septa of the alveoli.*

The interlobular connective tissue binding together the small lobules of the lung contains, in adults, not only fine elastic fibres and connective tissue cells, but also small granules of black pigment and even particles of carbon that have been inhaled. The lungs of children show the interlobular connective tissue highly developed, so that the pulmonary lobules are better seen.

Fig. 180.—Sections of lung—*A* and *B* from man, and *C* from a kitten nine days old. × 240 d. *A*, Mixed epithelium from a bronchiole; *B* and *C*, alveoli. The dark coloured walls of the alveoli are seen to be covered with the same kind of epithelium as in the clear part of the alveoli. The nuclei of the cells are not seen. (Method No. 64, Appendix).

The outer surface of the lung is covered with the *visceral layer of the pleura*, consisting of connective tissue and numerous elastic fibres, and it is covered on its free surface with a single layer of flat, polygonal endothelial cells. The *parietal layer of the pleura* shows the same structure but it is poor in elastic fibres.

The branches of the *pulmonary artery* run along the sides of the bronchi, bronchioles, and alveolar passages, and pass between the infundibula, where they are resolved into a very narrow meshed *capillary network*, situated immediately below the respiratory epithelium of the bronchiole, alveolar passages, and alveoli. The veins originate, one by one, at one side of the alveolus, and join together to form larger veins, which then run close to the bronchi and the arteries, thus form ing the *pulmonary veins.* The *bronchial arteries* divide into deep branches, which supply the glands and muscles, and superficial ones, which run in the *tunica propria.* The capillaries unite either to form bronchial veins, or they may anastomose with the capillaries of the pulmonary veins.

There is a rich plexus of *lymphatics* below the pleura, and this communicates with a deeper plexus in the interlobular connective tissue. From these spring lymphatic vessels, which, running along with the bronchi, carry the lymph of the lung to the bronchial glands.

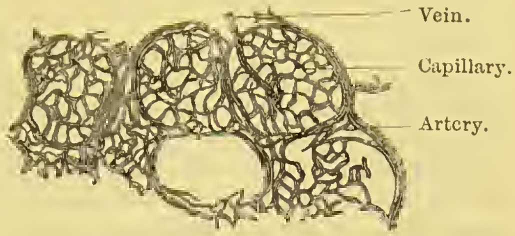

Fig. 181.—From the lung of a child injected through the pulmonary artery. × 80 d. The vessels of three alveoli have been completely injected. (Method No. 65, Appendix.)

Numerous nerve fibres, derived from the vagus and the sympathetic, are distributed in the lungs. On these minute nerves small ganglia are found. The nerve fibres are probably distributed to the muscular tissue of the bronchi, to the vessels, and to the epithelial surfaces, but the mode of termination is unknown.

Chap. III.—THE MECHANISM OF RESPIRATION.

The respiratory movements consist of rhythmic changes of volume of the thorax, produced partly by the contractions and relaxations of certain muscles, and partly by the elasticity of the structures involved.

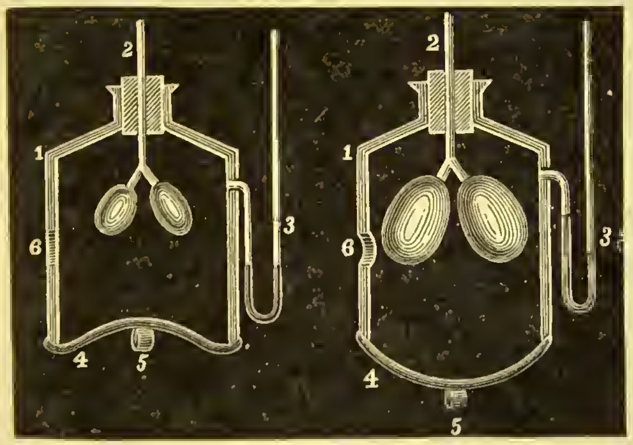

Fig. 182.—Diagrammatic view of apparatus to show the relations between the thoracic wall and the lungs. For description see the text.

As the cavity of the thorax, containing, and completely filled by, the lungs, heart, and other organs, is an air-tight cavity, and as the lungs are hollow and distensile organs lodged in this cavity, and communicating with the external air by the bronchial tubes and trachea, it is evident that any increase in volume of the thoracic cavity must be followed by an expansion, and any diminution in volume by a contraction, of the lungs. This will be clearly understood by studying the preceding diagram of an apparatus devised by Funke, of which various forms may be used.

Imagine a wide glass flask, 1, the bottom of which, 4, is made of strong india-rubber, having in the centre a wooden knob or cork, by which the membrane may be pushed upwards or pulled downwards at pleasure. A tightly-fitting cork is inserted into the neck of the flask, through which passes a glass tube, 2, dividing into two branches in the flask, and to the end of each tube a small india-rubber bag is attached. A mercurial manometer, 3, is inserted into an opening on one side of the flask, and an opening on the other side, 6, is covered by an india-rubber membrane. Suppose the membrane, 4, to be in the position shown in the figure on the left hand, the pressures on the inner and outer surfaces of the flask are equal, and consequently the mercury in the two limbs of the manometer is at the same level, and the india-rubber bags are collapsed. If, then, the cavity of the flask is increased, as in the right hand figure, by pulling down the membrane, 4, by the knob, 5, the pressure in the interior of the flask is diminished, and the india-rubber bags expand, the mercury rises in the shorter limb of the manometer, and the membrane, as at 6, is pressed inwards by the atmospheric pressure acting on 3, 2, and 6 being in excess of the pressure in the flask. When the membrane passes upwards, equilibrium of pressure is again established, as seen in the figure to the left. Imagine, further, that the capacity of the flask were increased, not only vertically by the movement of the membrane 4, but laterally and antero-posteriorly by an expansion of the wall of the cavity, we would then have an increase of capacity in every direction, and consequently the atmospheric pressure exerted through the tube, 2, would cause the bags to expand to a still greater extent.

In the mechanism of respiration this is what happens. By the action of the respiratory muscles, the capacity of the chest is enlarged in every direction; there is thus an excess of atmospheric pressure over the pressure on the outer surface of the lungs, and consequently a certain amount of air rushes into the air passages of the lungs, until equilibrium is again established. Ordinary inspiration is, therefore, essentially a muscular act. When the muscles relax in ordinary expiration, the elasticity of the lungs and of the thoracic wall causes these organs to recoil to their former position, and thus to force out a certain amount of air. Thus, ordinary expiration is not muscular, but is due to the elasticity of the structures involved. Any proof that the mechanism is of the nature just described is scarcely needed, but it is offered by what occurs when a puncture is made through the thoracic wall into the pleural cavity. When this occurs on one side, there is a collapse of the lung on that side and great difficulty in breathing; but if made on both sides, both lungs collapse and there is rapid asphyxia—the cause being that although the capacity of the chest is increased as before, the lungs do not likewise expand, as the atmospheric pressure exerted on their surface, through the hole in the thoracic wall, is of course equal to that in the respiratory passages.

After an inspiration has been made, the lungs may be said to be always over distended. Notwithstanding their great elasticity, the lungs cannot collapse so as to expel all the air, because the pressure on their inner surface, that of the air—say 760 mm. of mercury—is always greater than the elastic power of the lung and of the chest wall. This elastic power may be measured by connecting a manometer with the trachea of a dead subject, and opening the pleural cavity. The lungs collapse and the pressure of their retracting force may be measured in mm. of mercury. Donders thus was able to state the elastic force in the human being at 2 to 3 mm., but in life it may be twice or thrice greater, say 6 to 7·5 mm.; that is, about $\frac{1}{100}$th of the pressure of the atmosphere, or 30 mm., after a very deep inspiration, that is, $\frac{1}{25}$th of atmospheric pressure. Even in a dead subject the lungs do not become emptied when the pleural cavity is opened, because the elastic force is not of itself sufficient to expel all the air. In the living person the contractile force of the involuntary fibres in the bronchi also come into play, so that in life the force for expelling the air is greater than after death. When the chest expands, the lungs are distended because, as already stated, the pressure on the inner surface, atmospheric pressure, is now greater than that on their outer surfaces in the air-tight pleural sacs; but as they expand, the elastic force of the lung tissue becomes greater, so that, while in an ordinary inspiration it is only 7 to 9 mm. of mercury, after a deep inspiration it will rise as high as 30 mm. Finally, in expiration, the elasticity comes into play, the air in the alveoli is submitted to pressure; but as these communicate freely with the external atmosphere by the air passages, an equilibrium is quickly established, and it follows that with each expiration a quantity of air is expelled which corresponds with the diminished volume of the lung in expiration.

We have now to ask, by what muscular action is the capacity of the chest increased?

1. **In Ordinary Inspiration.**—The *vertical* diameter of the chest is increased by the contraction, and consequent descent, of the diaphragm, which is the chief inspiratory muscle. This muscle, in man, is a partition between the thorax and abdomen, of a vaulted form, the convexity

being directed towards the thorax. In the horse and ox the slope of this muscle is from above downwards and forwards. As its tendinous expansion is in the middle, when the muscular fibres contract, the centre descends to the extent of about 11·30 mm. in man, and the diaphragm becomes thus more flattened. The lateral parts, corresponding to the bases of the lungs, descend to a much greater extent than the central tendon, which is related on its superior surface to the pericardium and the heart. The downward pressure of the diaphragm is communicated to the contents of the abdomen, and these are pushed slightly downwards, but the pressure is chiefly expended on the anterior wall of the abdomen, which with an inspiration bulges outwards (Fig. 186). In long-bodied quadrupeds, like the horse, the bulging is chiefly seen in the lateral walls of the abdomen. At the same time, the *antero-posterior* and *lateral* diameters are increased by the elevation of the ribs by the *intercostales externi*, and by the portion of the *intercostales interni* found between the costal cartilages. The ribs are not only elevated, but slightly rotated, so that their lower borders are directed outwards, and at the same time the sternum is carried forwards. The *levatores costarum* (Fig. 185, 16) and *serrati postici superiores* (Fig. 185, 19)

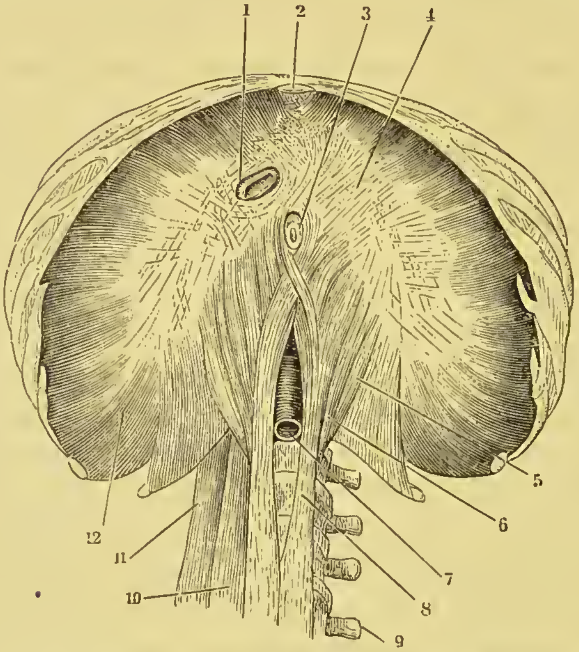

FIG. 183.—View of the inferior aspect of the diaphragm, according to Krause; ¼ nat. size. 1, *vena cava inferior;* 2, xiphoid process of the sternum; 3, œsophagus; 4, central tendon; 5, external crus; 6, middle crus; 7, descending abdominal aorta; 8, internal crus; 9, transverse process of 4th lumbar vertebra; 10, *psoas major*; 11, *quadratus lumborum;* 12, costal part of diaphragm. (Krause.)

passing from the spine to the ribs also assist in elevating the latter. In the horse and large quadrupeds the ribs are drawn forwards, their posterior edges are everted, and the ten pairs of false ribs are raised so as to be almost horizontal.

2. **In Forced Inspiration** the capacity of the chest is further increased by all the muscles which tend to fix the first rib, and thus allow the intercostals to contract with greater effect, or which act directly on the ribs from a fixed point, such as the shoulder. In some circumstances, the *quadrati lumborum* and *serrati postici inferiores*, by fixing the lower ribs and opposing the diaphragm, become muscles concerned in inspiration, although they are often grouped as expiratory muscles. Thus,

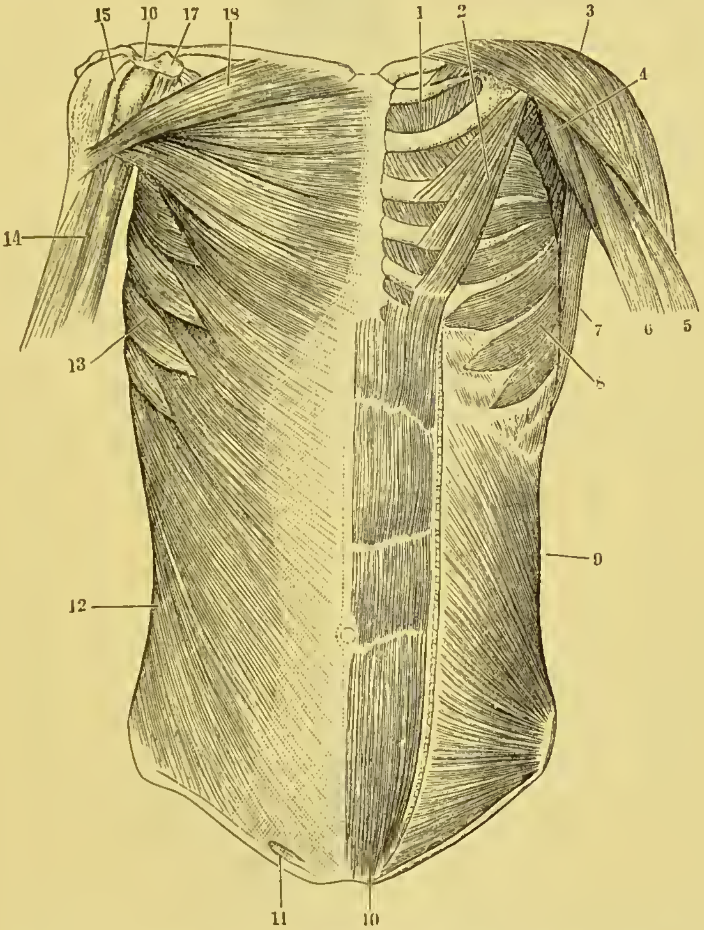

FIG. 184.—View of muscles in front of the body, showing some of the muscles of respiration, according to Krause. 1, internal intercostal; 2, *pectoralis minor;* 3, deltoid; 4, *coraco-brachialis;* 5, long head of *brachialis;* 6, short head of *brachialis;* 7, *latissimus dorsi;* 8, *serratus anticus major;* 9, *obliquus internus;* 10, *rectus abdominis;* 11, anterior inguinal ring; 12, *obliquus externus;* 13, *serratus anticus major;* 14, *brachialis;* 15, tendon of *brachialis;* 16, coraco-acromial ligament; 17, coracoid process; 18, clavicular portion of *pectoralis major.* (Krause.)

such muscles as the *scaleni*, the *sterno-cleido-mastoidei*, the *serrati postici superiores*, the *pectorales majores* and *pectorales minores*, and the *trapezei* and *rhomboidei* act as inspiratory muscles when deep forced inspirations are made. Lastly, inspiration is facilitated when the vertebral column

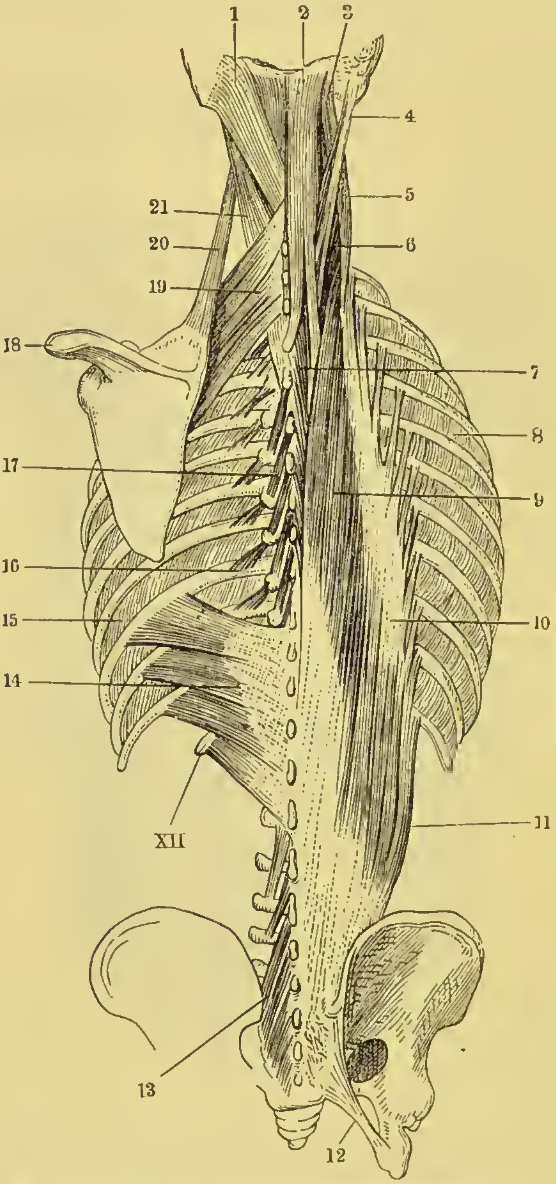

FIG. 185.—Muscles of back, showing certain muscles of respiration, according to Krause. One-sixth natural size. 1. *Splenius capitis;* 2, *biventer cervicis;* 3, *complexus;* 4, *longissimus capitis;* 5, *ilio costalis cervicis;* 6, *longissimus cervicis;* 7, upper portion of *spinalis dorsi;* 8, *intercostales interni;* 9, *longissimus dorsi;* 10, *ilio costalis;* 11, origin of *ilio costalis* from *fascia lumbo-dorsalis;* 12, *ligamentum sacro-tuberosum;* 13, *multifidus;* XII, twelfth rib; 14, *serratus posticus inferior;* 15, *intercostales externi;* 16, *levatores costarum breves;* 17, portion of *multifidus;* 18, acromion process; 19, *serratus posticus superior;* 20, *levator anguli scapulæ;* 21, *splenius cervicis.* (Krause.)

is straightened, as the ribs are then drawn from each other. This is accomplished by the *erectores spinæ*, including the *ilio-costales*, *cervicales ascendentes*, *longissimi dorsi*, *transversales cervicis*, *trachelo-mastoidei*, and *spinales dorsi*.

3. **In Ordinary Expiration**, the elastic recoil of the walls of the chest and of the lungs, following the relaxation of the inspiratory muscles, is quite sufficient to expel the air, but in *forced expirations* the ascent of the diaphragm is assisted by the contraction of the abdominal muscles compressing the viscera, and thus forcing up the floor of the chest. This action is assisted by all muscles which depress the ribs, such as the greater part of the *intercostales interni*, the *serrati postici inferiores*, *quadrati lumborum*, *obliqui interni et externi*, the *transversales abdominis*, and the *triangulares sterni*. Forced expiration comes into play in shouting, singing, blowing musical instruments, etc. In most of these actions, the abdominal muscles come powerfully into action. The abdominal muscles may, in a sense, be regarded as antagonists to the diaphragm. They also exert pressure on the contents of the abdomen and pelvis, in emptying the bowels, bladder, and the pregnant uterus.

The following are the points of special importance with reference to the muscles :—

1. **The Diaphragm** (Fig. 183).—This is the chief muscle of *inspiration*. When it contracts, the central tendon descends, and becomes less convex on its upper surface. Hence the vertical diameter of the thorax is increased, and the depth of the hinder part of the cavity is specially augmented. The diaphragm is supplied by the phrenic nerves, which are branches of the fourth and fifth cervical, and it also receives sympathetic filaments from the plexus running along with the phrenic arteries. Marckwald obtained contractions of the diaphragm of the rabbit by irritating the peripheral ends of the phrenic nerves for ·2 to ·3 of a sec., at intervals of 1 sec., and he arrived at the conclusion that the normal contraction of the diaphragm is a short tetanic spasm, and not a simple twitch.

2. **Levatores Costarum** (Fig. 185, 16).—Twelve on each side arise from tips of transverse processes of the seventh cervical and eleven highest dorsal vertebræ, and, passing downwards and outwards, are inserted into the outer surface of the rib belonging to the vertebra. They assist in raising the ribs. They are supplied by the intercostal nerves.

3. **Intercostales Externi** (Fig. 185, 15) consist of fibres passing between the ribs, running downwards and forwards. They extend from the tubercles of the ribs to the outer end of the cartilages. They raise the ribs. They are supplied by the intercostal nerves. The fibres of the *intercostales interni*, between the cartilages, also assist in raising the ribs.

4. **Sterno-cleido-mastoidei** pass from the sternum and clavicle to the mastoid process of the temporal bone. When their fixed point is the head, they raise the upper part of the chest in forced inspiration. They are supplied by the spinal accessory and a branch of the second cervical nerve.

5. **Scaleni Antici Medii et Postici.**—(1) *Scalenus anticus* passes from tubercles of transverse processes of third, fourth, fifth, and sixth cervical vertebræ to the first rib. (2) *Scalenus medius* passes from transverse processes of all the cervical vertebræ, also to the first rib. (3) *Scalenus posticus* passes from transverse process of three lower cervical vertebræ to the second rib. They all assist in drawing up first and second ribs, when the neck is fixed. All three are supplied by cervical nerves.

6. **Serrati Postici Superiores** arise from the *ligamentum nuchæ*, from the spines of the last cervical and two or three upper dorsal vertebræ, and from the supraspinous ligament, and passing downwards and outwards are inserted into second, third, fourth, and fifth ribs, slightly beyond their angles. They raise the upper ribs in forced inspiration. They are supplied by the intercostal nerves. In forced inspiration, if the scapula is fixed by the muscles, binding it to the trunk behind and above, the lower slips of the *serratus magnus* will dilate the chest by raising and everting the ribs. It is supplied by the posterior thoracic nerve arising from the fifth and sixth, and sometimes the seventh, cervical nerves.

7. **The Costal Portion of the Pectorales Majores and the Pectorales Minores** (Fig. 184, 2) will tend to raise the ribs in forced inspiration, if the shoulder is fixed. The *pectorales minores* spring from the third, fourth, and fifth ribs, near their cartilages, and pass to the coracoid processes. The pectorales are supplied by the anterior thoracic nerves.

8. **The Trapezei and Rhomboidei** assist in forced inspiration by raising the scapulæ, so that their bases are carried towards the dorsal spine. The coracoid processes are thus fixed, and the *pectorales minores* come into play. The *trapezei* are supplied by the spinal accessory nerves, and by branches from the third and fourth cervical. The *rhomboidei* receive branches from the fifth cervical.

9. **Erectores Spinæ** (Fig. 185).—These muscles, enumerated above, are directed longitudinally on each side of the vertebral column, and when they come into action they straighten the back, in forced inspiration. If, however, the spine be fixed, some of them, connected with the ribs, may depress these, and thus assist in forced expiration. They are all supplied by the posterior primary branches of the spinal nerves.

10. **Intercostales Interni** (Fig. 185, 8).—These consist of fibres running downwards and backwards from one rib to the next below it. They pass from the sternal ends of the cartilages to slightly beyond the angles of the ribs. As depressors of the ribs, they come into play as expiratory muscles. Many observers, however, are of opinion that they are inspiratory muscles. The view that commends itself to me is that neither the internal nor the external intercostals have much to do with raising or depressing the ribs, and that their chief action is to maintain pressure in the intercostal spaces. They are supplied by the intercostal nerves.

11. **Serrati Postici Inferiores** (Fig. 185, 14).—These arise from the spines of the last two dorsal and upper two or three lumbar vertebræ, run outwards, upwards, and forwards, and are inserted into the lower borders of the last four ribs. They draw the ribs downwards and backwards, and thus enlarge the lower part of the chest. If their first action preponderates, they must be regarded as expiratory muscles, but they may also act as inspiratory muscles in forced inspirations, where there are strong diaphragmatic contractions, by resisting the tendency of

the diaphragm to pull in the lower ribs. They are supplied by the intercostal nerves.

12. **The Musculi Abdominales** above enumerated, by compressing the abdominal organs, assist in pushing up the floor of the thorax, the diaphragm. They also draw down the ribs and contract the base of the thorax. Thus they come into play in forced expiration. They are supplied by the lower intercostal nerves.

13. **Triangulares Sterni**, lying behind the costal cartilages, arise from the deep surface of the ensiform cartilage, lower part of the body of the sternum, and cartilages of two or three of the lower sternal ribs, pass upwards and outwards, and are inserted into the cartilages of the ribs, from the sixth to the second. They depress the cartilages, and thus are muscles of expiration. They are supplied by branches of the intercostal nerves.

After an injury to the spinal cord, in the lower cervical or upper dorsal region, the intercostal and abdominal muscles are paralysed, but respiration is still carried on by the diaphragm, *serrati*, *sterno-cleido-mastoidei and trapezei.* The inspirations are then short and quick, and the expirations are not much disturbed. Injury about the level of the brachial plexus causes paralysis of all the muscles of respiration except the diaphragm. On the other hand, the diaphragm itself may be partially paralysed, and respiration is then carried on by the thoracic muscles. With each inspiration, in such cases, the diaphragm and abdominal organs are, as it were, sucked into the chest. If the cord is injured above the origin of the phrenics, death quickly occurs. It is remarkable, that rabbits more than four months old, which breathe almost entirely by the action of the diaphragm and abdominal muscles, may learn to breathe by the thorax, and live for a long time. Young rabbits quickly die after this operation, as they are unable to acquire the thoracic type of breathing.

Along with the movements of the chest in respiration, there are certain movements of the larynx and of the face. In calm inspiration and expiration the glottis is widely opened, and the muscles of the larynx are in a state of relaxation. When breathing becomes difficult, the larynx is pulled down by the action of the *sterno-hyoid* and *sterno-thyroid* muscles, supplied by the *descendens noni* branch of the 9th cranial nerve (hypoglossal), and the glottis is widely opened by the action of the *posterior crico-arytenoid muscles*, supplied by the inferior or recurrent laryngeal branch of the vagus. At the same time, in forced inspiration, or even in normal inspiration in some animals, as the horse and rabbit, the nares are distended by the *dilatores naris anteriores et posteriores* and the alæ are raised by the *levatores labii superiores alæque nasi*, and even the muscles concerned in opening the mouth come into action, *levatores anguli oris*, *levatores labii superioris*, *zygomatici minores et majores*, *levatores menti*, and *depressores anguli oris*, all supplied by the facial nerve. The soft palate also is elevated by the *levatores palati*, and the uvula is contracted by the *azygos uvulæ*, both supplied by the facial through the petrosal branch of the vidian nerve.

It thus appears that even in ordinary breathing, and still more so in forced breathing, a large number of muscles and of nerves come into play, and that the actions of these are co-ordinated through the intervention of spinal centres. The group of spinal nerves concerned in respiration forms the motor division of the respiratory system of Charles Bell.

FIG. 186.—Diagrams showing the extent of antero-posterior movement in ordinary, and in forced, respiration in male and female. The back is supposed to be fixed, in order to throw forward the movement as much as possible. The black line indicates, by its two margins, the limits of *ordinary inspiration* and *expiration*. In *forced inspiration* the body comes up to the dotted line, while in *forced expiration* it recedes to the smallest space indicated. The abdominal character of respiration in the male is distinctly shown. (Hutchinson.)

Varieties of Respiratory Movements.—When the action of the diaphragm predominates, as in the male, respiration is said to be *abdominal*, or *diaphragmatic*, the abdominal wall moves backwards and forwards, the vertical diameter of the chest is increased, and there is only a slight increase in the antero-posterior or in the transverse diameter. On the other hand, in the female, the capacity of the chest is increased in the transverse and antero-posterior directions, chiefly by movements of the ribs, and especially of the upper ribs, elevated by the *scaleni* muscles, causing heaving of the breast—the action of the diaphragm, and consequent movement of the abdominal wall, being much less than in man. In cases where a large tumour exists in the abdominal cavity, respiratory movements occur chiefly in the clavicular region. When the inspirations become very deep, the difference between the abdominal and costal types is not apparent, the enlargement of the thorax thus being almost wholly in the transverse and antero-posterior directions. During sleep, respiration is almost entirely thoracic in both sexes. The foregoing figure by Hutchinson illustrates these forms of respiratory movement (Fig. 186).

The antero-posterior diameter of the chest in an adult is on an average 165 mm. at its upper part, and 192 mm. at its base. The transverse diameter at the axillæ, about 260 mm. in man and 240 in woman. The mean circumference, passing the measure below the mammæ in front and the lower angle of the scapula behind, with the arms held over the head, is about 820 mm. at the close of expiration, and 900 at the close of a deep inspiration. The amplitude of movement is thus 80 mm. In an adult, the capacity of the thorax is increased by inspiration to the extent of ·083 to 0·142 of its capacity at rest, as indicated by a cord brought round the chest by the base of the heart (Valentin). Sibson gives the increase as ·1 in the region of the mammæ, and below the shoulders, ·083. This author also gives the increase in the antero-posterior diameter in the middle of the sternum as nothing in quiet breathing, in the middle of the abdomen in quiet breathing 7 to 10 mm., and in deep inspiration 30 mm. Ransome, who has made elaborate researches on this subject, states that the ends of the upper ribs may move forward in deep inspiration to the extent of from 12 to 30 mm. Colin states that in the horse the increase in the longitudinal diameter (vertical in man) of the chest in quiet breathing is 100 to 120 mm., and in the transverse direction, between the 11th and 12th pairs of ribs, as 30 mm.

Chap. IV.—REGISTRATION OF RESPIRATORY MOVEMENTS, FORCES, AND QUANTITIES.

Various instruments have been invented for recording the *movements* of the thorax. A simple form of recording apparatus is the *Pneumograph* of Marey, seen in Fig. 187.

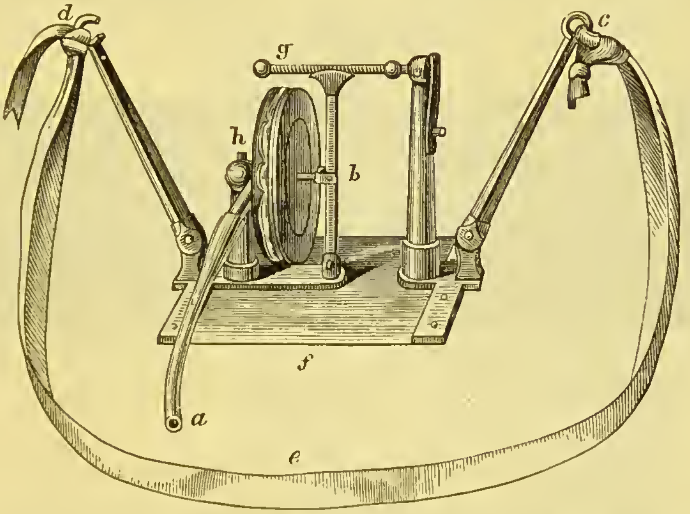

Fig. 187.—Marey's Pneumograph. *f*, very thin brass plate bearing a tambour, *h*, the aluminium disc of which is connected with the upright *b*, the upper end of which moves on a horizontal screw, *g*. The band *c e d* is placed round the body. During expansion of the chest, tension occurs between *c* and *d*, and acts on the tambour by the bending of the brass plate, *f*, and the movement is communicated to a recording tambour by *a*.

Tracings of the respiratory movements obtained by the pneumograph, and taken simultaneously with a sphygmograph and cardiograph, are shown in Fig. 188.

The *elasticity* of the *lungs* in ordinary respiration may be estimated by manometer (Fig. 29), according to the method already described (p. 305), to be from 6 to 8 millimetres of mercury, but in deep and prolonged inspirations it may amount to 30 to 40 millimetres.

The *contractility* of the lungs, which is comparatively small, and due chiefly to the muscular fibres of the bronchi, has been recorded by Paul Bert (Fig. 189).

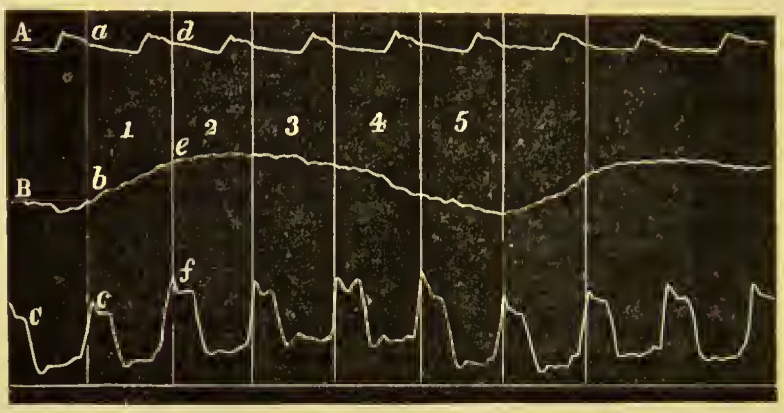

FIG. 188.—Simultaneous tracings taken by the pneumograph B, cardiograph C, and sphygmograph A, at the radial artery. The ascent of the curve in B corresponds to expiration, and the descent to inspiration. There are from four to five cardiac pulsations to each complete respiratory movement. Observe also that the pulsation at the wrist is a little later than the corresponding cardiac pulsation —thus *d*, in upper line A, corresponds to *c* in lower line C.

FIG. 189.—Tracings of pulmonary contraction from the dog. The two upper lines were obtained by direct galvanic stimulation of the lung, and the third by stimulation of the pneumogastric. *a*, *b*, *c*, indicate the moments of stimulation. (Paul Bert.)

These tracings afford a direct proof of the contractility of the lung, and show that it may be excited by stimulation of the vagus.

Movements of the Diaphragm.—Kronecker and Marckwald[1] have devised a method of registering the movements of the diaphragm which has been of great service in the experimental study of the innervation of breathing (Fig. 190). It consists of a small probe at the one end pointed, at the other, spoon-shaped, which is passed through the abdominal wall between the liver and the diaphragm, so as to follow the movement of the latter. A thread passes from the pointed end of the probe to a delicately adjusted lever (Fig. 190) brought to bear on the surface of a cylinder as seen in the figure. In Fig. 191 a specimen of the tracing is shown.

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[1] Max Marckwald, *The Movements of Respiration and their Innervation in the Rabbit.* Translated by T. A. Haig, with an introduction by John G. M'Kendrick. Blackie & Son. 1888.

Attempts have also been made to measure the *force* exerted by the inspiratory muscles. These muscles must overcome the following resistances: (1) the elasticity of the thorax, the value of which has not been ascertained; (2) the elasticity of the pulmonary tissue, which, as already stated, amounts to from 7 to 8 millimetres of mercury in calm inspirations, and 30 in deep inspirations. Measurements of these resistances are made if we insert (by a T-shaped junction) a tube passing from the short limb of a manometer into both nostrils and make an inspiration. The mercury will rise in the shorter limb, showing a negative pressure. In a calm inspiration this amounts to – 1 to – 3 mm. and in forced inspiration to – 30 to – 75 mm. Again, in a calm expiration there will be a positive pressure of 2 to 3 mm. and in a

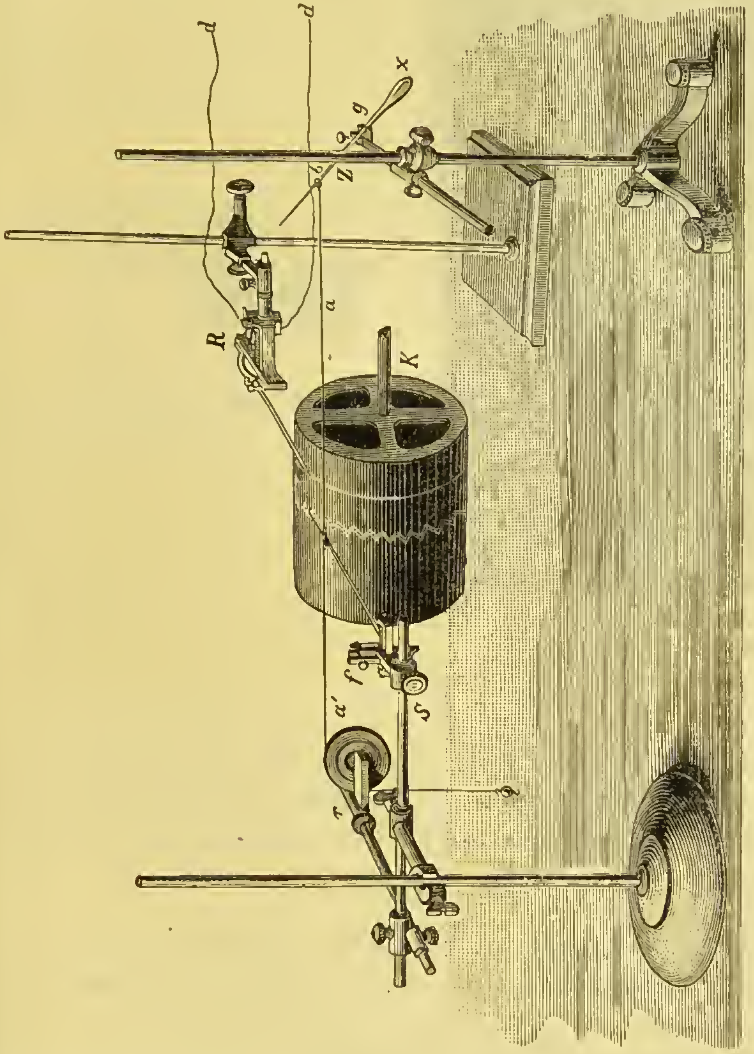

Fig. 190.—Kronecker and Marckwald's method of recording the movements of the diaphragm. *Z*, diaphragm probe or lever; *x*, spoon-shaped end; *g*, fork in which lever moves; *b*, movable knob for attachment of thread; *R*, chronograph; *S*, recording lever; *f*, adjusting screw; *K*, cylinder; *r*, wheel; *a*, *a'*, silk threads, *a* running from diaphragm lever to recording lever, and *a'* running from diaphragm lever over pulley to be attached to a weight; *d*, *d'*, wires of chronograph.

forced expiration 80 to 130 mm. of mercury. Thus, taking the mean of these figures, the inspiratory muscles have at least to overcome resistances represented by 8 + 2 = 10 millimetres in calm, and 30 + 52 = 82 millimetres in deep, inspiration. In forced expiration, as in loud speech, crying, or making a strong expulsive effort during severe muscular action, the force must overcome a resistance equal to the positive pressure in the lung in expiration, less the elasticity of the lung, or 105 - 30 = 75 millimetres of mercury.

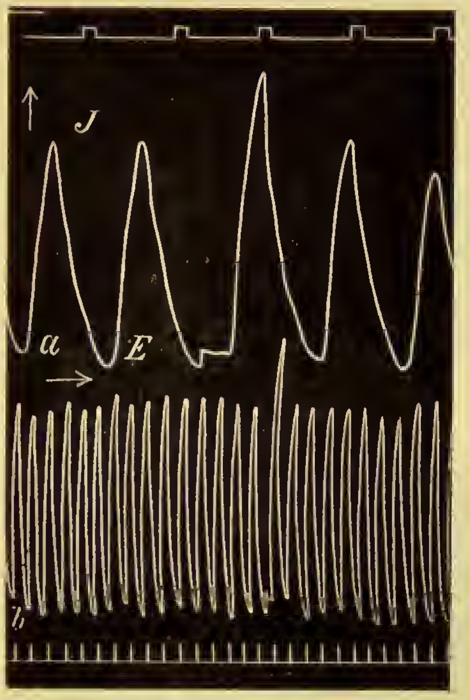

FIG. 191.—Normal movements of the diaphragm of a rabbit. *a*, with a quick, and *b*, with a slow movement of the drum. Curves to be read from left to right; inspirations from below upwards. *J*, inspiration; *E*, expiration. Chronograph marking seconds.

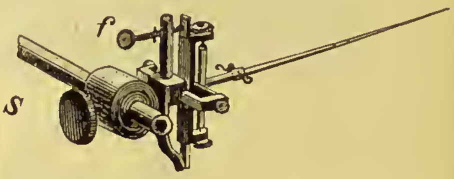

FIG. 192.—Minute construction of the recording lever.

Rhythm and Number of Respiratory Movements.—Each respiratory act consists of three periods: (1) a period of inspiration; (2) a period of expiration; and (3) a period in which there is no movement, usually termed the pause. In calm breathing expiration is longer than inspiration in the ratio of 5:6, but in some conditions, such as irritation of the vagi, the inspirations may become much longer (2-5 times) than the expirations. The pause may be long or short, its duration being apparently regulated by habit or by the amount of attention directed to it. In quiet breathing the pause occupies about ·25 of the time of a complete respiration. If the attention is directed to respiratory movements, they become more rapid, chiefly by diminution of the time of the pause, whereas the pause becomes much longer during sleep, unconsciousness, or even when the mind is in a state of abstraction. The number of respirations is smaller while lying than sitting and while sitting than standing. It is increased by active exercise. Thus at rest a horse will breathe 8 to 10 times per minute, but in trotting the number will rise to 50, and in the gallop to 60 (Colin). A man, after a quick race, may breathe 40 to 60 times per minute. In health, there are usually 15 respirations per minute in the adult. The following table by Quételet shows the effect of age—

Age.	Number of Respirations per Minute.		
	Maximum.	Minimum.	Mean.
Newly-born child,	70	23	44
1—5 years,	32	20	26
15—20 ,,	24	16	20
20—25 ,,	24	14	18
25—30 ,,	21	15	16
30—50 ,,	23	11	18

In very aged people, the number may fall even to 12 per minute. The number of respirations per minute in some animals is as follows:—whale, 4 to 5; horse, 8 to 10; ox, 12 to 15; sheep and goat, 12 to 20; dog, 15 to 18; cat, 20 to 30; rabbit, 50 to 60; rat and guinea-pig, 100 to 150 (Munk). Thus the larger the animal the fewer the number of respirations. The ratio of cardiac to pulmonary movements is seen in the curve—it is usually as 1 : 4 or 1 : 5 (Fig. 188).

Respiratory Sounds.—If a stethoscope be placed over the larynx and trachea of a healthy man, two sounds will be heard—one inspiratory, and the other expiratory.[1] These are called the *laryngeal and tracheal sounds.* If it be placed a little to the right or to the left of the manubrium of the sternum, the same sounds will be heard, but diminished in intensity. These are the *bronchial* sounds. If now we listen on either side of the chest, or on the back, over the posterior tube of either lung, two gentle rustling sounds are heard, termed the *vesicular respiratory murmurs.* All of these sounds become exaggerated during forced respiration, but in a state of health they never lose their soft character. They are produced by the passage of air through the trachea, larger bronchial tubes, finer bronchial tubes, and air-cells of the lung. Many modifications of the vesicular murmur are produced in disease, giving rise to various *souffles* and *râles*, to be studied in clinical wards. Again,

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[1] In connection with this subject the student is recommended to read the statement regarding the laws of sound given in discussing the functions of the ear.

if we listen in the same places whilst the individual speaks, there is a peculiar resonance of the voice noticeable over the trachea : it has been called *pectoriloquy*, as if the voice entered the ear directly from the chest ; over the bronchial tubes, *bronchophony*, as if the voice issued from a tube ; whilst in the regions occupied by lung tissue, voice sounds are scarcely audible. A peculiar modification of the quality of the voice is observed when there is an effusion of fluid into the pleural sac. It is heard over the middle and posterior region of the thorax, near the lower angle of the scapula, and from its peculiar trembling, acute, metallic character, like the bleating of a goat, it is termed *œgophony*.

The Capacity of the Lungs.—The amount of air which may pass into or issue from the lungs, or which they may contain after the fullest expiration or after the fullest inspiration, may be approximately measured by means of instruments called *spirometers*.

The most common is Hutchinson's spirometer, constructed on the principle of an ordinary gasometer for the storage of gas. Another excellent instrument is the spirometer of Cassella, on the principle of the anemometer used by meteorologists for registering the velocity of the wind. A third and convenient form, called the *anapnograph*, devised by Bergeon and Kastus, is shown in Fig. 193.

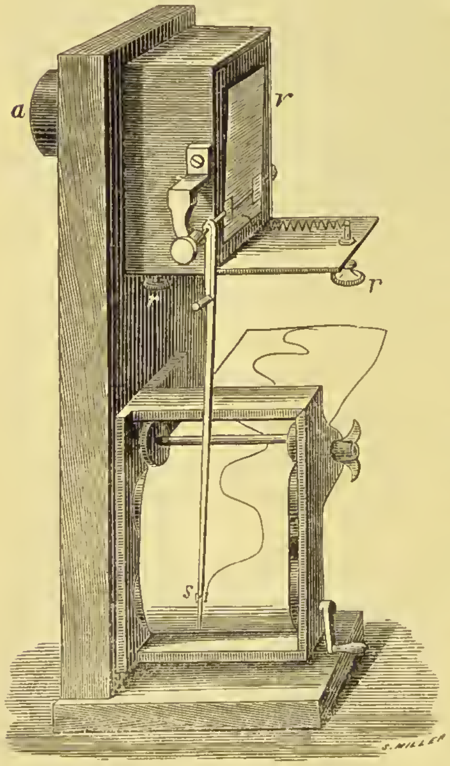

Fig. 193.—Anapnograph of Bergeon and Kastus.

A valve, or mobile plate of aluminium, r, forms one side of a rectangular box put into communication by *a* with a respiratory tube terminated by a mouth or nose-piece. The axis of rotation of the valve carries a very light lever, *s*, which writes on a stripe of paper moved by clockwork. If air is propelled through the tube into *a* with each movement of inspiration and expiration, the variations of the pressure of the air in the air passages are transmitted to the valve which, by the lever, inscribes on the paper. The instrument has been graduated so as to suit bands of paper divided into small squares, each square representing a certain amount of air. Thus the instrument registers not only the pressure of the air, but the quantity inspired and expired, and the rapidity of the current of air.

With such instruments it may be shown that when the lungs have been emptied as much as possible of air by the most powerful expiratory effort, they still contain a quantity over which we have no control, and which may be estimated at about 100 cubic inches. This has been termed *residual air.* In addition to this residual air, there are about 100 cubic inches constituting *supplemental air*, or the air that remains in the chest after an ordinary expiration, in addition to the residual air already mentioned. Thus there are 200 cubic inches of air in the chest after a gentle expiration. If, then, inspiration take place gently, from 25 to 30 cubic inches are introduced; these, constituting *tidal air*, are expelled by the next expiration. We find, therefore, that in ordinary respiration there are about 200 cubic inches in the lungs, and an inward and outward current of say 30 cubic inches; but, finally, it is possible, by a very deep and prolonged inspiration, to introduce 100 cubic inches more. This last quantity is called *complemental air.* After the deepest inspiration, there are therefore in the lungs 330 cubic inches of air, which number expresses the *maximum capacity* of the chest. These facts may be impressed on the memory by the following table, in which both English and metrical measures are given, the English measurements by Hutchinson, and the metrical by Gréhant.

		Cub. cent.	Cub. in.		
Maximum volume of air in the lungs, 4970 cubic centimetres, or 330 cubic inches.	Residual air, . . .	1200	100	Pulmonary capacity, 2800 cub. cent., or 200 cub. in.	
	Supplemental air, .	1600	100		Vital capacity, 3700 cub. cent., or 230 cub. in.
	Tidal air, ...	500	30		
	Complemental air, .	1600	100		

By *vital capacity* is meant the quantity of air expired or inspired in the strongest possible respiration. The vital capacity is somewhat less in women than in men; it increases up to 35 years, and afterwards diminishes. It also increases with the height and with the circumference of the chest: for each additional centimetre in height, there is an increase of about 52 cubic centimetres in the male, and 30 c.cm. in the female. Thus, the vital capacity in a man of 1½ metres in height is usually 2350 c.cm., and in a woman of the same height, 2000 c.cm. A man of a height of 1·70 metre will have a vital capacity of 3390 c.cm., and a woman, of the same height, 2600 c.cm. In emphysema it may fall as low as 2000, or even 1000 c.cm. Edward Smith also showed that movement increased the volume of air expired.

Influence of the Respiratory Movements on the Circulation.—This has already been referred to in another connection (p. 294), but the facts will be better appreciated after a study of the mechanism of inspiration. We have already seen that the walls of the air cells, or, in other words, the lungs, have an elastic force which is greater or less according to the amount of their distension. This elastic force, as was first shown by Donders, tending to cause collapse of the lung, exerts a certain pull or suction-like action on the other organs in the chest, and it is clear that this pull or negative pressure will become greater and greater as the lungs are distended. The negative pressure, or pull, thus defined, may be termed the *intrathoracic pressure*. Jakobson and Adamkiewicz give this pressure in sheep, dogs, and rabbits, at – 3 to – 5 mm. of mercury. Rosenthal found it in the thorax of a rabbit after the deepest inspiration to be – 20 mm. of mercury. In calm inspiration it was only – 3 mm. The pressure, therefore, on the organs in the chest of the rabbit in medium inspiration must have been atmospheric pressure, less the intrathoracic pressure, less again the increment of the elastic force of the lungs when distended, or $760 - 3 - 9 = 748$ mm. of mercury. In calm expiration, on the other hand, we have pressing on the organs in the chest, the atmospheric pressure, 760 mm., plus the positive pressure of a calm expiration, 2 mm., less the intrathoracic pressure, 6 mm., or in all 756 mm. (Munk). We see, then, that in calm respiration the pressure on the organs in the thorax, other than the lungs, is less than atmospheric pressure, or, in other words, the organs in the thorax are under a less pressure than the vessels outside of the thorax, the negative pressure being of course greater during inspiration. Thus, the blood is aspirated into the great vessels in the thorax both during inspiration and expiration, but more speedily during inspiration.

It will be evident, however, that in inspiration there will also be less pressure on the surface of the aorta, so that it will tend to become distended, thus diminishing the flow of blood through it, and causing a fall of blood-pressure. But the thick wall of the aorta yields much less than the thin walls of the veins, so that inspiration has not much effect on the former, and the little effect it has is much more than counterbalanced by the increased afflux of blood to the heart by the distension of the great veins. This increased supply of blood passes through the lungs from the right ventricle to the left ventricle, so that more blood is thrown into the aorta. Consequently the general effect of inspiration is to increase the blood pressure, while that of expiration is to diminish it. With very deep inspirations, as already explained, both the elastic force of the lung and the intrathoracic pressure are much increased, so that the pressure on the thoracic organs is much less than atmospheric pressure. On the other hand, forced expirations may cause a positive pressure of 130 mm. of mercury. This, added to 760, the ordinary atmospheric pressure, gives 890 mm.; but as intrathoracic pressure will then be reduced to 6 mm., we have $890 - 6 = 884$ mm. as the pressure on the thoracic organs. In these circumstances, the blood cannot readily flow to the heart, the veins become much distended, and a pulse-like movement may be seen in them with each forced expiration and inspiration.

This suction-like action of the thorax assists also in drawing the blood from the liver, for when the pressure on the inferior vena cava is reduced by inspiration, the flow through the hepatic vein and the slow circulation in the liver will be accelerated.

The movements of respiration also assist the pulmonary circulation. Inspiration, by causing diminished pressure on the thin walls of the pulmonary veins, favours the distension of these vessels, and consequently the flow of blood from the lungs to the left auricle, while it has not much effect on the pulmonary artery. The capillaries on the walls of the alveoli are also under a pressure greater than that on the pulmonary veins during inspiration, and thus the blood is forced onwards.

The aspirating action of the thorax may suck in air into a vein, and the air is carried to the right side of the heart and thence to the pulmonary capillaries. Here it may cause sudden death by plugging the capillaries, an accident liable to occur in a surgical injury to a vein in the neck.

CHAP. V.—THE CHANGES IN THE AIR DURING RESPIRATION.

The oldest writers do not appear to have had any clear notions even as to the necessity for respiration. Hippocrates dimly recognized that during breathing a *spiritus* was communicated to the body.[1] Many of the older anatomists, following Galen, thought that the "very substance of the air got in by the vessels of the lungs to the left ventricle of the heart, not only to temperate heat, but to provide for the generation of spirits." This notion of cooling the blood was held by Descartes (1596-1650) and his followers, and seemed to them to be the chief, if not the sole, use of respiration.

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[1] For a full account of the earlier ideas regarding respiration, see the author's lecture to the British Medical Association, published in the *British Medical Journal* for 1889.

About the middle of the seventeenth century clearer notions began to prevail. These rested partly on an anatomical and partly on a physical discovery. Malpighi (1621-1694) discovered that the minute bronchial tubes end in air-vesicles, or membranous cavities, as he termed them, on the walls of which, in the frog, he saw with his simple microscope the blood flowing through capillaries. This pulmonary plexus was for many years termed the "*rete mirabile Malpighii.*" The physical observations were made by the celebrated Robert Boyle (1627-1691), who made numerous experiments as to the behaviour of animals in the exhausted receiver of the air-pump. He showed that the death of the animals "proceeded rather from the want of air than that the air was over-clogged by the steam of their bodies." He also showed that fishes also enjoyed the benefits of the air, for, said he, "there is wont to lurk in water many little parcels of interspersed air, whereof it seems not impossible that fishes may make some use, either by separating it when they strain the matter thorow their gills, or by some other way."

Sanctorius, Professor of Medicine in Padua, who flourished from 1561 to 1636, was probably the first who made a quantitative estimate of substances escaping from the body. He constructed a balance by which he weighed himself repeatedly, and observed what he gained by food and what he lost by excretion. A celebrated experiment made by Robert Hooke, in 1667, showed that it was the fresh air, and not any alteration in the capacity of the lungs, which caused the renewal of the heart's beat. This was the first time artificial inflation of the lung was carried out.

Thus the necessity of a continual supply of fresh air was recognized as being essential to life. It was further surmised that the air imparted something to the blood, and received something in return; but no further advance was made in this direction until the researches of Mayow about 1674. By many ingenious experiments, he showed that combustion diminishes the volume of the air and alters its qualities; that respiration also affects the quality of the air; that an animal will die if kept in a confined space full of air, a fact to be explained, according to Mayow, by saying that the animal had used the respirable portion of the air, and that the residue was unfit for life; and, finally, he showed that an animal suffers if placed in an atmosphere, the qualities of which have been injured by combustion. Further, he gave the name of *nitro-aërial spiritus* to the "principle" in the air, which he said had to do with life, muscular action, and combustion. Thus, he no doubt came near the discovery of oxygen, made by Priestley nearly a century later.

The next step in the physiology of respiration was the discovery, in 1754, of carbonic acid by Joseph Black, in his investigation on magnesia. He showed that in the case of *magnesia alba* (carbonate of magnesia) the disappearance of the effervescence on treatment with an acid after heating was accompanied by a loss of weight. The substance thus given off he called "fixed air," or what we now term carbonic acid. This led to an examination of the salts of lime, and, in 1757, he made two important physiological discoveries, namely: (1) that the fixed air was injurious to animal life; and (2) that fixed air was produced by the action of respiration.

Fifteen years afterwards, namely, in 1772, Joseph Priestley examined the chemical effects produced by the burning of candles and the respiration of animals upon ordinary air; and he made the discovery that, after air had lost its power of supporting combustion, as by the burning of candles, this property might be restored by the agency of plants. He also found that air, deteriorated by the breathing of animals, might again become suitable for respiration by the action of plants. In 1774, Priestley obtained oxygen by heating red precipitate by means of the sun's rays concentrated by a burning glass. This led to an investigation of the constitution of the atmosphere, and it was shown that it consisted of two gases, and that its constitution was remarkably uniform.

Within a year after Priestley's discovery, a paper on respiration was written by Lavoisier (1743-1794), in which he showed that Priestley was correct in stating that the air lost oxygen in breathing, but Lavoisier pointed out that it had gained carbonic acid. Lavoisier was the first to make a quantitative examination of the changes produced in the air by breathing. In 1780, he performed an experiment, in which a guinea-pig was confined over mercury in a jar containing 248 cubic inches of gas consisting principally of oxygen. In an hour and a quarter the animal breathed with much difficulty, and, being removed from the apparatus, the state of the air was examined. Its bulk was found to be diminished by 8 cubic inches, and of the remaining 240 inches 40 were absorbed by caustic potash, and consequently consisted of carbonic acid.

About 1768, Spallanzani investigated respiration, more particularly in invertebrates. He showed that many such animals breathed by means of the skin as well as by the special breathing organs. He placed many animals, but more especially different species of worms, in atmospheres of hydrogen and nitrogen, and showed that, even in these circumstances, carbonic acid was produced. He also showed the production of carbonic acid by the dead bodies of such animals, and reasoned from this that the carbonic acid was produced directly from the dead tissues and not from the action of the oxygen of the air.

At the beginning of the present century it was recognized that expired air had lost oxygen, gained carbonic acid and aqueous vapour, and had become hotter. Since then many researches have been carried on to determine with accuracy the quantities of these substances. In all of these, the method followed has been to draw through a chamber containing the animal a steady, constant, stream of air, the quantity and composition of which are known. Thus, suppose a certain quantity of dry air, free from carbonic acid, and consisting only of oxygen and nitrogen, is passed through such a chamber. In the chamber some of the oxygen is consumed, and a certain amount of carbonic acid and of aqueous vapour is given up by the animal. The air is drawn onwards through bulbs or glass tubes containing substances such as baryta water to absorb the carbonic acid, and chloride of calcium or sulphuric acid to absorb the aqueous vapour. It is evident that the increased weight of these bulbs and tubes, after the experiment has gone on for some time, will give the amounts of carbonic acid and aqueous vapour formed. Thus Andral and Gavarret in 1843, Vierordt in 1845, Regnault and Reiset in 1849, Von Pettenkofer in 1860, and Angus Smith in 1862, determined the quantities both by experiments on animals and on human beings. We shall now consider the general results of such investigations.

The Air Inspired.—About half a litre, or 500 cubic centimetres, of air are taken into the lungs in each inspiration ; there are 15 inspirations per minute, therefore ·5 litre × 15 × 60 = 450 litres per hour, or 450 × 24 = 10,800 litres in twenty-four hours.

The *average* composition of atmospheric air, in 100 volumes, is as follows :—

$$\left.\begin{array}{ll} \text{O, - - - -} & 20{\cdot}93 \\ \text{N, - - - - -} & 78{\cdot}19 \\ \text{CO}_2\text{, - - -} & 0{\cdot}04 \\ \text{H}_2\text{O (vapour), - -} & 0{\cdot}84 \end{array}\right\} 100$$

Air may also contain traces of nitric acid, carburetted hydrogen, ammonia, particles of dust consisting of inorganic or dead organic matter, and the spores of minute organisms.

The amount of aqueous vapour depends on the temperature, being great when the temperature is high and small when it is low. Sometimes the air may be saturated with aqueous vapour at a given temperature ; if the temperature rise, more vapour may be taken up ; if it fall, some moisture will be deposited. The temperature and the pressure of the air have an influence on respiration. If the *temperature* is high, a rarefied air is breathed—that is, an air which per volume contains less oxygen than a condensed air. Consequently, to compensate for the expansion of the air by heat, the number and depth of the respirations are increased.

Thus a cubic metre of air at 0° C. will take up 4·8 grms. of H_2O; at 10°, 9·3; at 20°, 17·1; at 30°, 29·4; and at 37°, 42·2 grms. Air may be described as dry when it contains ·25 per cent. of H_2O, and damp when it is saturated. It usually contains about 1 per cent.

The Air Expired.—Contrast the percentage composition of the air inspired and the air expired, as follows:—

	Air inspired.	Air expired.		Difference.
O, - - -	20·81	16·03	–	4·78
N, - - -	79·2	79·3	+	0·1
CO_2, - - -	0·04	4·38	+	4·34

Note the following characters of expired air: (1) it contains one-fifth less oxygen; (2) it contains 100 times more carbonic acid; (3) it contains one-tenth per cent. more nitrogen; (4) it is saturated with aqueous vapour; (5) it may contain traces of ammonia, carburetted hydrogen (in herbivora especially), and of volatile substances; and (6) it is usually hotter. When air was inspired at a temperature of 6·3° C., the expired air had a temperature of 29·8° C.; when inspired at 15·20° C., the temperature of the expired air was 37·3° C.; and when at 41·9° C., the expired air showed a temperature of 38·1° C. In the latter case, the evaporation of water would account for the fall in the temperature. The temperature of expired air is usually about 37° C.; the volume of expired air is equal to, or even larger than, that of inspired air, in consequence of the expansion of the expired air by increase of temperature; but if the two volumes, inspired and expired, be reduced to the same temperature and pressure, the expired air will be found to be a little less than that of inspired air (a diminution of $\frac{1}{40}$th to $\frac{1}{50}$th of the total volume), and it has been ascertained that this is due to a disappearance of oxygen. From 800 to 2,000 grms. of water are given off by the breath in twenty-four hours. It is a doubtful point whether the whole of this is eliminated in the alveoli, or whether the greater part of it may not come from the moist walls of the upper air passages and the mouth. If a dry, or nearly dry, air passed over such warm, moist surfaces, it would quickly become laden with moisture.

The results are—*firstly*, the expired air, for its own temperature, is saturated with aqueous vapour; *secondly*, the expired air is less in volume than the inspired air, to the extent of about one-fortieth of the volume of the latter; *thirdly*, the expired air contains about 4 per cent.

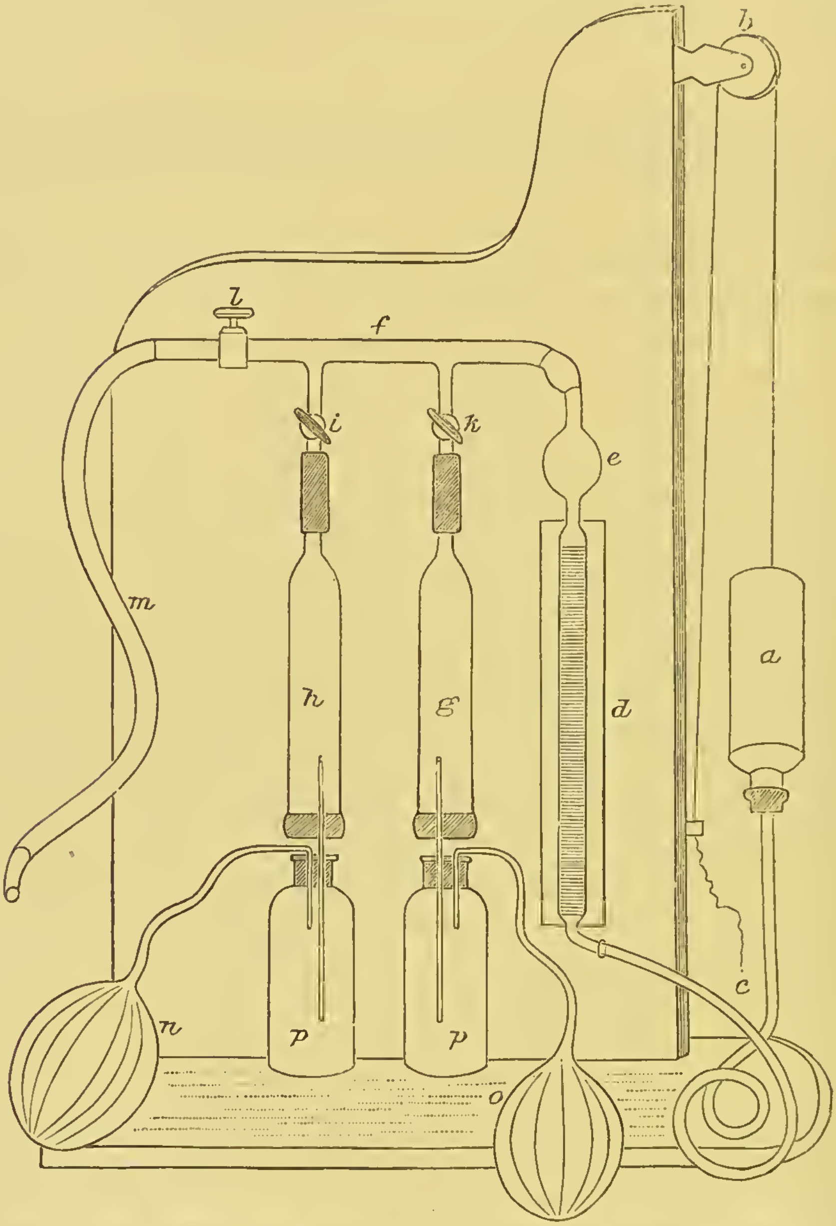

FIG. 194.—Apparatus for rapid analysis of air. *a*, pressure-bottle communicating by tube *c* with graduated tube *d*, having at top the bulb *e*. Air is breathed into tube *m*, stopcock *l* being open, by tube *f* into *e* and *d*, depressing water from *d* into *a*. Quantity is measured. Stopcock *l* is then shut, *a* is raised by string over pulley *b*, and air is forced from *d*, *e* into *g*, stopcock *k* being opened, containing strong caustic potash, to absorb CO_2. Then *a* is lowered, and air is forced back into *e*, *d* from *g*, aided by pressure on india-rubber bag *o*. The air is again measured in *d*, and the volume lost is CO_2. It is then forced into tube *h*, guarded by stopcock *i*. This tube contains ammonio-chloride of copper, which absorbs *o*. It is again forced back with aid of bag *n*. The diminished volume in *d* represents loss of oxygen, and the residue is nitrogen.

more carbonic acid, and from 4 to 5 per cent. less oxygen, than inspired air; *fourthly*, the total daily excretion of carbonic acid, by an average man, amounts to 900 grms. in weight, or 458 litres in bulk. This amount of carbonic acid represents 244 grms. of carbon, and 656 grms. of oxygen. The amount of oxygen, however, actually consumed, is about 700 grms.; so that nearly 44 grms. of oxygen absorbed are not returned by the lungs, but disappear in the body. It must be remembered, however, that carbonic acid escapes by the skin and other channels. These figures may be taken as averages, and are subject to wide variations, depending on nutritional changes.

Composition of the Air in the Bronchi and Lung Cells.—Having considered the composition of the air, inspired and expired, and the volumes of each, we have next to ascertain what is known regarding the condition of the air in the passages and in the ultimate air-cells of the lung. It has been shown by Vierordt that as we penetrate into the lung, the proportion of carbonic acid and of aqueous vapour increases, and that, if we divide the air of expiration into successive portions, the first expired contains less CO_2 than the second, the second than the third, and so on. It is difficult to estimate the percentage amount of CO_2 in the ultimate air-cells, but it may be as much as 7 or 8 per cent. After an inspiration, introducing, let us say, 500 cubic centimetres of air, the air passes only into the trachea and upper air passages, driving backwards and compressing the air in the lungs at the end of the previous expiration. Diffusion then quickly takes place, oxygen passing inwards and carbonic acid passing outwards. In the next expiration, 500 c.c. are returned, but of these, as has been ascertained by Gréhant, 170 c.c. consist of pure air which was introduced by the previous inspiration, and the remaining 330 c.c. consist of vitiated air returned from the lungs. The 330 c.c. of pure air not returned diffuse quickly with the air in the deeper passages of the lungs, and Gréhant has stated that this will probably take place in the time occupied by about five respirations.

Chap. VI.—THE CHANGES IN THE BLOOD DURING RESPIRATION.

The blood which reaches the lungs by the pulmonary artery is *venous*, whilst that carried back to the heart by the pulmonary veins is *arterial*. Arterial blood is of a rich vermilion colour, it coagulates readily, and it contains more oxygen and less carbonic acid than venous blood; venous blood is of a purple colour, and it contains more carbonic acid and less oxygen than arterial blood. The following table shows the percentage of gases in volumes that may be obtained from the two kinds of blood as measured at 0° C. and 760 mm. barometric pressure :—

In 100 vols of blood.	Oxygen.	Carbonic Acid.	Nitrogen.	Total.
Arterial, - -	20	39	1·2	60
Venous, - -	8-12	46	1·2	58

The Gases of the Blood.—These are removed from the blood, with the aid of heat, by means of a peculiar form of air-pump which thoroughly exhausts a receiver so as to allow the gases to escape *in vacuo*. As the fluid blood is introduced into the space from which the air has been removed, a portion of the water of the blood at once passes into the state of vapour, so that the gases do not really escape into a vacuum but into a space containing aqueous vapour, the tension of which depends on the temperature. Such an apparatus is shown in Fig. 195. It consists of a long barometrical tube, *e*, the height of which is greater than that of the ordinary barometrical column of mercury. The upper part of the tube opens into a large globe, *c*, with which two tubes, *g* and *h*, are connected ; one vertical, *h*, communicating with the external air, and the other horizontal, *g*, opening into a glass vessel or receiver, *a*, into which the blood is introduced. Stopcocks are placed at the openings into the globe of these two tubes. From the lower extremity of the barometric tube, *e*, a strong india-rubber tube, *f*, passes to another globe, *d*, which may be regarded as a reservoir of mercury of greater capacity than the first globe, *c*. This reservoir may be elevated or lowered by turning a strong band, passing over a pulley, round an axle, *l*. The object of this arrangement is to extract the air from the receiver, *a*, with great rapidity. This is accomplished as follows :—Open the stopcock, *g*, and shut the stopcock communicating with the receiver, *a ;* elevate the reservoir of mercury, *d*, above the level of the globe, *c ;* the air in the globe is expelled through the verticle tube, *g h ;* turn the stopcock of this tube at *g*, then lower the reservoir as far as it will go ; the mercury falls as it would do in a long barometrical tube so as to leave the globe, *c*, a vacuum, with the exception of some vapour of mercury ; the stopcock commanding the horizontal tube of the receiver, *a*, is then opened and immediately the air passes thence into the globe, *c* ; the stopcock at the opening of the horizontal tube is shut and that of the vertical tube opened, and, finally, by again elevating the reservoir, the gas obtained by the preceding experiment is expelled. The operation above described is repeated several times until the air in the receiver has been removed as far as possible. The next step is to introduce the blood into the receiver without allowing either to be influenced by the air. This is accomplished by preparing a tube filled with mercury and having a stopcock at each end. A canule is introduced into the vessel of the animal, with a slip-knot ligature on the cardiac side. The other end of the canule is connected with the mercury collecting tube by a short bit of india-rubber tubing. The ligature on the vessel is then loosened, the stopcocks on the collecting tube are opened, and the far end of the tube is lowered, so as to allow the mercury to flow out, while the blood flows in. When the tube is full of blood the stopcocks are closed, and one end of the collecting tube is then quickly connected by a short bit of india-rubber tubing, with the tube leading into the receiver. The stopcocks between the collecting tube and the receiver are opened, and on also opening the far away stopcock of the collecting tube, the blood is quickly sucked into the receiver. Care is taken that no air enters with the blood. The gases of the blood, now under a minimum of pressure, escape. They pass into the globe, from which they are expelled through the vertical tube by elevating the cistern, *d*, in the manner before indicated, and they are collected in

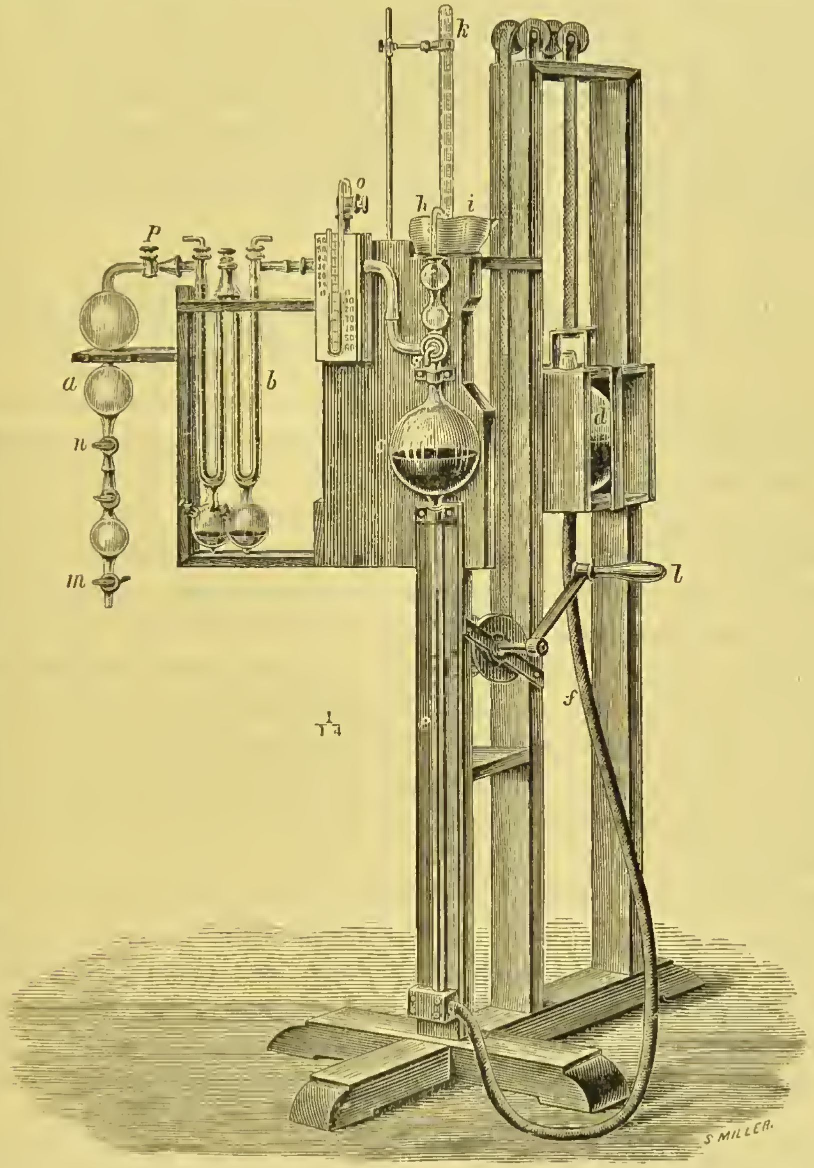

FIG. 195.—Pflüger's Pump for extracting the gases of the blood. *a*, receiver for blood; *b*, U-tubes, containing asbestos and H_2SO_4 for absorption of aqueous vapour; *c*, glass globe, containing mercury, communicating with *d*, a similar globe, by glass tube, *e*, and india-rubber tube, *f*; *h i*, mercury trough for collecting the gases in the tube, *k*; *l*, handle of crank for elevating globe, *d*; *m n*, stopcocks for regulating entrance into blood-receiver, *a*; *o*, pressure gauge of mercury, for ascertaining diminution of pressure in *a* and *b*; *p*, stopcock commanding the communication between blood-receiver, *a*, and gas-drying apparatus, *b*.

graduated tubes over mercury. By graduation, the amount of gas per volume of blood is readily ascertained. To assist in the liberation and escape of gas from the blood, the receiver is immersed in a water bath of about 40° C., and the liberation of carbonic acid is further accelerated by the addition of a small amount of a hot solution of tartaric acid. The total amount of gas having been ascertained, the percentage amount of each gas in the mixture is estimated by the ordinary methods of the volumetric analysis of gases—the carbonic acid being absorbed by a strong solution of caustic potash, whilst the amount of nitrogen is represented by what remains, and the oxygen by pyrogallate of potash produced by introducing a strong solution of pyrogallic acid. Eudiometrical methods of gas analysis may also be carried out with the usual precautions.

CHAP. VII.—THE INTERCHANGES BETWEEN THE BLOOD AND THE AIR IN RESPIRATION.

According to Lavoisier, respiration was a slow combustion of carbon and of hydrogen. The air supplied the oxygen, and the blood the combustible materials. The great French chemist, however, did not entirely commit himself to the opinion that the combustion occurred only in the lungs. He said that a portion of the carbonic acid may be formed immediately in the lung, or in the blood-vessels throughout the body, by combination of the oxygen of the air with the carbon of the blood. In 1791, Lagrange observed that, if heat were produced in the lungs alone, the temperature of these organs might become so high as to destroy them; and he therefore supposed that the oxygen is simply dissolved in the blood, and in that fluid combined with carbon and hydrogen, forming carbonic acid and aqueous vapour, which were then set free in the lungs.

Now, if the production of carbonic acid in a given time depended upon the amount of oxygen supplied in the same time, these views of Lavoisier and Lagrange would be correct; but Spallanzani had shown that certain animals confined in an atmosphere of nitrogen or of hydrogen exhaled carbonic acid to almost as great an extent as if they had breathed air. He said that carbonic acid previously existed in the body, and that its appearance could not be accounted for by the union of oxygen with the carbon of the blood. Spallanzani thought that in the lung there was an exhalation of carbonic acid and an absorption of oxygen. In 1830, Martigny stated that carbonic acid was secreted in the capillaries and excreted by the lungs.

Two theories of respiration were thus before physiologists—the one, that combustion occurred in the lungs or venous blood, furnishing carbonic acid and aqueous vapour, which were exhaled by the lungs (the *combustion theory*); the other, that there was no such combustion, but that oxygen was absorbed by the lungs and carried to the tissues, whilst in these carbonic acid was secreted, absorbed by the blood, carried to the lungs, and there exhaled (the *secretory theory*).

The difficulty felt by the older physiologists in accepting the secretion theory was the absence of proof of the existence of free oxygen and carbonic acid in the blood. This difficulty also met those who rejected the notion of combustion occurring in the lungs, and substituted for it the idea that it really occurred in the blood throughout the body, because, if this were true, free gases ought to be found in the blood. Consequently, so long as physiologists had no definite knowledge regarding gases in the blood, the combustion theory, in the most limited sense, held its ground. This theory, although fruitful of many ideas regarding respiration and animal heat, was abandoned in consequence of the evidence afforded by two lines of inquiry—namely, researches regarding the gases of the blood, and researches as to the relative temperature of the blood in the right and left cavities of the heart.

The remarkable change in the colour of the blood when it is exposed to, or shaken up with, air, was observed so long ago as 1665. Priestley was the first to show that the increased redness was due to the action of the oxygen of the air, and that the blood became purple when agitated with carbonic acid, hydrogen, and nitrogen. The presence of gas in the blood was first observed about 1672 by Mayow.

Gas was also obtained from the blood, in 1799, by Sir Humphry Davy, in 1814 by Vogel, in 1818 by Brand, in 1833 by Hoffmann, and in 1835 by Stevons. These observers, either by heating the blood, or by allowing it to flow into a vacuum, or by passing through it a stream of hydrogen, obtained small quantities of carbonic acid. Davy was the first to collect a small quantity of oxygen from the blood.

So long as the evidence in favour of the existence of gases in the blood was uncertain, the combustion theory of respiration held its own. At last, in 1836, appeared the researches of Magnus.

He first attempted to drive off carbonic acid from the blood by a stream of hydrogen, and thus obtained as much as 34 cubic centimetres of carbonic acid from 62·9 cubic centimetres of blood. He then devised a mercurial air-pump, by which it was possible to exhaust a receiver to a much greater extent than could be done by the ordinary air-pump. When blood was introduced into such a vacuum, considerable quantities of carbonic acid, oxygen, and nitrogen were obtained.

In order to appreciate the value of this evidence, and the method employed, we must study the laws regulating the diffusion of gases.

As a mass of gaseous matter has no independent form, like that of a solid body, nor a fixed volume like that of a liquid, but consists of an enormous number of molecules which, in consequence of their mutual repulsions, endeavour more and more to separate from each other, it is easy to see that if two masses of gas are brought into contact, they will mix, that is, their molecules will interpenetrate, until a mixture is formed containing an equal number of the molecules of each gas. The force by which the molecules repel each other, and by which they exercise pressure in all directions, is known as the pressure or tension of the gas. It is evident that the greater the number of gas molecules in a given space, the greater will be the tension of the gas, and from this it follows that the tension of a gas is in the inverse proportion to its volume (*Boyle's law*). Suppose now that two gases are separated by a porous partition; the two gases will mix, and the rapidity of the diffusion will vary according to the specific weight of the gases. Thus light gases, like hydrogen or coal gas, will diffuse more quickly than air, or chlorine, or carbonic acid.

It is important also to note the laws regulating the absorption of gases by fluids. If we allow a little water to come into contact with ammonia gas above mercury, the gas is rapidly absorbed by the water (1 volume of water absorbs 1180 volumes NH_3), all the gas above disappears, and in consequence of this the pressure of the outer air drives up the mercury in the tube. The higher the temperature of the fluid the less gas it absorbs. At the boiling point of the fluid its absorption = 0, because at that temperature the fluid itself changes into gas. The power of absorption of different fluids for the same gas and the absorptive power of the same fluid for different gases fluctuate between wide limits.

Bunsen defined the co-efficient of absorption of a fluid for a gas as that number which represents the volume of gas (reduced to 0° and 760 mm. barometric pressure) which is taken up by 1 volume of the fluid. Thus 1 volume of distilled water takes up the following volumes :—

Temp. Cent.	N.	O.	CO_2.	Air.
0	0·02	0·041	1·797	0·025
5	0·018	0·036	1·5	0·022
15	0·015	0·03	1·002	0·018
37	—	0·02	·569	—

Again, 1 volume of distilled water at 0° C. absorbs 0·00193 volumes of hydrogen, while it can take up no less than 1180 volumes of ammonia ; again, 1 volume of water at 0° C. absorbs only 0·2563 volumes of olefiant gas, but 1 volume of alcohol, at the same temperature, will take up as much as 3·595 volumes. The volume of gas absorbed is independent of the pressure, and the same volume of gas is always absorbed, whatever the pressure may happen to be. But, as according to Boyle's law the density of a gas, or in other words the number of molecules in a given space, is in proportion to the pressure, and as the weight is equal to the product of the volume and the density, so while the volume absorbed always remains the same, the quantity or weight of the absorbed gas rises and falls in proportion to the pressure (*law of Dalton and Henry*). It therefore follows that a gas is to be considered as physically absorbed by a fluid, if it separates from it not in volumes but in quantities, the weights of which are in proportion to the fall of pressure.

When two or more gases form an atmosphere above a fluid, the absorption takes place in proportion to the pressure which each of the constituents of the mixture would exercise if it were alone in the space occupied by the mixture of gases, because, according to Dalton's law, one gas does not exercise any pressure on another gas intermingled with it, but a space filled with one gas must be considered, so far as a second gas is concerned, as a space containing no gas, or, in other words, a vacuum. This pressure, which determines the absorption of the constituents of a gaseous mixture, is termed, according to Bunsen, the partial pressure of the gas. The partial pressure of each single gas in a mixture of gases depends, then, on the volume of the gas in question in the mixture. Suppose atmospheric air to be under a pressure of 760 mm. of mercury: as the air consists of 21 volumes per cent. of O and 79 volumes per cent. of N, then $\frac{760 \times 21}{100} = 159{\cdot}6$ mm. of mercury, will be the partial pressure under which the oxygen gas is absorbed, while the absorption of nitrogen will take place under a pressure of $\frac{760 \times 79}{100} = 600$ mm. of mercury. Suppose, again, that above a fluid containing a gas, say carbonic acid, which has been absorbed, there is an atmosphere of another gas, say atmospheric air, then as carbonic acid exists in the air only in traces, its tension is equal to zero, and carbonic acid will escape from the fluid until the difference of tension between the carbonic acid in the water and the carbonic acid in the air above it has been balanced, that is, until the carbonic acid which has escaped into the air has reached a tension equal to that of the gas still absorbed by the fluid. By the phrase "tension of the gas in a fluid" is understood the partial pressure in mm. of mercury which the gas in question has to exercise in the atmosphere, when no diffusion between the gas in the fluid and the gas in the atmosphere takes place. The terms "pressure" and "tension" mean the same thing.

The method followed by Magnus will now be understood. The blood being allowed to flow into an exhausted receiver surrounded by hot water, gases were set free. These were found to be oxygen, carbonic acid, and nitrogen. He further made the important observation that both arterial and venous blood contained the gases, the difference being that in arterial blood there was more oxygen and less carbonic acid than in venous blood. Magnus concluded that the gases were simply dissolved in the blood, and that respiration was a simple process of diffusion, carbonic acid passing out and oxygen passing in, according to the law of pressures just explained.

Let us apply the explanation of Magnus to what occurs in pulmonary respiration. Venous blood, containing a certain amount of carbonic acid at the temperature of the blood and under a certain pressure, is brought to the capillaries, which are distributed on the walls of the air-vesicles in the lungs. In these air-vesicles we have an atmosphere at a certain temperature and subject to a certain pressure. Setting temperature aside, as it may be assumed to be the same in the blood and in the air-cells, let us consider the question of pressure. If the pressure of the carbonic acid in the blood be greater than that of the carbonic acid in the air-cells, carbonic acid will escape until an equilibrium is established between the tension of the gas in the blood and the tension of the gas in the air-cells. Again, if the tension of the oxygen in the air-cells be greater than that of the oxygen in the venous blood, oxygen will be absorbed until the tensions become equal. This theory has no doubt the merit of simplicity, but it will be observed that it depends entirely on the assumption that the gases are simply dissolved in the blood. It was pointed out by Liebig that according to the experiments of Regnault and Reiset, animals used the same amount of oxygen when breathing an atmosphere composed of that gas alone as when they breathed ordinary air, and that the vital processes are not much affected by breathing the atmosphere of high altitudes where the amount of oxygen taken in is only about two-thirds of that existing at the sea level. It was also shown at a much later date, by Ludwig and W. Müller, that animals breathing in a confined space of air will use up the whole of the oxygen in the space, and it is clear that as the oxygen is used up, the partial pressure of the oxygen remaining must be steadily falling. Liebig urged the view that the gases *were not simply dissolved in the blood*, *but existed in a state of loose chemical combination* which could be dissolved by the diminished pressure in the vacuum, or by the action of other gases. He also pointed out the necessity of accurately determining the co-efficient of absorption of blood for the gases, that is, the amount absorbed under a pressure of 760 mm. of mercury by one volume of the gas at the temperature of the observation. The next important observations were those of Fernet, published in 1855 and 1857. He expelled the greater part of the gas of the blood (dog) by passing through it a stream of hydrogen and then submitting it to the action of the air-pump. He then introduced into the apparatus the gas under a given pressure, the absorption co-efficient of which he had to determine. He then estimated the amount of gas absorbed, under different pressures, and found in the case of oxygen that the amount absorbed with gradually decreasing increments of pressure was greater than what would have been the case had it been in accordance with Dalton's law of pressures. The oxygen was not then simply dissolved in the blood. Further, Fernet arrived at the conclusion that the greater portion of the oxygen was in a state of combination, whilst a small amount was simply dissolved according to Dalton's law.

It is evident, then, that while the amount of oxygen absorbed varies with the pressure, it does not do so according to Dalton's law. The amount decreases slowly with pressures below atmospheric pressure, and it increases rapidly with pressures above it. It is when the pressure in the vacuum is as low as one-thirtieth of an atmosphere that the oxygen is given up. The view that something in the blood is chemically united to the oxygen is strengthened by the fact that serum does not absorb much more oxygen than water can absorb, so that blood at a temperature of 30° C. would contain only about 2 volumes per cent. of oxygen gas were the latter simply dissolved in the fluid. It can also be shown that defibrinated blood takes up oxygen independently of the pressure, and that the quantity of oxygen taken up by defibrinated blood is about equal to the quantity absorbed by a solution of pure hæmoglobin containing as much of that substance as exists in the same volume of blood.

By similar experiments made with carbonic acid, Fernet determined that the greater portion of it was in a state of loose chemical combination, whilst a small amount was simply dissolved according to the law of pressures. Experiments with blood serum showed similar results as regards carbonic acid, with the difference that the co-efficient of absorption for oxygen was much less than with ordinary blood. He therefore concluded that nearly the whole of the carbonic acid was chemically retained in the fluid of the blood, whilst nearly the whole of the oxygen was combined with the red blood corpuscles. He then proceeded to investigate whether or not the three principal salts of the blood, carbonate of soda, phosphate of soda, and chloride of sodium, in any way influenced the absorption co-efficient of carbonic acid. He found (1) that the addition of these salts to distilled water in the proportion in which they exist in the serum slightly diminishes the absorption co-efficient; (2) that chloride of sodium has no influence on the absorption co-efficient; and (3) that carbonic acid combines with the carbonate and phosphate of soda.

In the same year (1855) Lothar Meyer published the results of a series of researches of the same nature. Under the direction of Bunsen, the blood was diluted with ten times its bulk of water, and the gases were collected by boiling the liquid in vacuo at a very gentle heat; a certain amount of gas was thus obtained. He also found that blood absorbs a much larger quantity of carbonic acid than pure water at the same temperature, and stated that when blood was exposed to oxygen at various pressures the quantity of that gas taken up might be regarded as consisting of two portions, one following Dalton's law and the other independent of it.

Further researches of a similar kind have been carried out by Setschenow, Ludwig, Alexander Schmidt, Bert, Pflüger, and others. The result has been to enable us to give the average composition of the gases of the blood as follows. From 100 volumes of dog's blood there may be obtained—

	Oxygen.	Carbonic Acid.	Nitrogen.
Arterial,	18·4 to 22·6, mean 20	30 to 40	1·8 to 2
Venous,	Mean 11·9	43 to 48	1·8 to 2

the gases being measured at 0° C. and 760 mm. pressure. The venous blood of many organs may contain less than 11·9 per cent. of carbonic acid, and the blood of asphyxia may contain as little as 1 volume per cent. It is clear, then, that the gases of the blood do not exist in a state of simple solution, but that they are largely combined with certain constituents of the blood. Take, for example, the case of oxygen. Berzelius showed long ago that 100 volumes of water will absorb, at a given temperature and pressure, 2·9 volumes of oxygen; while, in the same circumstances, 100 volumes of serum will absorb 3·1 volumes, and 100 volumes of blood will absorb 9·6 volumes. Something in the blood must have the power of taking up a large amount of oxygen.

The next step was the discovery of the important part performed in respiration by the colouring matter of the red blood corpuscles already discussed in Vol. I. p. 116, *et seq.* The colouring matter, hæmoglobin, was first obtained in a crystalline state by Funke in 1853, and subsequently by Lehmann. It has been analyzed by Hoppe-Seyler and Carl Schmidt, with the result of showing that it has a perfectly constant composition. Hoppe-Seyler's analysis first appeared in 1868.

In 1862, Hoppe-Seyler noticed the remarkable spectrum produced by the absorption of light by a very dilute solution of blood. The subject was investigated about the same period by Stokes, and communicated to the Royal Society in 1864.

Stokes came to the important conclusion that—

> "The colouring matter of blood, like indigo, is capable of existing in two states of oxidation, distinguishable by a difference of colour and a fundamental differ-

ence in the action on the spectrum. It may be made to pass from the more to the less oxidized state by the action of suitable reducing agents, and recovers its oxygen by absorption from the air."

To the colouring matter of the blood Stokes gave the name of cruorine, and described it in its two states of oxidation as scarlet cruorine and purple cruorine. The name *hæmoglobin*, given to it by Hoppe-Seyler, is generally employed. When united with oxygen it is called *oxyhæmoglobin*, and when in the reduced state it is termed *reduced hæmoglobin*, or simply hæmoglobin.

The spectroscopic evidence is, therefore, complete. Pure crystallized hæmoglobin absorbs and retains in combination a quantity of oxygen equal to that contained in a volume of blood holding the same amount of hæmoglobin.

Thus, 1 gramme of hæmoglobin absorbs 1·56 cubic centimetre of oxygen, at 0° C. and 760 millimetres pressure; and, as the average amount of hæmoglobin in blood is about 14 per cent., it follows that $1·56 \times 14 = 21·8$ c.c. of oxygen would be retained by 100 c.c. of blood. This agrees closely with the fact that about 20 volumes of oxygen can be obtained from 100 volumes of blood.

These researches have given an explanation of the function of the red blood corpuscles as regards respiration. The hæmoglobin of the venous blood in the pulmonary artery absorbs oxygen, becoming oxyhæmoglobin. This is carried to the tissues, where the oxygen is given up, the oxyhæmoglobin being reduced. Thus, the colouring matter of the red blood corpuscles is constantly engaged in conveying oxygen from the lungs to the tissues. Probably the union of hæmoglobin with oxygen, and its separation from it, are examples of dissociation, that is, of a chemical decomposition or synthesis, effected entirely by physical conditions.

Our knowledge as to the state of the *carbonic acid* in the blood is not so reliable. In the first place, it is certain that almost the whole of the carbonic acid which may be obtained exists in the plasma. Defibrinated blood gives up only a little more carbonic acid than the same amount of serum of the same blood. Blood-serum gives up to the vacuum about 30 volumes per cent. of carbonic acid; but a small part—according to Pflüger, about 6 volumes per cent.—is given up only after adding an organic or mineral acid. This smaller part is chemically bound, just as carbonic acid is united to carbonates, from which it can be expelled only by a stronger organic or mineral acid. The ash of serum yields about one-seventh of its weight of sodium; this is chiefly united to carbonic acid to form carbonates, and a part of the carbonic acid of the blood is united to those salts. It has been ascertained, however, that defibrinated blood, or even serum containing a large number of blood corpuscles, will yield a large amount of carbonic acid, even without the addition of an acid. Thus, defibrinated blood will yield 40 volumes per cent. of carbonic acid—that is, 34 volumes which would be also given up by the serum of the same blood (without an acid), and 6 volumes which would be yielded after the addition of an acid. Something, therefore, exists in defibrinated blood which acts like an acid in the sense of setting free the 6 volumes of carbonic acid. Possibly the vacuum may cause a partial decomposition of a portion of the hæmoglobin, and, as suggested by Hoppe-Seyler, acid substances may thus be formed.

But what is the condition of the remaining 30 volumes per cent. of carbonic acid which are obtained by the vacuum alone ? A portion of this is probably simply absorbed by the serum ; this part escapes in proportion to the decrease of pressure, and it may be considered to be physically absorbed. A second part of this carbonic acid must exist in chemical combination, as is indicated by the fact that blood-serum takes up far more carbonic acid than is absorbed by pure water. On the other hand, this chemical combination is only a loose one, because it is readily dissolved by the vacuum. There can be no doubt that a part of this carbonic acid is loosely bound to carbonate of soda, Na_2CO_3, in the serum, probably to form acid carbonate of soda, $NaHCO_3$. This compound exists only at a certain pressure. On a fall of pressure, it decomposes into sodium carbonate and carbonic acid, the latter becoming free. A third part of this carbonic acid is probably loosely bound chemically to disodium phosphate, Na_2HPO_4, a salt which also occurs in the blood-serum. Fernet has shown that it binds two molecules of carbonic acid to one molecule of phosphoric acid. This salt occurs in considerable quantity only in the blood of carnivora and omnivora, while in that of herbivora, such as in the ox and calf, only traces exist. It cannot be supposed in the latter instances to hold much carbonic acid in chemical combination. There must exist, therefore, other chemical substances for the attachment of the carbonic acid of the blood, and it has been suggested that a part may be connected with the albumin of the plasma.

According to B. W. Richardson and Zuntz, the blood corpuscles themselves retain a part of the carbonic acid, as the total blood is able to take up far more carbonic acid out of the gaseous mixture rich in carbonic acid or consisting of pure carbonic acid, than can be absorbed by the serum of the same quantity of blood. No compound, however, of carbonic acid with the blood corpuscles is known.

The *nitrogen*, which is contained in the blood to the amount of from 1·8 to 2 volumes per cent., is probably simply absorbed, for even water is able to absorb 2 volumes per cent. of this gas.

The general law is that for all kinds of breathing the pressure of the oxygen should be nearly that of the oxygen in ordinary atmospheric air, namely 157 mm. Whilst the absorption of oxygen by the hæmoglobin has nothing directly to do with the pressure, it is striking that any atmosphere contains enough oxygen by weight for the hæmoglobin in the blood, when the partial pressure of the oxygen is near 157 mm. On each side of this median line life can be supported with considerable differences of pressure. Thus the pressure may be gradually reduced until the point of the dissociation of oxyhæmoglobin is reached—that is to say, down to from $\frac{1}{10}$th to $\frac{1}{30}$th of an atmosphere. On the other hand, animals may breathe an atmosphere containing two or three times the normal amount of oxygen (50 to 70 per cent.) without appearing to be affected. This was first noticed by Regnault and Reiset, and the observation has been much extended by Paul Bert. The latter distinguished physiologist found that an increase even up to 8 or 10 atmospheres did not produce any apparent effect, but on reaching the enormous pressure of 20 atmospheres, death, with severe tetanic convulsions, was the result. He also showed that the additional increment of oxygen absorbed by the blood under the influence of each atmosphere of added pressure was very small. Thus, with a pressure of 1 atmosphere the amount of oxygen absorbed by the blood was about 20 per cent by volume; a pressure of two atmospheres caused an increase of only 0·9 per cent., of 3 atmospheres 0·7 per cent., of 4 atmospheres 0·6 per cent., of 5 atmospheres 0·5 per cent., of 6 atmospheres 0·2 per cent., of 7 atmospheres 0·2 per cent., of 8 atmospheres 0·1 per cent., of 9 atmospheres 0·1 per cent., and of 10 atmospheres 0·1 per cent. Thus from 1 atmosphere to 10 atmospheres the increase was only to the extent of 3·4 per cent., so that the blood now contained 23·4 per cent. by volume instead of 20 per cent. These facts indicate that when all the hæmoglobin has been satisfied with oxygen it becomes indifferent, within limits, to any additional oxygen that may be forced into the blood under pressure, and thus the blood of animals breathing an atmosphere richer in oxygen than ordinary air is not more highly oxygenated than normal blood. On the other hand, the percentage of oxygen in air may fall to 14 vols. without any noticeable effect on an animal breathing the air. Distress appears when the percentage approaches 11, and death will soon occur if it fall as low as 7 per cent.[1]

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[1] Suppose the shorter limb of a manometer to be connected by a tube with the trachea of an animal, during inspiration the mercury would rise in the shorter limb, and during expiration it would rise in the longer limb—that is, during inspiration the pressure in the air passages is less than the pressure of the air, and during expiration it is greater. This amount has been found to be—

In calm inspiration, - - - - -	− 1	mm.
In deep inspiration, - - - - -	− 57	,,
In calm expiration, - - - - -	+ 2 to 3	,,
In forcible expiration, - - - -	+ 87	,,

From these data, it is easy to calculate the partial pressures of the gases in the two states.

The absorption of *oxygen*, therefore, probably takes place as follows: the inspired air is separated in the alveoli of the lung by delicate epithelial cells and the endothelial wall of the pulmonary capillaries from the blood which circulates in the latter. The exchange of gas takes place through these thin porous membranes, so that the velocity of the transit must be practically instantaneous. As the oxygen is bound loosely to the hæmoglobin of the corpuscles, the laws of diffusion can have only a secondary influence on its passage, and only so far as it has to pass into the plasma so as to reach the blood corpuscles. The plasma will absorb, at 35° C., about 2 volumes per cent., if we take the co-efficient absorption of the plasma as equal to that of distilled water. Many of the blood corpuscles of the pulmonary blood have just returned from the tissues with their hæmoglobin in the reduced state, and the latter at once withdraws oxygen from the plasma. In an instant more oxygen passes out of the pulmonary air into the plasma, from which the oxygen is again quickly withdrawn by the hæmoglobin of the corpuscles, and so on. If the oxygen did not exist in loose chemical combination, it would only be absorbed, and its amount would depend on the barometrical pressure at the moment, and would follow each fluctuation of pressure through a range, say, of one-fourteenth of the total pressure. Such an arrangement could not fail in affecting health. If, on ascending a high mountain, say 15,000 to 20,000 feet above the

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Thus: Let P = partial pressure, H the pressure of the air inspired or expired, and Q the quantity of gas in 100 volumes—

$$P = \frac{H \times Q}{100}.$$

Suppose H = 760 mm. and Q = 20·8, then $\frac{760 \times 20{\cdot}8}{100} = 158.$

The great difficulty is to state precisely the partial pressure of the gases in the ultimate air-cells. This is attempted as follows by Beaunis:—

		Oxygen.			Carbonic Acid.	
		Percentage.	Partial Pressure in mm. of Mercury.		Percentage.	Partial Pressure in mm. of Mercury.
Inspiration.	Calm,	17	129	...	4	30
	Deep,	20	140	...	1	7
Expiration,	Calm,	16	121	...	5	38
	Deep,	13	110	...	8	67

The above table is to be thus read: After a calm inspiration, the pressure of O in the ultimate air cells = 129 mm. of mercury, or the pressure which would be exerted by a gaseous mixture containing 17 per cent. of O at the same temperature.

The enormous respiratory surface presented by the red blood corpuscles has already been alluded to (p. 186).

level of the sea, the pressure sank to nearly one-half, the blood would then contain only half its normal quantity of oxygen, and disturbances in the functions of the body would be inevitable. High-flying birds, soaring in regions of the air where the pressure falls below half an atmosphere, would suffer from want of oxygen; but in deep mines and on high mountains men and animals live in a state of health, and the quick-breathing bird has a sufficient amount of oxygen for its expenditure of energy, because the amount of oxygen in the blood is independent of the factor which exercises an immediate influence on the gas contents of the fluid, namely, the partial pressure.

The conditions regulating the exchange of *carbonic acid* are quite different. We have seen that the carbonic acid is almost exclusively contained in the blood plasma, the smaller part being simply absorbed, and the greater part chemically bound, a portion existing in a fairly firm combination with the sodium carbonate of the plasma, and another portion in a loose, easily decomposable combination with the acid sodium carbonate, and a third portion with the sodium phosphate. Carbonic acid is contained in air only in traces, and its tension in the air is almost nothing. The air contained in the lungs is not wholly expelled by each respiration, but a part of the air of expiration, rich in carbonic acid, always remains in the lung. It is evident, then, that by the mixing of the air of inspiration with the air in the alveoli, the latter will become richer in oxygen and poorer in carbonic acid. The air in the alveoli, however, will always contain more carbonic acid than atmospheric air. Pflüger and Wolffberg have drawn the air out of the small bronchi and air-cells by a catheter. They found the amount of carbonic acid in alveolar air to be about 3·5 volumes per cent., therefore its tension will be $\frac{3{\cdot}5 \times 760}{100} = 27$ mm. of mercury. The tension of the carbonic acid in the blood of the right ventricle (which may be taken as representing venous pulmonary blood), amounts, according to Strassburg, to 5·4 per cent. = 41 mm. of mercury, and is 14 mm. higher than that in the alveoli. Carbonic acid will, therefore, pass by diffusion from the blood into the alveolar air until the tension of the carbonic acid has become the same in the blood and in alveolar air. Before the state of equilibrium is reached, expiration begins and removes a part of the air out of the alveoli, so that the tension of the carbonic acid again becomes less than that in the blood. During the expiration and the following pause, the elimination of carbonic acid continues. This physical arrangement has the advantage for diffusion, that by expiration the whole air is not driven out of the lungs, for, if expiration had emptied the lungs of air, the diffusion would have ceased altogether during expiration and the following pause, and diffusion have been possible only during inspiration. There would thus have been an incomplete separation of the carbonic acid from the pulmonary blood. But as air remains in the lungs, the stream of diffusion between pulmonary blood and pulmonary air goes on steadily, and fluctuations occur only in regard to its velocity.

Chap. VIII.—THE GASEOUS INTERCHANGES BETWEEN THE BLOOD AND THE TISSUES.

If we then regard the blood as a respiratory medium, having gases in solution, we have next to consider what is known of the breathing of the tissues themselves. Spallanzani was the first to observe that animals of a comparatively simple type used oxygen, and gave up carbonic acid. But he went further, and showed that various tissues and animal fluids, such as the blood, the skin, and portions of other organs, acted in a similar way. These observations were made before the beginning of the present century, but they appear to have attracted little or no attention until the researches of Georg Liebig on the respiration of muscle, published in 1850. He showed that fresh muscular tissue consumed oxygen, and gave up carbonic acid. In 1856, Matteucci made an important advance, by observing that muscular contraction was attended by an increased consumption of oxygen, and an increased elimination of carbonic acid. Since then, Claude Bernard and Paul Bert, more especially the latter, have made numerous observations regarding this matter. Paul Bert found that muscular tissue has the greatest absorptive power (Fig. 196). Thus we arrive at the conclusion that the living body is an aggregate of living particles, each of which breathes in the respiratory medium passing from the blood.

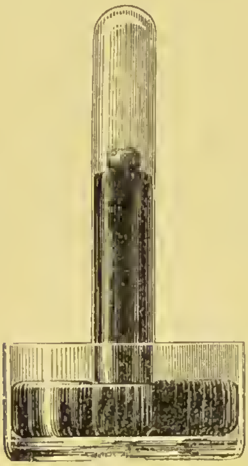
Fig. 196.—Apparatus for demonstrating the absorption of oxygen by living tissues, consisting of test tube filled with oxygen, with the mouth in mercury. The tissue is then introduced, and, as the oxygen is absorbed, the mercury rises. A bit of solid caustic potash may then be introduced to absorb CO_2, and the mercury will rise higher.

As the blood, containing oxygen united with the colouring matter (hæmoglobin), passes slowly through the capillaries, fluid matter transudes through the walls of the vessels, and bathes the surrounding tissues. The pressure or tension of the oxygen in this fluid, being greater than the tension of the oxygen in the tissues themselves, in consequence of the oxygen becoming at once a part of the living protoplasmic substance, oxygen is set free from the hæmoglobin, and is appropriated by the living tissues becoming part of their protoplasm. Whilst alive, or, at all events, whilst actively discharging their functions, as in the contraction of a muscle, or in those changes we term secretion in a cell, the living protoplasm undergoes rapid decompositions, leading to the formation of comparatively simple substances. Amongst these is carbonic acid. As it has been ascertained that the tension of the carbonic acid in the lymph is less than its tension in venous blood, it is difficult at first sight to account for the absorption of carbonic acid by venous blood; but its tension is higher than that of carbonic acid in arterial blood, and it must be remembered that the lymph has had the opportunity, both in the connective tissues and in the lymphatic vessels, of modifying its tension by close contact with arterial blood. Strassburg fixes the tension of the carbonic acid in the tissues as equal to 45 mm. of mercury, while that of the venous blood is only 41 mm. We may assume that, as the carbonic acid is set free, it is absorbed by the blood, uniting loosely with the carbonates and phosphates of that fluid, thus converting it from the arterial into the venous condition. This constitutes respiration of tissue.

In connection with the respiration of tissues, as determined by the analysis of the blood gases and of the gases of respiration, there arises the question of the ratio between the amount of oxygen absorbed and the amount of carbonic acid produced, and striking contrasts among animals have thus been determined. Thus, in herbivora, the ratio of the oxygen absorbed to the carbonic acid produced, or the *respiratory quotient*, as it is termed by Pflüger, $\frac{CO_2}{O}$, amounts to from 0·9 to 1·0, while in carnivora it is from 0·75 to 0·8. Omnivora, of which man may be taken as the example, come between; $\frac{CO_2}{O} = 0{\cdot}87$. The quotient is greater in proportion to the amount of carbohydrate in the diet, whether the animals are carnivora, herbivora, or omnivora. The respiratory quotient becomes the same, about 0·75, in starving animals, a proof that the oxidations are kept up at the cost of the body itself, or, in other words, the starving animal is carnivorous. The activity of respiration in different animals is well shown in the following table, in which the amount of oxygen used is given per kilogramme of body-weight per hour.[1]

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[1] Munk, *op. cit.* p. 82.

Animal.	O in grammes.	Respiratory Quotient. $\frac{CO_2}{O}$
Cat	1·007	0·77
Dog,	1·183	0·75
Rabbit,	0·918	0·92
Hen,	1·300	0·93
Small Singing Birds,	11·360	0·78
Frog,	0·084	0·63
Cockchafer,	1·019	0·81
Man,	0·417	0·78
Horse,	0·563	0·97
Ox,	0·552	0·98
Sheep,	0·490	0·98

Smaller animals therefore have, as a rule, a greater intensity of respiration than larger ones. In small singing birds the intensity is very remarkable, and it will be seen that they require ten times as much oxygen as a hen. On the other hand, the intensity is low in cold-blooded animals. Thus a frog requires 135 times less oxygen than a small singing bird. The need of oxygen is therefore very different in different animals. Thus a guinea-pig soon dies with convulsions in a space containing a small amount of oxygen, while a frog will remain alive for many hours in a space quite free of oxygen. It is well known that fishes and aquatic animals generally require only a small amount of oxygen, and this is in consonance with the fact that sea water contains only small quantities of this gas. Thus, according to the elaborate researches of Dittmar, on the gases of the sea water brought home by the *Challenger* Expedition, collected in many parts of the great oceans, and from varying depths—"The ocean can contain nowhere more than 15·6 c.c. of nitrogen, or more than 8·18 c.c. oxygen per litre; and the nitrogen will never fall below 8·55 c.c. We cannot make a similar assertion in regard to the oxygen, because its theoretical minimum of 4·30 c.c. per litre is liable to further diminution by processes of life and putrefaction and processes of oxidation."[1]

As a matter of fact, a sample of water from a depth of 2,875 fathoms gave only 0·6 c.c. per litre of oxygen, while one from a depth of 1,500 fathoms gave 2·04 c.c. per litre. Taking 15° C. as an average temperature, one litre of sea water would contain only 5·31 c.c. of dissolved oxygen, that is, about 0·5 c.c. in 100 c.c. Contrast this with arterial blood, which contains 20 c.c. of oxygen in 100 c.c. of blood, or there are about forty times as much oxygen in arterial blood as in sea water. At great depths the quantity of oxygen is very much less, and yet many forms of life exist at these great depths. Fishes have been dredged from a depth of 2,750

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[1] Dittmar. *Proceedings of Phil. Soc. of Glasgow*, vol. xvi. p. 61.

fathoms, where the amount of oxygen was probably not so much as 0·06 c.c. per 100 c.c., or 300 times less than that of arterial blood. Making allowance for the smaller quantity of oxygen in the blood of a fish than that of a mammal, it will still be evident that the blood of the fish must contain much more oxygen than exists in the same volume of sea water. No doubt we must remember that the water is constantly renewed, and that the oxygen in it is in the state of solution, or, in other words, in a liquid state. But the question remains, Where do these deep sea creatures obtain the oxygen? Probably by a method of storage. Biot has found in the swimming bladder of such fishes 70 volumes per cent. of pure oxygen, a gas in which a glowing splinter of wood is relit. This oxygen probably oxygenates the blood of the fish when it plunges into the dark and almost airless depths of the ocean.

Aquatic breathers, however, if they live in a medium containing little oxygen, have the advantage that they are not troubled with free carbonic acid. One of the most striking facts discovered by the *Challenger* chemists is that sea water contains no free carbonic acid, except in some situations where the gas is given off by volcanic action from the crust of the earth forming the sea bed. In ordinary sea water there is no free carbonic acid, because any carbonic acid formed is at once absorbed by the excess of alkaline base present. The fish obtains the oxygen from the sea water by the chemical affinity of its hæmoglobin, which snatches every molecule of oxygen it may meet with, while it gets rid of its carbonic acid easily, because there is not only no tension of carbonic acid in the sea water to prevent its escape, but there is always enough of base in the sea water to seize hold of the carbonic acid the moment it is formed.

It is a remarkable fact that, in certain circumstances, tissues and even organs may continue their functions with little or no oxygen.

Thus, "Kronecker and MacGuire found that the heart of the frog pulsates just as powerfully with blood deprived of its gases as with that containing oxygen, while the blood of asphyxia, or blood containing reduced hæmoglobin, soon stops its action."[1]

Further, Kronecker has found that dogs bear the substitution of two-thirds to even three-fourths of their blood by 0·6 per cent. solution of common salt, and Von Ott withdrew $\frac{14}{15}$ths of the blood of a dog, and replaced the same with serum from the horse, free from corpuscles. For the first day or two after the transfusion, the dog had only $\frac{1}{55}$th part of the normal number of red blood corpuscles, so that it had only $\frac{1}{55}$th part of its normal amount of oxygen. But this dog showed no symptoms except weakness and somnolency, nor did it suffer from distress of breathing, a remarkable fact when we consider that the blood of an asphyxiated dog still contains 3 per cent. of oxygen, and that it may show great distress of breathing when there is still $\frac{1}{6}$th part of the normal amount of oxygen in its blood.

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[1] Max Marckwald, in his work on the *Innervation of Respiration in the Rabbit* (translated by T. A. Haig, with introduction by Dr. McKendrick. Blackie and Son. 1888).

Chap. IX.—QUANTITATIVE ESTIMATES OF THE GASES OF RESPIRATION.

1. **Oxygen.**—From 600 to 1,100 grms. of O have been absorbed by an adult man in twenty-four hours. The average amount is about 700 grms.

2. **Carbonic Acid.**—Various estimates have been given of the amount of CO_2 exhaled by an adult man in twenty-four hours, varying from 700 to 1,300 grms. From 800 to 900 grms. are the average quantities. The following table, compiled by Munk, gives the relative quantities of O and CO_2 in grms. in various animals :—

	Weight of Body in Kilogs.	O.	CO_2.
Ox,	600	7,950	10,900
Horse,	450	6,100	9,560
Man,	75	750	900
Sheep,	70	820	1,140
Dog,	15	425	440
Cat,	2·5	60	64
Rabbit,	2·0	45	57
Hen,	1·0	31	39
Frog,	0·03	0·067	0·05

Numerous researches have shown that various circumstances affect the elimination of CO_2, of which the following are the chief :—

(1) *Number and Depth of Respirations.*—If we increase the number of respirations, and keep their depth as far as possible the same, the amount of CO_2 eliminated is increased. Again, if we keep the number the same and increase the depth, the amount is increased. As already seen, ordinary breathing eliminates about 4·3 per cent. of CO_2 in each breath. Slow, deep breathing may increase the percentage to 5, but the total amount of CO_2 exhaled, say in five or ten minutes, is diminished by slow breathing. Quick breathing, on the other hand, causes an increased elimination, although the percentage of CO_2 in the air of each breath will be less than 4·3.

(2) *Length of the Respiratory Pause.*—If we collect samples of the air of expiration from the air of one expiration, we find that the air first expelled contains less CO_2 than the last expelled. Thus the first may have only 3·7 and the last 5·4 per cent. of CO_2, but the mean will be nearly the normal amount, 4·4. If the time of the respiratory pause be increased, the amount of CO_2 separated is greater, indicating that the elimination of CO_2 from the blood into the air cells is going on even during the pause. When the air is retained in the lungs for say 1·25 minute, the amount of CO_2 in the alveoli, and in the expired air at the end of that period, may rise to even 8 per cent. This Vierordt found to be the case in man, but in the dog the amount does not rise past 3·6 per cent., even after the stoppage of breathing for three minutes.

(3) *Age and Sex.*—The amount of CO_2 exhaled increases in both sexes until the time of puberty. In women it may remain stationary after that period, but in men it increases until thirty years of age, and afterward diminishes. More is excreted during pregnancy.

(4) *Food.*—The nature of the food, as has been shown by the laborious observations of Edward Smith, has a marked effect. The amount of CO_2 increases with the carbon contained in the food, carbohydrates and vegetable acids yielding more than fats and albuminates. Starvation, or a state of hybernation, diminishes the amount of CO_2 to a minimum, which remains constant for a considerable time.

(5) *Muscular Action.*—This increases the amount of CO_2, as has been ascertained by researches conducted by Pettenkofer, Voit, Parkes, etc., and is what might have been expected, as it is well known that muscular activity cannot take place without the production of CO_2. Pettenkofer states that in man the increase caused by active muscular exercise may amount to 60 per cent., and Lassaigne has shown that in the horse the amount may be doubled, rising from 342 grms. per hour to 745 grms. per hour.

(6) *Sleep.*—During this condition the amount of CO_2 is diminished to the extent of 25 per cent.

(7) *Period of the Day.*—The amount eliminated is smallest in the morning, rises during the forenoon, reaches its maximum about three or four o'clock, especially if a mid-day meal has been taken, and falls off towards night. This diurnal variation is seen even during fasting, so it does not entirely depend on the food taken.

(8) *Temperature of Medium.*—If the temperature raises the temperature of the body then the amount of CO_2 rises, and if the temperature lowers the temperature of the body then the amount of CO_2 falls.

(9) *Pressure.*—Rapid lowering of the pressure of the atmosphere allows the gases of the blood to assume the form of minute bubbles in the capillaries of the lung, less CO_2 is exhaled, and death will soon occur. The effects of increased pressure on the elimination of CO_2 have not been sufficiently studied.

Nitrogen.—As already stated, the air expired always contains a little more nitrogen than the air inspired. From 7 to 8 grammes are thus eliminated daily, which may be derived partly from the nitrogen of the food, and partly from the nitrogen contained in the air introduced into the alimentary canal along with the food. More nitrogen is eliminated by herbivora than by carnivora. Rabbits have been found to secrete ·3 to ·5 milligramme of nitrogen per kilog. of their body weight.

Aqueous Vapour.—About 300 grammes of aqueous vapour are eliminated by the lungs daily. This amount is derived from two sources: (1) the water of the blood, and (2) the water contained in the air previously inspired. The amount of water separated from the blood will depend on the hygrometric state of the air inspired, and upon the depth of the respirations. The absolute amount of watery vapour separated by the lungs increases with the depth and duration of the respirations: whilst cold, a low barometrical pressure, and dryness of the air, produce the same effect.

CHAP. X.—PRINCIPLES OF VENTILATION.

If an animal is placed in a confined space, where the renewal of air is impossible, the air loses by degrees its oxygen, and becomes more and more highly charged with carbonic acid. When the proportion of oxygen does not fall below 15 per cent., respiration is normal; from 15 to 7 per cent., respiration becomes deep and prolonged; from 7 to 4½ per cent., respiration is carried on with great difficulty; and below this amount, there is risk of immediate asphyxia. After death, the blood is still found to contain some oxygen, and the tissues continue to absorb the oxygen of the blood for some time. The rapidity of asphyxia will depend on the quantity of oxygen in the confined space. Thus a ligature applied tightly round the trachea, by diminishing the space containing oxygen, produces almost immediate asphyxia. It is important to observe that when an animal is placed in a confined space, there appears to be a kind of tolerance gradually established, by which it will live in an atmosphere fatal to another of the same species introduced directly from without. Thus, Claude Bernard placed a bird under a bell-glass over mercury; three hours afterwards, he introduced another bird into the same space; the second bird died in convulsions in a few minutes, while the first continued to respire.

But, as already stated, not only is the oxygen removed, but the percentage of carbonic acid increases. Other gases and volatile substances, such as carburetted hydrogen, sulphuretted hydrogen, volatile fatty acids, etc., are also separated from the body. These latter give to the air the peculiar odour and "stuffy" character observed in crowded apartments. The object of ventilation is not only to introduce fresh oxygen, but to dilute the carbonic acid and matters just mentioned to their normal amount. Pure air contains of CO_2 about ·4 volumes in 1,000. It has been ascertained that air containing one volume per 1,000 of CO_2 has a sensible odour, and may be regarded as impure, and it has been established as a principle in ventilation that the amount of CO_2 present ought never to pass ·7 per 1,000.

If we take 900 grms. as the weight of carbonic acid expired in twenty-four hours, it is easy to calculate its volume, thus :—1 grm. of H at standard temperature and pressure = 11·2 litres. Then 22 grm. CO_2 = 11·2 litres, $\therefore \frac{900 \times 11{\cdot}2}{22} = 458$ litres in twenty-four hours, or $\frac{458}{24} = 19$ litres per hour. Again 44 grms. of CO_2 contain 12 grms. of C., $\therefore \frac{900 \times 12}{44} = 245$ grms. of carbon (7·7 oz. avoird) are separated by the lungs in twenty-four hours. About 700 grms. of oxygen are used in

C	+	O_2	=	CO_2
1 vol.		2 vols.		2 vols.
12		32		$\frac{44}{22}$

twenty-four hours; 16 grms. of O = 11·2 litres at standard temperature and pressure, $\therefore \frac{700 \times 11\cdot2}{16} = 490$ litres of O, or $\frac{490}{24} = 20\cdot4$ litres of O per hour. Thus, about 20 litres may be taken as the amount of carbonic acid expired per hour as the basis of a calculation as to the quantity of air required to dilute it, so as to make the atmosphere fit for respiration. To dilute 20 litres of CO_2 so that there will be 1 part in 1,000 requires 20,000 litres of air. But there must not be more than ·7 per 1,000 of CO_2 in the air, so to dilute it to this extent 28,000 litres of air per head per hour will be required. As 1,000 litres = 1 cubic metre, and as 1 cubic metre = 1·308 cubic yards, $\therefore 1\cdot308 \times 28 \times 27 = 988\cdot85$, or say 1,000 cubic feet; to dilute from ·07 per cent. to ·04 per cent. (the amount of CO_2 in *pure* air) would require about twice as much, or say 2,000 cubic feet of pure air per head per hour, the quantity stated by Von Pettenkofer.

It is evident that even a larger quantity is necessary in the wards of hospitals and in sleeping apartments. The practical problem in ventilation is to supply this amount of air by such arrangements as secure freedom from colds and draughts.

CHAP. XI.—ABNORMAL RESPIRATION.

1. **Apnœa.**—When the blood is saturated with oxygen, respiratory movements are arrested. This may be observed during the process of performing artificial respiration by means of bellows, or other appliances, as requires frequently to be done in the course of physiological research. If the interval between the successive insufflations be gradually diminished, the respiratory movements become slower, and may even be altogether arrested, whilst other movements, as those of the heart and reflex actions, continue. The condition is caused by the presence in the blood of a great excess of oxygen, and of only a small amount of carbonic acid. The action of blood in this condition will be pointed out when we treat of the influence of the nervous system on respiratory movements.

2. **Dyspnœa.**—By this term is meant difficulty in breathing, which may arise either from (1) puncture of the pleural cavity, preventing expansion of the lungs; (2) obstruction in the air passages, preventing the free passage of air to and from the lungs, as by strangulation; (3) profuse hæmorrhage, the loss of blood interfering with the normal action of the respiratory centre to the *medulla oblongata;* and (4) weakening of the circulation, so that the medulla does not receive an adequate supply of blood, as occurs in fatty disease of the heart, in valvular disease, or when there is the pressure of a tumour in the neck interfering with the flow of blood in the carotids or jugulars. It may also be caused by any conditions of the lung, such as congestion, pneumonia,

tubercular solidification, etc., which diminish the extent of respiratory surface. It may occur either from want of oxygen, as in breathing in a confined space, so that the oxygen tension becomes much reduced, or from excess of carbonic acid. The latter course is not uncommonly seen, and it is well known that dyspnœa may be excited by breathing an atmosphere containing a large amount of carbonic acid, although more than the normal percentage of oxygen may be present. If the blood flowing to the brain be above the normal temperature, dyspnœa is excited. Dyspnœa is characterized by increased rapidity and depth of the respiratory movements, so that numerous muscles come into play. Thus, in addition to the ordinary inspiratory muscles—the diaphragm, external intercostals, etc.—other muscles, such as the *scaleni* and *serrati postici*, take part. The ribs are forcibly elevated and depressed; and the larynx, which is almost motionless in ordinary respiration, is drawn upwards and downwards through a considerable distance.

3. **Asphyxia.**—This is the state produced by interruption of the respiratory process, so as to lead to the accumulation of CO_2 in the blood. It may come on gradually, as when an animal is placed in a confined space, or suddenly, as by complete occlusion of the trachea. In either case, it may be divided into three stages: (*a*) *First stage*—This is characterized by dyspnœa, or difficulty in breathing. The respiratory movements are hurried, somewhat irregular, and they soon become deeper and laboured; the inspiratory and expiratory muscles, more especially the former, contract powerfully, and the muscles of the thoracic and abdominal regions contract spasmodically. At the end of about one minute, the spasmodic movements extend more or less to the muscles of the extremities, chiefly affecting the flexors. During this period the oxygen is being used up, the blood is becoming more and more venous, and the respiratory centres in the *medulla oblongata* are excited by the venous blood. (*b*) *Second stage*—The convulsions cease, and the movements of inspiration are scarcely perceptible, while those of expiration come powerfully into action. The second stage also lasts about one minute, and its phenomena are due to the action of the highly venous blood on the *medulla oblongata* and the spinal cord. (*c*) *Third stage*—The pupils are now dilated; the eyelids do not shut on touching the eyeball; consciousness is abolished; reflex movements cease; the muscles become loose or flaccid, and there is a state of calmness, which presents a striking contrast to what was observed a minute before. The ordinary inspiratory muscles act more feebly, and at longer intervals of time, whilst the accessory inspiratory muscles occasionally contract spasmodically, so as to produce a series of con-

vulsive gasps; similar convulsive movements now and then occur in the muscles of the extremities, more especially in the extensors, the head is bent backwards, and the body may also be arched in the same direction; the nostrils are dilated; the heart becomes paralysed, its right cavities are very distended with venous blood, and the venous blood also enfeebles the cardiac muscular tissue; the pulse cannot be felt, and, after one or two convulsive movements, death ensues. This period lasts from two to three minutes, and the whole of the stages may be completed in five or six minutes. The heart, however, may beat for seven minutes. Recovery from asphyxia may take place if artificial respiration is set up *before* the heart ceases to beat. In cases of drowning, complete submersion for three or four minutes is fatal. Newly-born animals sustain immersion for a longer time than adults. On examining the body, the venous system generally, the right cavities of the heart, and the capillaries of the lungs are found to be full of dark venous blood, whilst the arterial system is nearly empty, the elasticity of the great vessels driving the blood onwards. The blood is very dark coloured, and its colouring matter is almost entirely in the form of reduced hæmoglobin.

The blood-pressure rises during the first and second stages, owing to the peripheral resistance being increased by contraction of the smaller vessels, caused by stimulation of the vaso-motor centre in the *medulla oblongata.* At the same time, the heart beats more strongly, and it is influenced also by stimulation of the cardio-inhibitory centre, diminishing the number of its beats, while it strengthens their force. This period of increased action of the heart quickly passes, and the organ beats more feebly, in consequence of its tissue being supplied by venous blood. All the cavities are engorged, and the left ventricle is unable to drive the blood onwards against the great peripheral resistance. Then begins the third stage, when the pressure falls to zero. This is accounted for by the venous blood paralysing the vaso-motor centre in the medulla. The smaller vessels become relaxed, the blood flows from them into the veins, and it engorges the right side of the heart. The left ventricle also beats feebly, as the cardiac muscle is injured by the venous blood, and thus the weak action of the left ventricle, along with the diminished peripheral resistance, causes an enormous fall in arterial pressure.

CHAP. XII.—BREATHING OF FOREIGN GASES.

We shall here shortly consider the relation of certain gases to respiration. Animals may breath nitrogen or hydrogen with impunity provided a sufficient amount of oxygen is present. Thus, hydrogen may replace the nitrogen of air, but in pure hydrogen or pure nitrogen, animals quickly perish from the want of oxygen. Such gases as hydrochloric acid gas, sulphurous acid, nitric acid gas, ammonia, nitrous acid, and chlorine are practically irrespirable, because they produce spasmodic closure of the glottis, and their irritant action has nothing to do with respiratory exchanges. Other gases reach the lungs and there either interfere with the normal gaseous exchanges, or, entering the blood, combine with one or other of its constituents, or have a poisonous action on the tissues. Under this category we may include carbonic acid, carbonic oxide, sulphuretted hydrogen, phosphuretted hydrogen, cyanogen, and arseniuretted hydrogen. The effects of carbonic acid have already been considered (p. 346). Carbonic oxide, formed during the imperfect combustion of carbon, is a poisonous gas affecting breathing, even when existing in the atmosphere to the small amount of ·001 per cent., and rapidly destroying life when present to the extent of 1 per cent. Its poisonous effects are due to the formation of CO-hæmoglobin, by which the hæmoglobin is prevented from performing its function of being an oxygen carrier. The blood becomes scarlet red, redder than ordinary arterial blood, and it shows the characteristic spectrum. (Vol. I. p. 124.) It is said that when two-thirds of the hæmoglobin are combined with carbonic oxide, the animal begins to suffer from a deficient supply of oxygen, and the motions of the heart and of respiration become weaker, until death occurs. The breathing of pure air, or of oxygen, if not too long deferred, will still decompose the CO-hæmoglobin and save life. Nitrogen monoxide (N_2O) may be breathed if mixed with oxygen in the proportion of 2 vols. of N_2O with 1 vol. of O, and it then produces a peculiar condition of intoxication, which has earned for it the name of laughing gas. When breathed in a pure condition it quickly produces a state of asphyxia, with unconsciousness. Sulphuretted hydrogen robs oxyhæmoglobin of its oxygen, the hydrogen combining with the latter so as to form water, sulphur being set free—$O + H_2S = H_2O + S$. According to Hoppe-Seyler, the blood becomes of a greenish hue, and a sulphur-compound is formed which gives an absorption band like that of reduced hæmoglobin. Thénard states that horses die if they breath an atmosphere containing ·4 per cent. of this gas. The breathing of ozone, the allotropic condition of oxygen in which three vols. are condensed to two vols., interferes with the elimination of carbonic acid by irritating the air passages, and probably by injuring the endothelial lining of the alveoli. This occurs even when the amount of ozone present in the air breathed, is not more than 3 or 4 per cent.

Chap. XIII.—INNERVATION OF RESPIRATION.

The whole of the brain, with the exception of the *medulla oblongata*, may be removed from an animal without arresting the movements of breathing. They also continue after section of the spinal cord below the origin of the phrenic nerves. Such experiments led Legallois and Flourens to state that a respiratory centre exists in the *medulla oblongata*, and the latter observer defined its position to be at the lower end of the *calamus scriptorius* (at the point of the V in the grey matter), in the floor of the fourth ventricle, inasmuch as he found that destruction of this part at once arrested the movements and caused death. Hence he termed the centre the *nœud vital*, and he stated its diameter at 5 mm. It is difficult to define its exact position, and it is sufficiently correct to state that it is a spot of limited dimensions near or at the deep origin of the *vagi*.

The question whether or not there are also centres in the spinal cord affecting respiration has given rise to much controversy. Brown-Séquard, in 1855, showed that excision of the *nœud vital* was not necessarily fatal, and, in 1874, Rokitansky and Schroff found that respiratory movements occurred in rabbits poisoned by strychnine, even after division of the spinal cord where it joins the *medulla oblongata*. At a later period, Langendorff stated that respiratory movements occurred in newly-born animals after division of the *medulla oblongata* a few mm. below the point of the *calamus scriptorius*. It was accordingly concluded that a respiratory centre or centres exist in the spinal cord, working both automatically, and by reflex influences coming from the periphery, and the stoppage of breathing, after destruction of the *nœud vital* was said to be due to an inhibition of the spinal centres from irritation of nerve fibres passing to them from above.

Marckwald, on the other hand, has never seen normal respiratory movements after division of the medulla at its lower part, and he shows that the movements observed by Langendorff were of a spasmodic character and were not true respiratory movements. The movements of Langendorff were produced by irritation of the skin or pinching of the limbs. They were in reality reflex spasms produced by a summation of impulses from the periphery, and they happen more readily in decapitated animals, or in animals in which the reflex excitability of the cord has been heightened by strychnine. Marckwald produced movements of a similar character by intermittent electrical stimulation of the spinal cord, and it is well known that in certain conditions of nervous centres, even continuous stimulations produce rhythmic effects. We may therefore conclude that there are no respiratory centres in the cord.

Other writers have asserted the existence of centres higher up in the cerebro-spinal system. Thus Christiani locates a centre in the wall of the lateral ventricle and Martin and Booker and Christiani and Steiner have placed centres in the *corpora quadrigemina*. Christiani identified a small mass of nervous matter about 1 mm. in diameter in the lateral wall of the third ventricle, the stimulation of which quickens respiration, deepening both inspiration and expiration but chiefly inspiratory in its action, and he also places, for similar reasons, an expiratory centre in the two anterior bodies (the *nates*) of the *corpora quadrigemina*. Further, Martin and Booker place an inspiratory centre lower down, in the upper part of the *pons Varolii* and *medulla oblongata*. There are no good reasons, however, for holding that because stimulation of a particular spot causes inspiratory or expiratory movements, we must therefore conclude that the spot is a respiratory centre, and the results can be explained by supposing that the stimulation irritated nerve fibres passing downwards from these localities to the true respiratory centre in the *medulla oblongata*. To prove the existence of a respiratory centre in a particular spot, it is necessary to show, first, that destruction of that spot arrests or modifies the respiratory movements, and, second, that the spot has nerve fibres passing to and from it, in connection with the respiratory mechanism. The view of the existence of the higher centres above noticed will not bear this criticism. We may therefore conclude that the respiratory centre exists in the *medulla oblongata* and in it alone.

We have next to consider the mode of action of the centre. Following older observers, Rosenthal showed that even if the *medulla oblongata* be removed from the influence of all centripetal nerves, by dividing it below the *corpora quadrigemina*, and also cutting the posterior roots of the spinal nerves, and the vagi, that still respiratory movements continue. These movements Marckwald regards as inspiratory and expiratory spasms. The conclusion is that the respiratory centre in the medulla can act automatically in the sense of producing such spasms, but that in ordinary breathing it is influenced in a reflex manner, by centripetal impressions. By the study of the effects of direct electrical stimulation of the *medulla oblongata*, Marckwald showed that the respiratory centre consists of two portions, an inspiratory and an expiratory, and by modifying the intensity of the shocks, the time of the respiratory movement in which they were applied, and the position of the electrodes, he could call forth an inspiration or an expiration. These movements, however, were not produced by stimulation of motor but of sensory fibres, and consequently they were of a reflex character, so that it was possible to maintain an artificial respiration by rhythmic electrical stimulation. The inspiratory centre was more easily called into action than the expiratory, and it was also observed that, in a manner similar to the effect of induction shocks on the frog's heart, a minimal stimulus produced a maximal effect, and also that after repeated stimulations, the excitability of the centre was raised so that stimuli which were too weak before now produced an effect.

The respiratory centre in the *medulla oblongata* may be influenced by impulses passing along nerve tracts from the upper part of the brain, or by impulses passing from the mouth and pharynx along the glosso-pharyngeal nerves, or by impulses passing from the larynx and lungs by the vagi nerves, or by impulses reaching it from any sensory surface on the periphery of the body, or by impulses coming from the abdominal organs by the splanchnic nerves, and lastly, it may be influenced by the nature of the blood circulating through it.

1. It is a matter of common experience that the movements of respiration are to a certain extent under the control of the will, a fact implying the action of *higher centres* on the respiratory centre. We also know that a strong stimulation of any nerve of *special sense* will influence the movements of respiration. Thus, a strong stimulation of the optic and auditory nerves causes an inspiration, while stimulating the olfactory nerves has an expiratory effect. Strong irritation of the sensory branches of the 5th nerve is followed by an expiratory movement. Thus we have the familiar phenomenon of sneezing, which is a series of strong reflex expiratory movements, caused often by irritation of the sensory filaments of the 5th in the mucous membrane of the nose. The other sensory nerves of the head, especially when so irritated as to cause sensations of pain, may cause both inspiratory and expiratory movements. These various nerves carry impressions to the brain, and these impressions may then be carried down to the centres in the *medulla oblongata*, exciting or depressing the activity of these centres. If the *medulla oblongata* is cut across high up in the floor of the fourth ventricle so as to sever it from the encephalon, the respiratory movements cease for an instant or two and then begin, or sometimes artificial

respiration must be resorted to before breathing movements are restored. Then breathing goes on with much regularity as to rhythm, but the amplitude of the movements increases and diminishes at regular intervals, as occurs during sleep. When the transverse incision is made lower down, respiration becomes more laboured, and when the incision is made near the apex of the *calamus scriptorius*, the movements acquire a periodic character, showing long pauses, then a deep respiration, followed by two or three shallower ones, the amplitude of each successive respiration being less than the one before it. During this phase of periodic breathing, Marckwald has found that irritation of the sensory nerves of the skin removes the periodicity, so that respiration becomes normal. Further, it can be shown that mere pressure on the *medulla oblongata* will not cause periodic breathing, and that the condition for obtaining it is that some of the stimuli that descend normally from the brain be prevented from reaching the centre of respiration. This phenomenon of periodic movement is of much interest as throwing light on the cause of a peculiar mode of breathing familiar to physicians in some affections of the heart or brain, known as the *Cheyne-Stokes' respiration.* Here we find long pauses in the breathing, lasting from ·5 to ·75 of a minute, followed by from twenty to thirty respirations—the first shallow, the next deeper, the next still deeper, and finally the remainder again shallow, each successive respiration being slightly deeper in the first half of the series, and slightly shallower in the second half. In the lower animals, when respiration becomes periodic, there is an absence of the ascending series, that is, of those in which the respirations become deeper and deeper. This form of respiration is the type of breathing in hybernation. The long pause is not due to a diminished excitability of the respiratory centre, as respiratory movements may be liberated in the time of the pause by stimulating the skin, thus exciting reflex breathing. It has also been observed that during the pause in the Cheyne-Stokes' breathing of man, respiratory movements may be excited by addressing the patient and arousing his attention. Division of the vagi at once causes periodic breathing to disappear, and in its place there are irregular respiratory spasms. It is clear, therefore, that periodic breathing occurs when the upper nervous tracts are inactive and when, in these circumstances, the vagi convey impressions to the respiratory centre. Hence it is that the Cheyne-Stokes' phenomenon appears when the higher nervous centres are totally or partially inactive, or, at all events, when the upper tracts are not conveying impressions downwards.

2. We have next to consider the influence of the *glosso-pharyngeal* nerves. Division of the glosso-pharyngeal nerves does not alter the respiratory movements, nor has division of the nerves before or after division of the vagi any effect. Marckwald has ascertained that stimulation of the nerves arrests respiration for a time equal to that occupied by the three preceding respirations, and then breathing begins with an inspiration which starts from the position occupied by the diaphragm at the moment of arrest. This nerve may therefore be regarded as an inhibitory nerve of breathing, and it comes into play in this manner at the beginning of deglutition. It is well known, from the experiments of Kronecker and Meltzer, that in the mechanism of deglutition, the centre of which is in the *medulla oblongata*, there is first a stimulation and then an inhibition of the mechanism. The stimulation is excited by the sensory nerves of the tongue, mouth, and pharynx, other than the glosso-pharyngeal, and the inhibition is brought about by the action of fibres in the glosso-pharyngeal. The object gained by the inhibitory action of the glosso-pharyngeal in swallowing is that it makes it possible to have a number of swallowing movements in quick succession, as in drinking. If it did not come into play, the stimuli transmitted by the sensory nerves would so excite the centre of deglutition as to cause a spasm of the muscles of deglutition, but the centre is excited for a time sufficient to excite the mylo-hyoid muscles, which are the muscles brought into action in the first stage of deglutition, and then it is at once and momentarily inhibited. But it is well known that during deglutition breathing is arrested, although it is only lately, and more especially by the researches of Marckwald, that the nervous mechanism by which this is accomplished has been made apparent. If breathing were not arrested during deglutition, it is evident that there would be a risk of foreign matters being aspirated into the lungs. This is prevented, however, by the *glosso-pharyngei* inhibiting the respiratory centre, and thus there is a short stoppage of breathing during swallowing. The exact mechanism appears to be that nervous currents irradiate from the centre of deglutition to the centre of respiration which arouse an inspiratory movement, but this is at once inhibited by the glosso-pharyngeal, so the so-called "breathing of swallowing" consists of a remarkably short inspiration, followed by a longer period of inhibition. When the bolus or fluid has passed down the œsophagus, so that all danger of its entering the glottis is over, then the inhibition ceases, and breathing goes on as before.

3. Influences passing along the *vagi* have an important action on the respiratory centre. After separating the *medulla oblongata* from the

upper centres, if the *vagi* are cut, there is a prolonged inspiratory spasm, then irregular spasms of the muscles of inspiration and expiration, and death soon occurs. On the other hand, if the *vagi* are divided first, the respirations are regular in rhythm, but slower and deeper, with some dyspnœa, and if the *medulla oblongata* is then divided, respiratory spasms immediately come on, as in the last experiment. It is evident therefore that impressions passing from the brain to the respiratory centre can compensate for the absence of impressions passing upwards by the *vagi*, and *vice versâ*. Cut off the influence of the one set of impressions and the centre is not affected as to rhythmic action; cut off the remaining set and its action at once becomes unrhythmical. Both then, *vagi* and upper tracts, are the channels of influences which are the regulators of respiratory rhythm, but the difference between them is that influences are constantly passing along the *vagi* while they are intermittent along the upper tracts. Along the latter flow impressions called forth by volition, emotion, intellectual action, and the strong stimulation of the organs of special sense. Along the *vagi* flow impressions from the lungs which tend to liberate rhythmical movements. This view of the action of the *vagus* is supported by the results, arrived at by stimulation of its trunk below the origin of the superior laryngeal branch. Traube first showed that stimulation of the *vagus* in the neck caused deep inspirations, and that a tetanic condition of the muscles of inspiration may be induced if the irritations are strong, and it was accordingly concluded that the *vagus* contained inspiratory fibres. Other observers, however, have found that expirations were frequently produced, and they were obliged to assume that the *vagus* contained expiratory as well as inspiratory fibres. The discrepancy in the evidence on this matter has been removed by Marckwald, who finds that irritation of the *vagus* may liberate sometimes an inspiratory and sometimes an expiratory movement, according to the moment in the rhythm of the respiratory movement that the stimulus is applied. He agrees with Traube in holding that when expirations occur they are due to the stimulation of sensory nerves causing pain, but he differs from him in asserting that the vagus contains no inspiratory fibres in the sense of fibres, the stimulation of which normally liberates inspirations. Marckwald's view is that the respiratory centre is automatically active, but when not influenced by the *vagus* it only liberates respiratory spasms. The impressions passing along the *vagi* fibres so stimulate the respiratory centre as to cause rhythmic discharges of nervous energy by which both inspiratory and expiratory movements are effected. The vagus is in constant stimulation, that is, impressions are constantly flowing along its fibres from the lungs to the respiratory centre and rhythmic discharges are the result. According to this view, the vagus acts on the respiratory centre as a discharger which prevents the tension in the respiratory centre increasing beyond a certain limit. Thus the respiratory centre in the *medulla oblongata* is influenced from above by the upper tracts and from below by the *vagi.*

From the *vagi*, sensory branches pass to the larynx termed the *superior laryngeal* nerves. Rosenthal found that stimulation of these causes expirations, and, if the stimulation is sufficiently strong, there is stoppage of respiration with tetanus of the expiratory muscles. With a weak stimulation, we find slowing of respiration and a lengthening of the pause, and with stronger shocks there is arrest of respiration in a position of expiration. The superior laryngeal nerves appear to be true nerves of expiration, and they differ in their action from the sensory nerves of the skin in acting as expiratory nerves, even when the *medulla oblongata* has been severed from the upper parts of the brain, while, in these circumstances irritation of the nerves of the skin always excites inspirations. They act only occasionally when irritation is applied to the mucous membrane of the larynx, and they have not a constant influence like that of the *vagi.*

4. The respiratory centre in the *medulla oblongata* is also influenced by impressions transmitted to it along the *sensory nerves of the skin.* Gentle irritation of a sensory nerve has no marked influence, but if the irritation is so strong as to cause pain, there is quickening of the respiratory movements and a tendency to inspirations and the stoppage of expirations. Sprinkling the face or chest with cold water, slapping the chest with a wet towel, plunging into a cold bath, all excite inspirations by stimulating the sensory nerves of the skin. These are reflex influences, and they are more marked when the *medulla oblongata* has been divided above the respiratory centre. Irritation of the *splanchnic nerves* causes strong expirations, and irritation of the abdominal branches of the *vagi* also causes expirations. These influences, however, are not constant, and they affect the rhythm of the respiratory movements only occasionally.

5. The respiratory centre is also influenced by the *gases in the blood* circulating through it. The first to recognize this kind of influence was Marshall Hall, who supposed that the accumulation of carbonic acid in the venous blood carried to the lungs excited the pulmonary branches of the *vagi* and thus caused an inspiration. Volkmann extended the influence of the carbonic acid to the sensory nerves in all parts of the

body. Valentin supposed that the cause of inspiration was not the carbonic acid in the blood circulating through the *medulla oblongata*, but the deficiency of oxygen, a view also supported, at a later date, by Rosenthal. Traube, again, was in favour of the carbonic acid being the stimulating agent. Rosenthal's theory was that the activity of the respiratory centre depended on the presence of oxygen in the blood flowing through it, and that the nerves modified the impulses emanating from the centre. According to this view, the pulmonary branches of the vagus conveyed influences which favoured inspiratory movements by diminishing the tension supposed to exist in the nerve centre, while the branches of the superior laryngeal increased the tension and favoured expirations. Lastly, it has been established by Pflüger that both deficiency of oxygen and excess of carbonic acid excite the respiratory centre—blood poor in oxygen causing inspirations, and blood rich in carbonic acid causing expirations. These theories of respiration are all founded on the supposition that the exciting cause of the respiration movements is the gases in the blood circulating through the centre. As opposed to this chemical explanation, we have a mechanical theory, advocated chiefly by Schiff, Hering, and Breuer, that the mechanical distension of the lungs in inspiration irritates fibres of the *vagi*, which carry impressions to the centre and excite expiration, while collapse of the lungs in expiration, by irritating other fibres, so excites the centre as to call forth inspiration. This view cannot be correct, because the movements of respiration may continue after removal of the lungs themselves. Lastly, Gad holds that the pulmonary branches of the vagus, when the lungs are distended, inhibit the centre and thus allow an expiration to follow.

Considering these various and contradictory theories, the question arises as to which is best supported by experimental evidence. The fact that the saturation of the blood with oxygen produces apnœa appears at first sight to support Rosenthal's view that the deficiency of oxygen in the blood is the cause of inspiration; but it is contradicted by the observation that the blood of an apnœic animal may contain less and not more oxygen than that of a normally breathing animal. It is also a point to be noted that it is difficult to produce apnœa in an animal in which the *vagi* have been divided, and when it is produced in these circumstances it lasts only for a short time. This appears to be irreconcilable with the view that apnœa is caused by excess of oxygen in the blood in the *medulla oblongata*, because one cannot see how division of the *vagi* can influence the circulation in the medulla. The theory urged by Marckwald is the most tenable. It may be expressed thus:—With some modifications, the normal stimulation of the respiratory centre does not depend either on deficiency of oxygen or on excess of carbonic acid, as animals, such as a hybernating marmot, may be eviscerated and still the movements of respiration go on breathing even without a circulation. Breathing continues also after profuse hæmorrhage. The centre works for a time, like the isolated heart, nourished by its interstitial fluids. When anabolism reaches a certain point, the molecular structure of the protoplasm gives way (katabolism) with the result of the liberation of a series of impulses that causes a respiratory spasm. Then these katabolic changes are succeeded by another series of anabolic changes, and so on, each splitting up of the protoplasm being attended by a molecular discharge. The nerve filaments specially influencing katabolism are the pulmonary branches of the vagi, and by their constant effect they prevent respiratory spasm, and cause rhythmic discharges. If anabolism is arrested, then we have apnœa, hence it is that this condition is brought on with difficulty after division of the *vagi*, because these nerves bring about the katabolism on which respiratory movements depend.

The respiratory centre, as we have seen, is sometimes influenced by impressions reaching it by other nerves. These conclusions may be summarized as follows:—

1. Upper brain tracts. Liberate rhythmic movements, like the *vagi*, whose action they may replace.
2. If the upper brain tracts are at rest, while the *vagi* act alone, we have the Cheyne-Stokes' breathing.
3. The pulmonary branches of the *vagi* act continuously, and they are the chief regulators of breathing.
4. The sensory nerves of the skin, by reflex action, excite respiratory movements, but they cannot replace the action of the *vagi* and of the upper tracts.
5. The fifth cranial nerve, the superior laryngeals, and the glosso-pharyngeal nerves, act occasionally as inhibitory nerves of respiration. They do not act in normal respiration.
6. The fifth cranial nerves, the superior laryngeals, the olfactories, and the splanchnics slow respiration and stop it in the state of expiration.

As already stated, many observers have stimulated the *medulla oblongata* directly, and certain peculiar forms of dyspnœa have been observed. In Fig. 197 we see a curve of the movements of the diaphragm of a rabbit when a little common salt was placed on the cut surface of the *medulla oblongata*. The respirations become very quick and irregular, and at the same time larger waves occur, on which the respirations appear as teeth, so that the diaphragm is quivering and at the same time making a considerable excursion. This condition has been called *common salt dyspnœa*. By cooling the *medulla oblongata* to −5° C., Marckwald found similar quiverings of the diaphragm, along with groups of larger movements, and when the *vagi* were cut, respiratory spasms appeared. This he terms *cold dyspnœa*. Finally, by warming the medulla, or passing heated blood through it, Gad and other observers have found irregular movements of the diaphragm. This condition has been termed *heat dyspnœa*. The important inference Marckwald draws from these observations is that probably fibres pass from the brain down the *medulla oblongata* and upper part of the cord to the phrenic nerves and thence to the diaphragm, and that probably by these fibres the diaphragm is partially under the control of the will or may be affected by psychical states.

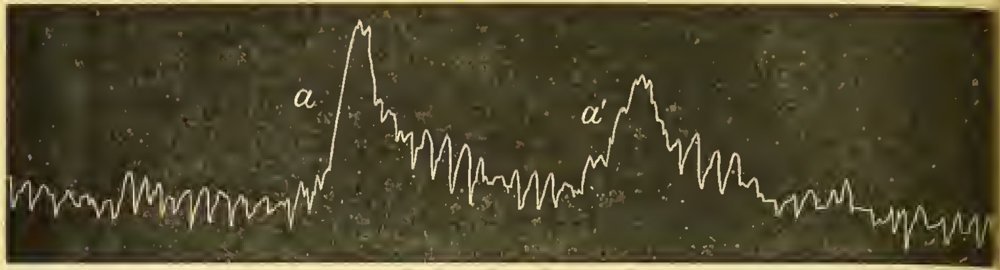

FIG. 197.—Movements of the diaphragm of a rabbit during direct stimulation of the *medulla oblongata* by common salt. At *a* and *a′* there are natural respiratory movements. (Marckwald.)

Anomalous Respiratory Movements.—Such movements as coughing, sneezing, laughing, moaning, etc., may be explained by a disturbance of the equilibrium between the exciting and inhibiting arrangements of the respiratory nervous mechanism. Thus, in *coughing*, usually arising from an irritation in the laryngeal passage, the irritating effect of the sensory filaments of the larynx reaches a certain intensity, there is then a deep inspiration, which is followed by sudden and strong expirations. *Sneezing* is produced in an analogous manner, but the irritation commences in the nasal passages. The other respiratory movements, such as laughing, groaning, sighing, yawning, etc., which frequently originate in psychical states, are associated with movements of the diaphragm. Thus, in laughing, there is a short inspiration, then a pause, and afterwards a rapid series of expiratory actions; in groaning or blowing the nose, the expiratory action is much more prolonged; and in sighing and yawning the inspiratory and expiratory actions are both prolonged and of about equal length.

SECTION VI.

ASSIMILATION OR NUTRITION.

Chap. I.—GENERAL STATEMENT.

Having studied the formation of blood, the mechanism by which it circulates through the body, and the arrangements by which it receives oxygen, and at the same time has carbonic acid removed, we have next to direct our attention to the exchanges taking place between the blood and the tissues. As has been already seen, every tissue is brought into close relation with the circulating blood by capillary arrangements. Any portion of living tissue may be regarded as being surrounded on all sides by capillaries in which a nutritious fluid is slowly flowing. In proportion to the activity of the tissue, the capillary plexus is more or less close and intricate. Thus, such tissues as constitute the grey matter of the brain or voluntary muscle are supplied with so rich a plexus of capillaries as to bring each portion of the tissue into almost immediate contact with the circulating blood. On the other hand, in cartilage, where vital phenomena occur with comparative slowness, the ultimate elements of the tissues exist at a considerable distance from the blood, and they are nourished by the transudation of fluids. In all tissues, however, matters are absorbed from the blood by the living protoplasmic elements. These matters may, under the influence of the tissue, either be converted into matter of the same nature as the tissue itself, be elaborated into more complex, or be split up into simpler, substances. For example, when a muscle works, chemical changes occur in it which lead to destruction or degradation of the protoplasm—the result being the formation of simpler chemical compounds. In this condition, the muscle is in a state of fatigue, which is recovered from when new materials are absorbed from the blood, and are used up in the renovation of the muscle-substance. Matters thus taken from the blood are converted into muscle-protoplasm. On the other hand, the protoplasm of a fat cell absorbs materials from the blood, which it elaborates into fat, either directly or indirectly, by first changing them into protoplasm and then into fat.

1. **Interstitial Phenomena in Nutrition.**—It was remarked by Claude Bernard, that the blood may be regarded as an *internal medium*, in relation to which all the phenomena of nutrition take place. It is in a state of perpetual change, receiving on the one hand new materials from the outer world, or from the tissues; and on the other, giving up, in addition to the matters returned to the outer world by the various excretory channels, substances required for the nutrition of the tissues. It receives new materials by various channels of absorption, and it gives up other matters by processes of elimination occurring in the lungs, skin, liver, kidneys, and bowels; and, as already mentioned, it supplies new materials to the tissues.

During its passage through the tissues, the blood gives up oxygen and matters required for their repair. Each tissue selects from these substances such as are required for its existence; but it need scarcely be said that this expression does not imply the existence of any special power in the tissues, but simply that in accordance with physical and chemical laws, when any tissue is brought into relation with nutritive matters, these combine with the tissue. This power has been termed the *selective affinity of the tissues.* The process by which nutritive matters pass from the blood to the tissues is physical, governed by the laws which regulate the passage of matters from a moving fluid through an organic membrane. In the capillaries, such matters pass through a thin organic wall. The rapidity of such diffusion will partly depend on the pressure of the blood in the capillaries, partly on the resistance offered by the tissues themselves, and partly on the pressure in the lymphatic channels. As to the rationale of the selective influence of the tissues, we are in ignorance. It is only known, for example, that a fat cell takes up materials to form fat, but the nature of the processes is still hidden.

The tissues also give up to the blood carbonic acid and waste matters. The proof of this statement is, that the blood returned from an active tissue contains an excess of these materials; but it is impossible to say whether the matters thus met with in the blood represent all the products of the tissue changes, inasmuch as there is another fluid, the lymph, conveyed from the tissues, in which some of the waste products are found. Thus each particle of living tissue gives up to, and receives from, the blood certain materials, and in particular each absorbs oxygen and eliminates carbonic acid. There is thus a true respiration of tissues, and each living element, from this point of view, behaves like a microscopic aquatic organism.

2. **Ultimate Changes in Nutrition.**—The ultimate phenomena of nutrition are grouped under the terms anabolism and katabolism. By anabolism is understood those changes by which the living tissues convert dead matter into matter similar to themselves; and by katabolism, we mean those changes by which living matter, of complex chemical constitution, is resolved into simpler forms, in consequence of the activity of the tissue.

ANABOLIC CHANGES IN THE TISSUES.

(*a*) **Origin of Albuminous Matters.**—All albuminates are derived from nitrogenous foods. It has already been seen that the various albuminous articles of food are converted by digestive processes into peptones, and these peptones are converted into the albumin of the blood. (See Vol. I. Chap. III. p. 5.)

(*b*) **Origin of Fats.**—The principal portion of the fats stored up in the body is derived from the fatty matters introduced in the food. In carnivora the greater portion of the fat is thus obtained; but in herbivora, and in many other animals, its appearance cannot thus be accounted for. Thus, bees form wax, a kind of fat, from saccharine substances obtained from flowers; and geese feeding on grain, which contains only a small amount of fat, store up large quantities of this substance. Dumas states that the Indian corn or maize on which a goose is fed contains 9 per cent. of fat, and on calculating the quantity consumed, he found less fat in it than was sufficient to explain the increased weight of the goose.

These conclusions were confirmed by the observations of Boussingault. Liebig made several experiments upon swine. He says that three pigs, to be fattened in thirteen weeks, require 1,000 lbs. of pease and 6,825 lbs. of boiled potatoes. These contain together 26 lbs. of fat—21 lbs. in the pease, and 5 lbs. in the potatoes. One fattened pig gives on an average 50 to 55 lbs. of fat—that is, the three together, 150 to 165 lbs. Each animal, before being fattened, contains, on an average, 18 lbs. of fat—that is, 54 lbs. for the three. If to these 54 lbs. we add 26 lbs. from the food, we get 80 lbs.; and if we subtract these from 150 lbs. to 165 lbs., there is a remainder of 70 to 85 lbs. of fat produced from the starch, etc., contained in the food. These experiments have been confirmed by the researches of Lawes and Gilbert, who found that, in fattening pigs, for every 100 parts of fat in the food, the animals stored up from 400 to 450 parts of fat in their bodies.

It is evident, therefore, that fats may be formed from other substances than the fat introduced in the food. Liebig suggested the theory that they were derived from carbohydrates. Chemists have, as yet, found it impossible to transform carbohydrates into fats. On the other hand, the carbohydrates may not contribute directly to the formation of fat, but indirectly, by assisting in the decomposition of albuminates (p. 30).

It is now generally accepted by physiologists that a considerable part of the fat of the body is formed from albuminates. This view is supported by various well-known facts. Thus, when albuminous tissues in the dead body are subjected to the action of water, a fatty substance called *adipocere* is frequently formed. Animals have also been fattened on a diet of pure casein. Pettenkofer and Voit have shown that, after a flesh diet, all the nitrogen appears in the excretions, whilst a proportion of the carbon is retained in the organism; entering, probably, into the formation of fat (p. 30). Further, any albuminous substance may be supposed capable of being decomposed into a nitrogenous portion of simpler constitution, and into a non-nitrogenous residue, which may become transformed into fat.

There are thus evidently two sources of fat: (1) the fat contained in the food, and (2) from transformations in the albuminous matters of food. The part played by the carbohydrates is to combine with a certain quantity of oxygen, forming carbonic acid and water, thus preventing oxidation of the non-nitrogenous residue already alluded to, as proceeding from decomposition of albuminates. It is well known that such circumstances as hinder the decomposition of nitrogenous tissues and interfere with processes of oxidation (a small amount of muscular exercise and breathing a vitiated atmosphere) favour the formation of fat.

When the amount of fat in the body passes a certain limit, the condition is termed *obesity*. To remove this state, it is necessary to attend to the following points: (1) no fat should be taken in the food; (2) active muscular exercise should be indulged in for the purpose of increasing oxidation processes; and (3) no carbohydrates, but only albuminates, in the form of lean meat, should be taken, so as to allow the oxygen introduced in respiration to attack the non-nitrogenous residue produced by the decomposition of the albuminates, and thus prevent the formation of fat.

KATABOLIC CHANGES IN THE TISSUES.

These are carried on in the presence of oxygen, and we must therefore assume, that one of the first steps is the liberation of oxygen from oxyhæmoglobin. The oxygen thus liberated enters into combination with certain of the elements of the tissues, so as to produce numerous chemical compounds; and, as the result of this union, energy is set free under various forms, such as heat, movement, etc. Activity of tissue is always associated with the production of simpler chemical compounds than existed in the tissue itself. The chemical nature of the substances thus formed has already been described in Vol. I. Sect. I., treating of the chemistry of the tissues, and the physiological processes by which they are formed are discussed in relation to the various organs.

CHAP. II.—CONDITIONS OF HEALTHY NUTRITION.

The conditions of healthy nutrition are as follows:—

1. **A Proper Supply of Blood.**—If the principal vessel of a limb is ligatured, the limb becomes cold and powerless until the circulation is re-established through collateral vessels; but if the supply of blood is entirely cut off suddenly, as by ligaturing all the vessels, moist gangrene soon appears; if more slowly and gradually, by pathological changes in the vessels, dry gangrene is the result, as may be seen in the senile gangrene of aged people, or in the form caused by the action of ergot of rye. On the other hand, actively-growing parts have always a rich supply of blood.

2. **A Proper Quality of Blood.**—As already explained, this implies that all the processes of nutrition are properly performed. If one of these processes is disturbed, the nutrition of the body as a whole, or of an organ of the body, is affected. By the due performance of all of these processes, the blood is maintained in a healthy state. It is remarkable that, in a vigorous individual, if the blood becomes vitiated, there is an effort on the part of the various excretory organs to get rid of the noxious matter. Thus, during the course of fevers, and more especially in what physicians have long recognized as the *critical stage*, or *crisis*, there may be diarrhœa, profuse diaphoresis or sweating, epistaxis, or bleeding at the nose, or the appearance of large quantities of urates in the urine, after which the individual may proceed towards recovery. Paget has pointed out interesting examples of how the nutritive changes occurring in one organ may affect the whole body. Thus, the development of the beard in men, of the mammæ in women, and the changes in form more or less of the whole body, are examples of nutritive changes associated with the appearance of the capacity for reproduction at the age of puberty, indicating that there is a correlation between the nutrition of the reproductive organs and of other parts o the body. The same fact is illustrated by what is seen in the lower animals. Thus, in the majority, the two sexes are alike until the time of puberty, when a divergence occurs, as may be seen in the greater

size of the male, and in the development of various epidermic appendages, such as the mane of the lion, the comb of the common cock, and the magnificent tail feathers of many birds. These facts have been included under the term *complemental nutrition*, the idea being, that the nutrition of one part is the complement of the other, and is intimately associated with it.

It would appear also that all tissues are liable to the two following influences: (1) if the nutrition of a tissue is affected by an external influence, such as the action of the vaccine virus, or the poison of any of the eruptive fevers (small-pox, scarlet fever, measles), the nature of the tissue is so profoundly altered as to give it an immunity from the action of the virus for a considerable time; and (2) that a tissue so altered tends slowly to revert to its original condition, just as a reversion to some ancestral form may be observed in artificial races of pigeons and dogs. These views afford a rational explanation of the influence exerted by vaccination over the body, an influence so profound as to secure the individual against an attack of unmodified small-pox for sixteen or seventeen years, beyond which time, however, the tissues slowly return to their original state.

Again, if we consider the phenomena of nutrition as consisting essentially of molecular changes, it is necessary to assume, as an explanation of the persistence of form for perhaps many years, that each living element of tissue so operates upon the nutritive matter brought to it by the blood, as to convert it into matter almost precisely similar to itself. Thus, we may conceive particle by particle removed, and the edifice still having the same form, inasmuch as fresh particles precisely similar are introduced. But it is significant that slow changes do occur. A tissue apparently is not kept in exactly the same condition for any length of time. During the early period of life, it advances to a condition of greater strength and higher vitality; but afterwards, when a maximum has been reached, it slowly retrogrades until the tissues of old age are unlike those of youth.

3. **A Healthy State of the Tissue itself.**—A healthy tissue will continue in this state unless a strong influence be exerted upon it. If it becomes what we term unhealthy, that is, if nutritive changes of a different kind or of a different intensity are induced, this morbid condition also tends to become perpetuated. Thus we may explain the persistence of tumours, either simple or what are called malignant, and the inveteracy of many diseases of the skin. But even in pathological conditions, the same law of a tendency of a reversion to what may be called the normal type may be observed.

4. **A certain Influence of the Nervous System.**—Section of a motor nerve is followed by wasting of the muscles supplied by it. Section of a nerve supplying the blood-vessels of an area of mucous membrane or of skin causes ulceration and destruction of the part. The limbs of the paralytic waste, unless the muscles are frequently artificially excited to contract. These facts show the influence of the spinal cord and motor portions of the nervous system; but it is not easy to account for the well-known influence of psychical conditions. There is scarcely an organ of the body the functions of which may not be more or less affected by various conditions of the mind. Thus joy or sorrow, a light heart or a mind brooding with anxiety, exercises an influence over the nutrition of the body. As a rule, a contented and happy frame of mind and freedom from care favour nutrition, whilst worry or melancholy diminishes it. Again, hope and confidence seem to be favourable towards recovery even from serious diseases, but fear and foreboding of evil may aggravate even simple maladies and tend to make dangerous ones fatal.

Growth.—Growth may be either special or general. Thus we may have growth of a particular organ, as the increase in the size of the uterus during pregnancy, or the increase in the size of the muscles of the arm following severe but regular muscular exercise. When growth is limited, it may be termed *hypertrophy*, or increase of growth, as opposed to *atrophy*, or diminution. Again, growth may be general, affecting not one tissue or one organ, but the whole body, as occurs in early life. Regarding nutrition as consisting essentially of processes of anabolism and katabolism, it will be seen that when the former is in excess there is growth; when both are equal, there is cessation of growth; and when the second is in excess, there is wasting.

From the histological point of view, growth may consist: (1) of an increase in the volume of tissues already existing; (2) of the development of the elements of other tissues which previously existed in an undeveloped state; and (3) of both of these changes. Thus, the walls of the uterus, in the virgin state, are thin and contain only a comparatively small number of involuntary fibres. During pregnancy, however, numerous fibres are probably produced from nucleated protoplasms hitherto in an undeveloped state, so that the wall of the organ becomes thick and powerful. The same phenomenon, though to a less degree, occurs in voluntary muscle (see vol. I. p. 433).

The following conditions favour growth: (1) activity; (2) increased supply of blood; (3) integrity of the nervous system. The mode of growth termed *secretion* has already been described (Vol. I. p. 297, and Vol. II. p. 35).

SECTION VII.

GLYCOGENESIS.

The phenomena of nutrition are intimately related with the formation by the liver of a substance called *glycogen*, and with the changes which it undergoes in the tissues. The first step towards the discovery of this function of the liver was made in 1848 by Claude Bernard when he ascertained that a considerable quantity of sugar exists in the liver after death. He completed the discovery in 1857 by showing that during life a substance of the nature of a carbohydrate, named *glycogen*, is formed in the liver, and that this is readily changed into sugar by the action of a diastatic ferment.

In 1858, Pavy demonstrated that if the liver be examined as quickly as possible after death, only glycogen will be found, with occasionally a mere trace of sugar. He also found that the blood of the hepatic vein is not richer in sugar than that of the portal vein, and thus doubt was thrown on Claude Bernard's view that the glycogen is changed into sugar in the liver. MacDonnell made the important observation that glycogen abounds in young, actively growing, embryonic tissues.

1. *Nature of Glycogen.*—If the liver is quickly removed from the body of a well nourished animal during digestion, cut in pieces, and thrown into boiling water, the morsels become in a few minutes firm and crisp, and an opalescent or yellowish brown solution is obtained. The solution contains glycogen, named by Pavy, *Bernardin*, in honour of its discoverer. The methods by which the substance may be obtained from this solution, and its general characters, are described in Vol. I. p. 160. It is a carbohydrate, having the general formula $n\ (C_6H_{10}O_5)$, and it is quickly changed into sugar by the action of dilute mineral acids and by the ferments of the saliva and of pancreatic juice.

The amount of glycogen in the liver has been found to vary in different species of animals. Thus, according to MacDonnell—

	Ratio of weight of body to weight of liver.		Percentage of Glycogen.
Dog,	30·1	...	4·5
Cat,	19·1	...	1·5
Rabbit,	35·1	...	3·7
Guinea-pig,	21·1	...	1·4
Rat,	26·1	...	2·5
Pigeon,	44·1	...	2·5

Glycogen has also been found in the liver of invertebrate animals. It exists in greatest amount two or three hours after a full meal, and it is diminished by fasting. Prolonged fasting may cause its disappearance from the liver, in dogs after fourteen to eighteen days, and in rabbits after five days. After death, it quickly disappears, being converted into glucose.

2. *Origin of Glycogen.*—The amount of glycogen formed is influenced by the nature of the food. Carbohydrates are converted by the digestive fluid into maltose, and the maltose passes into the portal system. In the hepatic cells, a dehydration occurs, with the result of forming glycogen. Thus—

$$\underset{\text{Maltose.}}{C_6H_{12}O_6} - H_2O = \underset{\text{Glycogen.}}{C_6H_{10}O_5}$$

Bernard found that the injection of glucose into the portal vein is followed by an increased formation of glycogen. Starch, grape sugar, cane sugar, fruit sugar, and milk sugar in the food increased the formation of glycogen by the liver. But the substance may be produced even after the careful exclusion of all carbohydrates from the food, and in all probability it is then formed from proteid matters. The injection of albumin into the stomach is followed by no increase; but Claude Bernard and Kühne hold that in the liver albuminous matters may split up into a nitrogenous portion—possibly urea—and a non-nitrogenous portion, which may become glycogen. This is illustrated by the following comparative analysis :—

	Albumin.	Urea.	Non-nitrogenous residue.
Carbon,	53·50	6·64	46·86.
Hydrogen,	7·00	2·21	4·79.
Nitrogen,	15·50	15·5	—
Oxygen,	22·00	8·85	13·15.
Sulphur,	1·60	—	1·60.
Phosphorus,	0·40	—	0·40.
	100	33·20	66·80
		100	

But a small amount of glycogen may be formed even during complete starvation. It would thus appear that glycogen may be formed independently of matters furnished from the alimentary canal. The presence of glycocin in one of the bile acids (glycocholic) has suggested to Kühne and Heynsius the notion that it may split up into urea and glucose, the latter being afterwards converted into glycogen; and they have found that the introduction of glycocin directly into the blood is followed by an increase in the amount of urea in the liver and urine, and of glycogen in the liver.

The statement on which there is no uncertainty is, that carbohydrates are the bodies from which glycogen is chiefly formed. By their conversion into glycogen, highly soluble carbohydrates are changed into a less soluble carbohydrate, which is stored up in the cells of the liver, to be used by certain of the tissues of the rest of the body during periods when these cannot receive fresh supplies of nutritious matter from the alimentary canal. The consumption of carbohydrate matter by the tissues will also save the consumption of such nutritious matters as albumin and fats.

3. *Sugar of the Liver.*—If a few morsels of liver, an hour or two after the death of the animal, be thrown into boiling water, so as to make an infusion, and the infusion be tested for sugar, it will be found that a large amount of this substance is present. A still more satisfactory demonstration may be obtained by introducing the nozzle of a syringe into the portal vein, so as to wash out the liver with cold water—the washings being collected at intervals from the hepatic vein. On testing the washings, it will be found that the first portions contain a large amount of sugar, and that the amount diminishes in each successive portion, until no reaction is obtained. If, however, the operation be repeated two hours afterwards, the presence of sugar will be again indicated. As a rule, a perfectly fresh liver, that is, one removed quickly from an animal just killed, and thrown into boiling water, shows only faint traces of sugar; but if it be left for even a few minutes at a temperature of 15·5° C., sugar is present in abundance. Immediately after death, there is apparently a rapid transformation of glycogen into sugar. Thus, Dalton found 1·8 of sugar per 1,000 after five seconds, 6·8 after fifteen minutes, and 10·3 after an hour. Pavy in his earlier writings held that the formation of sugar is a post-mortem phenomenon, and that it never exists during life; a view which was contested by Claude Bernard. Another view, urged by Seegen, is that there is a true liver sugar, distinct from the sugar derived from glycogen. He has always found about ·5 per cent. of sugar in infusion of fresh liver, whatever the nature of the diet may have been, and he states that after death sugar undoubtedly increases, but not at the expense of the glycogen present. Further, this sugar, according to Seegen, does not disappear even although the animal be starved or fed entirely on fatty food, and he holds that *liver sugar* is formed from peptones, for after feeding with peptones, its amount is increased three-fold. He found also that in the experiment the blood of the portal vein contained ·13 per cent. of sugar, while that of the hepatic vein contained ·25 per cent. and the blood of the carotid artery and crural artery showed only ·15 per cent.

Bernard showed that even in the living animal, whilst the blood of the portal vein gives no trace of sugar, the blood of the hepatic vein contains a small quantity. The fact appears to be that during life a very minute quantity may be present, and that the amount increases rapidly after death. The author, in class demonstrations, has found it impossible to prove to students the entire absence of sugar from a perfectly fresh liver.

More recently, by the use of his gravimetric process (Vol. I. p. 156), Pavy obtained quantities of sugar from the liver taken at the moment of death, varying from ·056 to ·545 per 1000 in the cat, from ·069 to ·597 in the rabbit, and ·315 in the dog.

4. *Transformation of Glycogen into Sugar.*—In 1857, Claude Bernard showed that glycogen is transformed in the liver into glucose under the influence of a ferment which exists in the liver itself. He also pointed out that the transformation is at once arrested by plunging the liver into water at 100° C. or into water at 0° C.; and he explained these facts by stating that the extremes of heat and cold coagulated, or otherwise changed, the fermentive matter. The isolation of this ferment presented great difficulties, but Bernard succeeded in extracting it from the liver by Von Wittich's glycerine process. It is interesting also to find that he proved the identity as regards chemical activity between the ferment thus separated from the liver and the diastase of germinating grain. Thus, Claude Bernard has discovered another point of resemblance between animal and vegetable organisms. He was the first to show that a substance similar to starch was formed in the animal body; and he completed his labours by demonstrating the existence in the animal body of a fermentive matter similar to that which converts the starch of the germinating grain into sugar.

Glycerine-extracts of liver readily convert starch into sugar, and glycerine-extracts of other organs, such as lung, brain, spleen, and muscle, have sometimes the same effect, though to a feebler degree. The extract of muscle rarely fails. These observations indicate that the ferment may exist in other organs than the liver.

5. *Sugar in the Blood.*—The presence of sugar in the blood of diabetic patients has been long known, but its relation to the glycogenic function of the liver was first pointed out by Claude Bernard. If a dog be fed with flesh free from sugar, whilst the blood of the portal vein will contain no sugar, some will be found in that of the hepatic vein, the inferior vena cava, the right heart, and the arterial system generally. In this case, therefore, the sugar does not disappear in the lungs, but in the capillary system. On the other hand, if the diet supplies a

considerable quantity of maltose, it is absorbed, and is found in variable amount in the portal vein. Sometimes even the amount in the portal vein is greater than in the hepatic vein, but the amount in the general system of vessels is not proportionately increased. Thus it would appear that the amount of sugar in the portal vein depends on the nature of food, whilst the amount in the hepatic veins and general system depends on the activity of the liver. Claude Bernard has found ·9 per 1,000 in the blood of man, 1·7 in the ox, ·99 in the calf, and ·91 in the horse.

By the employment of his gravimetric method, Pavy obtained the following quantities per 1,000:—Dog's blood, ·787; sheep's blood, ·521; and bullock's blood, ·543. Pavy also gives the following important figures:—In dog's blood, immediately after death, mean in arterial blood from ·795 to ·926 per 1,000; the mean in venous blood from ·792 to ·900; and in dog's blood collected during life, arterial ·941, and venous ·938, showing an excess in arterial blood of ·003.

When the amount is largely increased, it is separated by the kidneys and the state is known as glycosuria or diabetes. Pavy found in the blood of a fever patient suffering from diabetes amounts ranging from 1·543 to 5·763 per 1,000, the minimum being reached when the patient had a restricted diet, containing only a small amount of carbohydrate.[1]

The quantity of sugar produced in such cases is sometimes very great. For example, in one of Pavy's cases, in which the blood contained 5·763 per 1,000, no less than 751·6 grms. (10,600 grains) were eliminated by the kidneys in twenty-four hours, and even in the case containing 1·543 per 1,000 of sugar in the blood, the quantity in the urine was 27·9 grms. (431 grains) in twenty-four hours. Even in the highest case, the amount of sugar in the blood was only a little more than ·5 per cent.; but so great is the quantity of blood passing through the liver in a given time, that if the amount of sugar in the blood of the hepatic vein is increased by only ·1 per cent., from 100 to 200 grms. of sugar will pass into the general circulation.

6. *Transformation of the Sugar in the Blood.*—It was at one time supposed that the sugar entirely disappeared by oxidation in the lungs, a view which was apparently supported by the anatomical arrangements, and by the fact that glucose (maltose) is very oxidizable, more especially in an alkaline fluid, such as the blood. But it is negatived by the fact that the quantity of sugar in the blood of the left heart is not less than that in the right heart, and that sugar is also found more or less in the blood of all tissues, and especially in muscles. Glycogen is also found in muscle, but the muscle may be contractile although glycogen is absent. Nasse has found as much as 1 per cent. in mam-

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[1] F. W. Pavy. *Croonian Lectures on Diabetes.* 1878.

malian muscle, and ·4 per cent. has been found in frog's muscle. Even after starvation, muscle may still contain a store of glycogen. On the other hand, as shown by Külz, muscular action uses up the store of glycogen in the liver itself. Muscular contractions are accompanied by a gradual diminution of the glycogen or sugar in the muscle. Physiologists generally are now of opinion that the glycogen first changed into sugar is used up in the muscles, and that it is one of the substances required for the upbuilding of the contractile substance. The appearance of diabetes during the action of curare, which completely paralyses all voluntary muscles, has been accounted for by supposing that the inactive muscles do not consume the sugar supplied to them, and that consequently this substance accumulates in such quantities in the blood as to be eliminated by the kidneys. This, however, is a doubtful explanation, and the appearance of glycosuria might be accounted for by the curare causing vaso-motor paralysis. As regards the rôle of sugar in supporting animal heat, no satisfactory evidence has yet been afforded, the only experimental fact being the alleged fall of temperature in animals from which, by a strict diet, all external supplies of carbohydrates have been cut off. Finally, it is not at all improbable that a portion of the glycogen or sugar may contribute to the upbuilding or histogenesis of tissues, a statement which is supported by the well-known fact that these substances abound in embryonic tissue, where histogenetic changes occur with great rapidity.

7. *Relation of the Nervous System to Glycogenesis.*—Claude Bernard was the first to point out that a puncture of the floor of the fourth ventricle, at the origin of the pneumogastric nerves, produced temporary diabetes, that is, the appearance of sugar in the urine. The seat of the puncture (*la piqûre*) is shown in Fig. 198.

After the operation, the vessels of the liver are dilated and engorged with blood. There appears to be a vaso-motor paralysis in the liver. Diabetes has also been observed to follow injury of the cerebral lobes in man, of the cerebellum, of the cerebral peduncles, *pons Varolii*, middle peduncle of the cerebellum, and of the cervical sympathetic cord and sciatic nerve.

FIG. 198.—Posterior view of the *medulla oblongata* and part of the cerebellum of a rabbit, *a*, situation of the puncture followed by diabetes.

As has already been seen in studying the innervation of blood-vessels, p. 291, the vaso-motor centre from which constant stimuli pass to all the vessels of the body, so as to keep these in a state of moderate contraction, is situated in the *medulla oblongata.* The vaso-motor fibres for the liver pass from the centre down the spinal cord for a certain distance, issue thence into the sympathetic, and by it through the splanchnics to the liver. Cyon and Aladoff state that they leave the cord by fibres which accompany the vertebral artery, passing in them to the lower cervical ganglion. Thence they proceed in two bundles, one of which passes on either side of the subclavian artery, forming the *annulus of Vieussens*, to the first dorsal ganglion, and thence through the gangliated cord of the sympathetic to the cœliac ganglion, and along the hepatic vessels to the liver. If these nerves be divided at any point, it is evident that vasomotor paralysis will occur in the liver, the vessels dilate, the flow of blood through the liver is increased, and there may be an increased production of sugar. It appears that section of the sympathetic cord between the tenth and twelfth ribs, and section of the splanchnics, may be performed without sugar appearing in the urine, a somewhat perplexing fact which has received an explanation from Cyon. This explanation is thus given in the words of Lauder Brunton:

> "It is not mere dilatation of the hepatic vessels, but increased circulation through them, which accelerates the formation of sugar; and the width of the vessels is of little consequence unless there be sufficient blood to fill them. Now, the vessels of the intestine, especially when the digestive canal is long, as it is in rabbits, are so capacious that, when dilated, they can hold as much blood as all the rest of the vascular system put together, and their vasomotor nerves are also contained in the lower part of the cord and in the splanchnics. Consequently, when these are divided, the vaso-motor nerves of the intestine become paralysed as well as the hepatic ones, the vessels themselves dilate, and retain so much blood that there is not left enough to increase the flow of blood through the liver, even though its vessels may be standing wide open to receive it. But if the vessels of the liver be first dilated, and the cord and splanchnics be then cut, the formation of sugar is not arrested; for the liver, having once a brisk circulation established in it, keeps it up, although the intestinal vessels may have become dilated."[1]

It is evident also that the hepatic vessels may become dilated not only by direct interference with the vaso-motor centre, but by an inhibitory effect on this centre exercised by sensory nerves. Thus if the pneumogastric is cut in the neck, stimulation of the lower end produces no effect on the liver; but if the upper end is irritated, the vessels of the liver dilate, the circulation increases, and sugar appears in the urine. This is to be explained by certain fibres of the pneumogastric exercising an inhibitory influence over the vaso-motor centre. The hepatic

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[1] T. Lauder Brunton, Lecture, *Brit. Med. Jour.* 1874, p. 40.

vessels may also be reflexly dilated by irritation applied to the vagus, either at its ends in the lungs, liver, or intestine, in its trunk or at its roots in the medulla, or to the cerebrum, cerebellum, pons, and probably some of the sympathetic ganglia. Any marked increase in blood pressure affecting the vessels of the liver may cause increased production of sugar, and its appearance in the urine. Interference with the vaso-motor centre or nerves will chiefly affect the calibre of the hepatic artery, which becomes dilated. As this is followed by increased production of sugar, the inference is that the blood of the hepatic artery may carry to the liver the materials for forming the glycogenic ferment. Another view, first suggested by Pavy in 1875, is that blood rich in oxygen, or in other words, arterial blood, when passed through the liver in larger quantities than normal, causes glycosuria. He found that the injection of defibrinated arterial blood into the portal vein was followed by the appearance of sugar in the urine, and he supposes that "blood, either unnaturally charged with oxygen or impregnated with carbonic oxide, acts upon the amyloid substance [glycogen] in such a manner as to lead to its abnormal transformation into sugar." Pavy does not see the necessity for the existence of a special ferment, but that a body or bodies capable of converting glycogen into sugar exist in the liver there can be no doubt.

Formation of Fat by the Liver.—If we examine the hepatic cells of any of the domestic animals, especially those kept in confinement, fat globules are always seen in considerable numbers. Again, it is well known that in what is termed by pathologists *fatty liver*, the cells are filled with fat. This tendency to the formation of fat is connected with the production of glycogen. Thus, it has been supposed that glycogen in the liver may not only be transformed into sugar, but, in some circumstances, also into fat. If the fat be removed as quickly as it is formed, it may be oxidized in the tissues, or it may be stored up in the adipose tissue of some other organ; but if, from interference with oxidation processes, it is not consumed, it apparently remains in the hepatic cells, which become swollen, so that the aggregate size of the liver becomes increased. Thus there appears to be a relation between oxidation changes, or, in other words, activity of respiration, and the formation of fat by the liver. In the embryo, and in fishes, where respiration is not active, the liver is large; whereas in birds, which have an active respiration, the liver is small. If a goose be kept from exercise, and fed with food rich in oils and carbohydrates in a hot and close atmosphere, the liver becomes fatty, increases enormously in size, and constitutes *paté du foie gras.* We also observe similar changes, though to a less degree, in the liver of many residents in tropical countries, where they breathe a rarefied atmosphere, if they live on a rich diet and take too little exercise.

SECTION VIII.

EXCRETION.

We have seen that the tissues are nourished by a fluid which passes out of the thin walled capillaries into the fine spaces that exist among the elementary tissues, and that the excess of this fluid, along with various matters produced by the disintegration of tissue, to be regarded as waste products, is carried off by the lymphatics, and constitutes the lymph. We have also seen that the lymph is carried back to the blood, so that the blood receives a considerable quantity of waste products, substances which are not only of no further use in the body, but if they collect in the blood to any great extent, become actually injurious to the living tissue elements. These matters are eliminated from the blood and constitute *excretions.* Such are the matters escaping by the skin in the form of sweat, the substances eliminated by the kidneys as urine, and the carbonic acid and aqueous vapour separated chiefly by the lungs, and to a smaller extent by the skin and kidneys. It may be briefly stated here that nitrogen is eliminated by the kidneys chiefly in the form of urea, and that the other excreted matters consist principally of water, carbonic acid, and salts. These waste products are separated by five channels, namely, the lungs, the intestinal canal, the liver, the skin, and the kidneys. The excretory functions of the first three have been fully discussed, and it remains to consider the functions of the skin and of the kidneys.

A.—The Skin.

Chap. I.—THE STRUCTURE OF THE SKIN AND OF ITS EPIDERMIC APPENDAGES.

The skin consists of two layers, a deeper layer formed of connective tissue, and termed the *corium*, *derma*, or *cutis vera*, and a superficial layer formed of epithelium, known as the *epidermis.* In the skin we also find two kinds of glands, and various appendages, the hairs and nails, which are developed from the epidermis.

1. The upper surface of the **Corium** or true skin shows delicate furrows crossing each other, so as to form small lozenge-shaped areas, or the

furrows may run parallel for a considerable distance so as to form a series of grooves. The lozenge-shaped arrangement is seen on the surface of the skin of the body, while the furrows or grooves are best seen on the palmar aspect of the hand and fingers. On the little areas, or on the ridges separating the furrows, we find small prominences termed the *papillæ*, the number and size of which vary much in different parts of the body. Papillæ are most numerous and attain the greatest size (even as much as ·2 mm. in length) in the palm of the hand and the sole of the foot, and they are small and few in number in the skin of the face. The corium is a feltwork of connective tissue, with elastic fibres intermingled, and here and there we find connective tissue cells and plain muscular fibres. The most superficial strata show the connective tissue in a very condensed condition, but in the deeper strata the bundles of connective tissue are wide apart and cross each other in all directions, so as to form an irregularly meshed network. Thus we have in the corium two strata, the superficial *stratum papillare*, and the deep *stratum reticulare*, insensibly merging into each other. In the deepest layer of the *stratum reticulare*, we find in the meshes groups of fat cells, and below this we have the subcutaneous tissue in which fat is abundant. The subcutaneous tissue, containing fat, constitutes the *panniculus adiposus.* The subcutaneous tissue merges into the fascia of the muscles, or into the periosteum of bone. The elastic fibres are finest in the

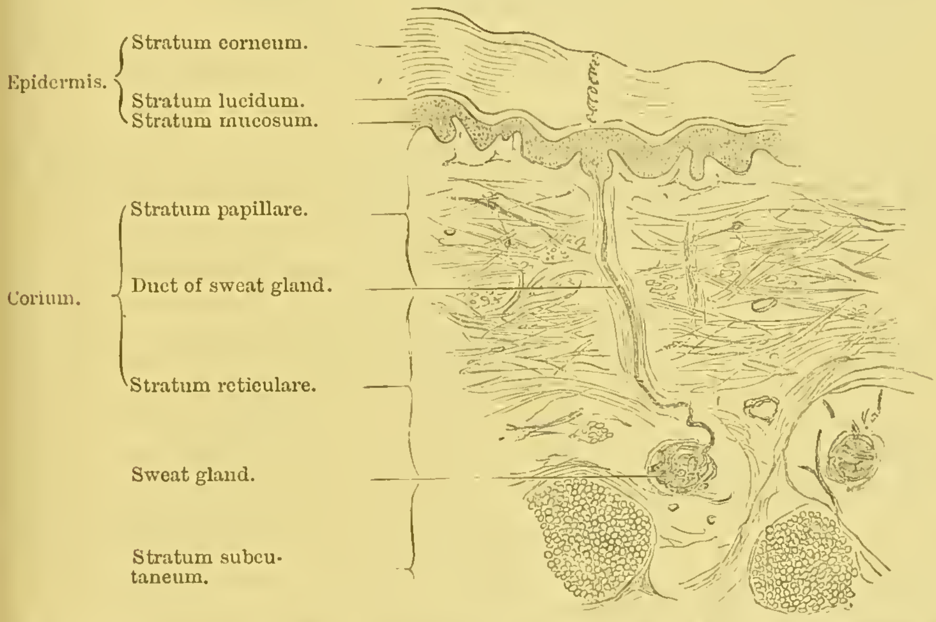

FIG. 199.—Perpendicular section of the skin of finger of an adult man. × 25 d. (Method No. 66, Appendix.)

stratum papillare, and thickest in the *stratum reticulare*. The cells are flat or spindle-shaped, and they may be connective tissue cells, leucocytes, or cells destined to become fat cells. The plain muscular fibres are chiefly connected with the sheaths of the hairs; but in some parts they form a distinct layer, as in the neighbourhood of the nipple and in the *tunica dartos* of the scrotum.

2. The **Epidermis** is formed of stratified pavement epithelium. Two strata are easily seen, as they are sharply defined—a deeper stratum, soft in character, and filling up the spaces between the papillæ, termed the *stratum mucosum* or *stratum Malpighii*, and a superficial and denser stratum known as the *stratum corneum*. Both strata are formed of epithelial cells, which change their appearance as we pass from below upwards. The cells in the *stratum mucosum* are cylindrical, and possess an oblong nucleus; above these we find cells of a more or less round form, having prickly borders, and hence called *prickle cells*. The prickles are delicate thread-like processes, passing from cell to cell through a small amount of cement substance. The term *intercellular bridges* has also been applied to these processes uniting cell to cell. The cells of the next higher layer are more flattened, and contain strongly refractive granules, believed to be a substance called *eléidin* or *keratohyalin*. In the *stratum mucosum* a rapid multiplication of cells takes place by karyokinesis, and it has, for this reason, been appropriately termed the germ-stratum of the skin. The *stratum corneum* is formed of flat polygonal cells which have lost their nucleus, and the cells of the most superficial layer are continually being shed by abrasion. The young cells developed in the *stratum mucosum* gradually become those of the *stratum corneum*, and older cells are pushed upwards by younger ones. In situations where the epidermis is very thick, as on the palm of the hand and sole of the foot, a transparent strip may be seen between the *stratum mucosum* and the *stratum corneum*, known as the *stratum lucidum*. The true nature of this intermediate stratum has not yet been satisfactorily explained. The pigment of the skin, on which its colour depends, exists as fine granules in the cells of the deeper layer of the *stratum mucosum*.

3. The **Nails** are horny plates, which lie on specially modified portions of the skin, termed the *bed of the nails*. The bed is bounded laterally by two pads flattened towards the front, the *nail pads*, and between the nail pads and the nail bed we have the *nail groove*, in which the *edge* of the nail is fixed. The posterior border of the nail, termed the *root* of the nail, springs from a deeper groove, and the tissue from which the nail is developed is termed the *matrix*. The nail bed is formed of corium, covered with epithelium, and the bundles of the connective tissue of the

corium run either longitudinally or they spring from the periosteum of the terminal phalanx, and pass perpendicularly to the surface of the corium. In the bed, the corium has no papillæ, but there are delicate grooves which run longitudinally from

Fig. 200.—Dorsal half of a transverse section of the third phalanx of the finger of a child × 15 d. The grooves on the nail bed appear in a transverse section as papillæ. (Method No. 67, Appendix.)

the matrix, the lips of the groove increasing in height until we reach the spot where the nail suddenly rises from its bed. The epithelium of the bed consists of several layers of cells like those of the *stratum mucosum*, and these fill up the grooves on the corium, but the uppermost layer of epithelium is sharply defined from the under surface of the nail. It is only the epithelium of the matrix that passes into the substance of the nail. The nail is formed by the growth of epithelium from the matrix. The matrix shows the usual structure of epidermis; cells are developed from the layer corresponding to the *stratum mucosum*, and as these are pressed upwards and forwards, they become horny. The cells become firmly cemented together, and they differ from the cells in the upper layers of the epidermis of the skin in containing a nucleus (Fig. 201).

Fig. 201.—Elements of human nail. × 240 d. (Method No. 68, Appendix).

4. Hairs are flexible elastic structures found on the surface of the skin. The part projecting from the skin is the shaft, *scapus;* the part passing obliquely into the skin is the root, *radix pili ;* and at the end of the root we find a bulb, *bulbus pili*, having a hollow underneath filled with a tissue belonging to the corium, and termed the *papilla.* The root is surrounded by a modified portion of skin, termed the *follicle*, in the formation of which we find both corium and epidermis. The epidermal portion forms the *sheath* or *sheaths.* From two to five glands open into the follicle, termed *sebaceous glands.* A few bundles of plain muscular fibre pass obliquely from the side of the follicle to the under surface of the corium. These constitute the erector muscle of the hair (*musculus arrector pili*). When they contract towards the corium, they pull on the sheath and erect the hair, as in goose-skin. A hair is formed entirely of epidermal cells, which are arranged in three strata : (1) the *cuticle*, which covers the surface ; (2) the *cortex*, forming the mass of the hair ; and (3) the *medulla*, or *pith*, in the centre (Figs. 203 and 204). The cuticle is formed of small, non-nucleated, transparent, tile-shaped, hard cells, the edges of which sometimes project from the surface, so as to make the hair rough. The cortex of the shaft is composed of more elongated, nucleated,

horny cells, intimately cemented together; in the root, the cells are softer, and more of a round form, and they become rounder as we approach the bulb. Many hairs show no medulla, and even in thick hairs, where it is present, it does not extend the entire length of the hair. It is formed of cubical, finely-granular, epithelial cells, closely packed in a double row, and having a small nucleus. Coloured hairs contain pigment, in the form of fine granules, in the cells of the cortex; the pigment may also be diffused through the hair. Fully-grown hairs also contain minute globules of air among the cells, both of the cortex and of the medulla. The follicle of fine, woolly hairs is formed entirely of the epidermal layers surrounding the root, but that of stronger hairs is partially formed by the corium. A hair follicle usually shows the following sheaths or strata: (1) most externally, a longitudinal layer of connective tissue fibres, and rich in vessels;

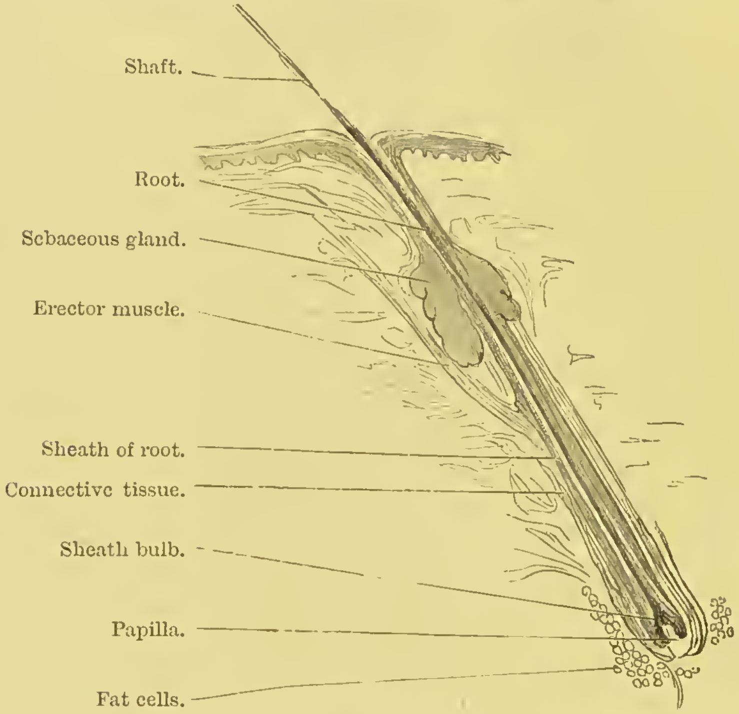

Fig. 202.—Hair seen in a section of human scalp. × 20 d. (Method No. 69, Appendix.)

(2) a thicker middle layer of delicate bundles of connective tissue, arranged circularly; and (3) most internal—a transparent elastic layer. These three strata are formed entirely of connective tissue, and belong to the corium. Next to the innermost layer of the corium we find a layer of stratified pavement epithelium, continuous with the *stratum mucosum*, and termed the *external root sheath*. Lining this, in the upper part of the follicle, we find the *internal root sheath*, which represents the *stratum corneum*. Below the orifices of the sebaceous glands, the inner root sheath divides into two layers or strata. The outer of these, termed *Henle's sheath*, consists of a single or double layer of non-nucleated epithelial cells, and the inner, known as *Huxley's sheath*, is formed of a single layer of nucleated cells. The inner surface of Huxley's sheath is lined by a cuticle like that covering the hair. The external root sheath becomes thinner, and gradually disappears in the lower part of the follicle, and the internal root sheath becomes less marked, and gradually merges into the round cells forming the hair bulb.

The development of a hair and of a hair follicle begins about the end of the third month of embryonic life, in the form of a small knob or prominence on the

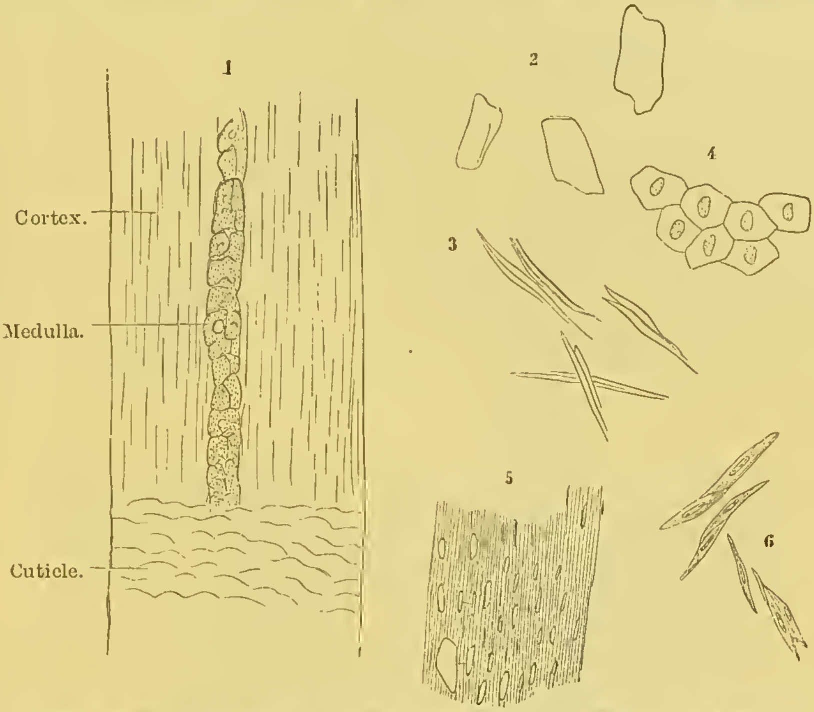

Fig. 203.—Structural elements of human hair and of hair follicle. × 240 d. 1, white hair; 2, epidermal cells of the cuticle; 3, cells of cortex of the shaft; 4, cells of Huxley's layer; 5, cells of Henle's layer, appearing as a fenestrated membrane; 6, cells of cortex of the root. (Method No. 70, Appendix.)

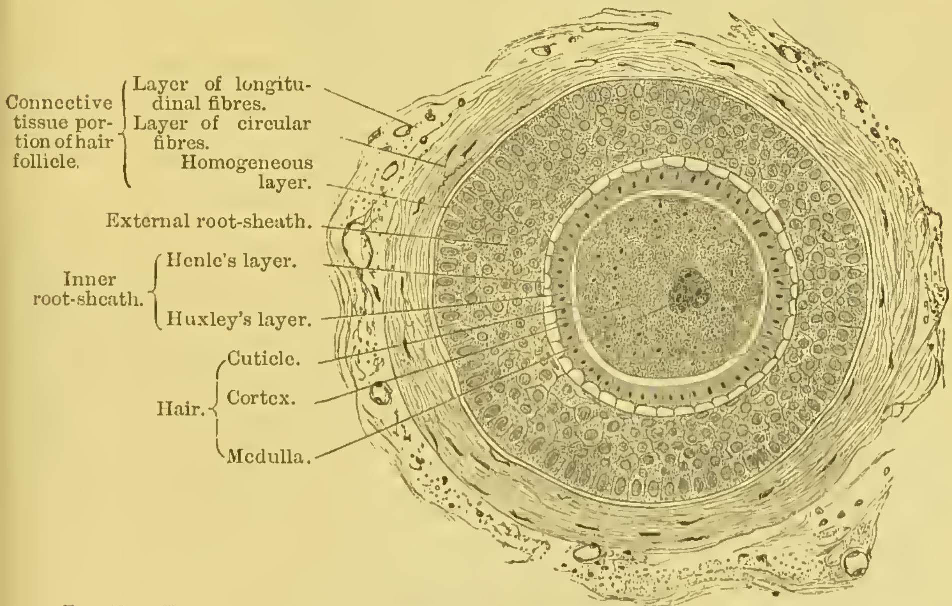

Fig. 204.—Transverse section of a hair and hair follicle in the lower half of the root. From skin of scalp. (Method No. 71, Appendix.)

epidermis (Fig. 205), and, at the same time, of a condensed mass of epidermal cells growing into the corium (Fig. 205, *A*, *B*, *hk*), and termed the *germ* of the hair. The papilla disappears, while the germ becomes longer, and a knob or bulb appears at its lower end (Fig. 205, *C*). At the same period, a *papilla* makes its appearance on the upper surface of the corium (Fig. 205, *C*, *p*). The connective tissue portion of the follicle also develops (Fig. 205, *C*, *hb*). The germ next divides into an outer layer and a cord, in the axis of the germ (Fig. 205, *D*, *s*). The outer layer becomes the external root sheath (*aw*), and the outer part of the axial cord becomes the internal root sheath, while its centre is transformed into the hair (*h*). The sebaceous glands are local outgrowths from the external root sheath.

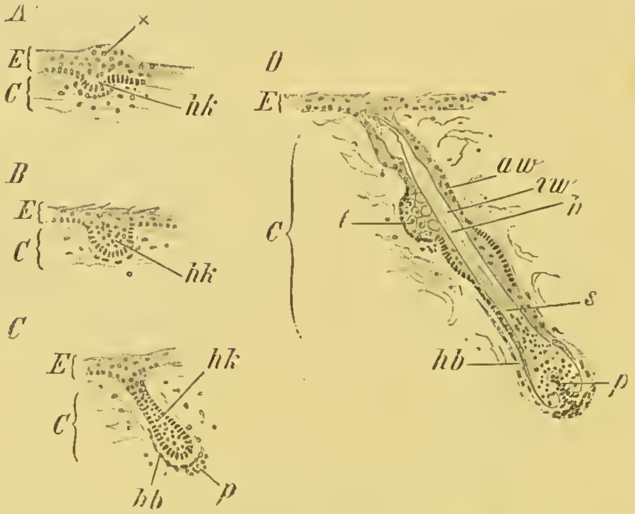

FIG. 205.—From perpendicular sections, *A*, of skin of cheek of human embryo of fourth month. *B*, *C*, *D*, of skin of the forehead of human embryo of five and a half months. × 80 d. *E*, epidermis, still consisting of nucleated epithelial cells; *C*, corium; ×, knob; *hk*, hair germ; *hb*, connective tissue layer of follicle; *p*, papilla; *aw*, external root-sheath; *s*, axial cord, in the upper part of which, the separation into *iw*, the inner root-sheath and *h*, the hair is seen; *t*, beginning of sebaceous glands. (Method No. 72, Appendix.)

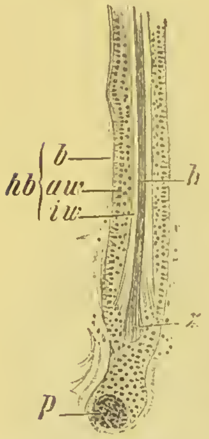

FIG. 206.—From a perpendicular section of eyelid of a new-born child. × 80 d. The lower half of a hair follicle is shown. *h b*, hair follicle; *b*, connective tissue layer; *a w*, external, and *i w*, internal, root sheath; *p*, papilla; *h*, hair; *z*, bulb, raised up. (Method No. 73, Appendix.)

The hairs found on the skin at birth are soon shed, and other hairs are developed. In the adult each hair has a limited duration of life, and an old hair gives place to a new one. The cellular elements of the hair bulbs become horny, and the bulb itself becomes detached from the papilla and rises in the follicle. The inner root sheath is folded backwards, and the lower portion of the follicle, being empty, collapses, a cord-like structure is formed, and then a series of changes similar to those of embryonic life occurs. The young hair pushes upwards, opens up the follicle, and presses close to the old hair, until the latter falls out (Fig. 207).

5. The **Sebaceous Glands** are either simple or compound pear-shaped follicles, of a racemose type. We observe a short duct (Fig. 207, *A.*, *a*), and the body of the gland, formed

of a variable number of tubes or acini. The duct has its wall formed by a continuation of the external root sheath, and is lined by stratified flat epithelium which, by a gradual diminution of its layers, merges into the epithelial lining of the pouches of the gland. The opening of the gland is lined by short cubical cells (*B*, 1); farther in, the cells are more polygonal (2, 3, 4), and fill the lumen of the gland. These cells usually show various stages in the process of secretion. The sebaceous matter (*sebum*) is a fatty matter mixed with the debris of broken down cells. The sebaceous glands of large hairs are appendages of the follicles, but in the case of the soft woolly embryonic hairs, the hairs are really appendages of the glands. The glands are found everywhere in the skin except on the palm of the hand and sole of the foot. The sebaceous glands reach their greatest size in the skin of the negro races, where they may be found so large as to dip into the subcutaneous fatty tissue. Some sebaceous glands are not connected with hair follicles, as on the red margins of the lips, the *labia minora*, and the *glans* and *preputium penis*. In the latter situations they are known as *Tyson's glands*. The glands are always found in the superficial stratum of the corium, the *stratum papillare*. They vary in size from ·2 to 2·2 mm., the latter being found in the skin of the nose, where their ducts are visible to the naked eye.

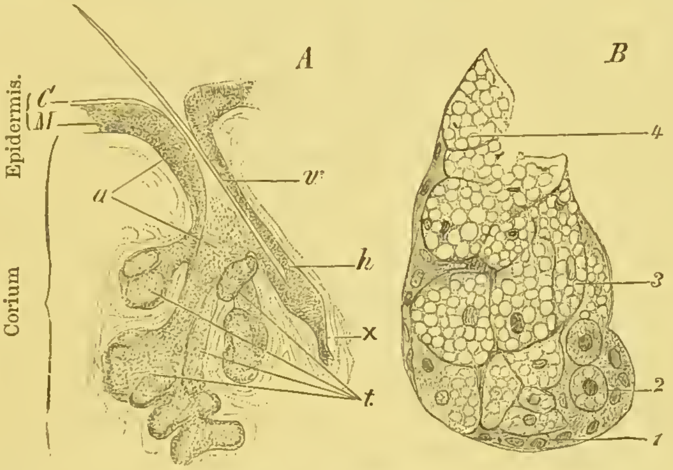

FIG. 207.—*A*. Vertical section through the ala of the nose of a child. × 40 d. *C*, *stratum corneum*; *M*, *stratum mucosum*; *t*, sebaceous gland consisting of 4 tubes or *acini*; *a*, duct; *w*, first kind of hair, falling out; *h*, follicle showing at the bottom × the formation of a new hair.

B. Portion of gland in same situation as *A*. × 240 d. Gland cells are seen in various stages of secretion. 1, cubical cells; 2, large round cells, showing secretion in drops at 3; 4, cell with a shrivelled nucleus. (Method No. 74, Appendix.)

6. The **Sweat** or **Sudoriparous** glands, first discovered by Malpighi, are long tubes coiled up at their lower ends so as to form a ball

or clew. The duct pursues a straight or slightly winding course through the corium, passes between two papillæ into the epidermis, runs spirally through the epidermis, and opens on its upper surface by a circular pore. The wall of the duct while it passes through the corium is formed of a stratum of cubical cells, outside of which bands of connective tissue run longitudinally. The duct has no wall in passing spirally through the epidermis. The ball is formed of a single coiled tube, lined with a single layer of cubical cells containing pigment and granules of fat, and the wall of the tube is formed of a delicate *membrana propria.* In large sweat glands, smooth muscular fibres are found between the *membrana propria* and the gland cells. The secretion of the gland at rest is a fatty fluid which lubricates the skin, and it is only under the influence of nervous stimuli that the watery fluid, known as perspiration or sweat, is formed. Sweat glands are found everywhere except on the *glans penis* and on the inner surface of the *preputium penis*, and they exist in largest numbers on the palm of the hand and the sole of the foot. In these latter situations they may number 2,736 to the square inch. In the same area on the back of the hand Krause counted 1,500; on the forehead and neck, 1,250; on the breast, belly, and arms, 1,100; on the cheeks and thighs, 500 to 600; and on the back, 400. Krause states that, taking the surface of the skin of the whole body at 15 square feet, about 2,500,000 sweat glands exist. They are also found in the skin of the ox, and in the pads of the feet of dogs and cats. They attain a great size in the pig's snout. The nose and upper lip of ruminants, and of the dog and cat, contain racemose glands that secrete a clear, watery, alkaline fluid.

7. The **Arteries** of the skin spring from vessels in the underlying fasciæ, and they run vertically towards the surface. They form three sets of capillaries: the deepest belong to the adipose tissue (Fig. 208, a'), the next form a basket-like network (a'') winding spirally round the sweat glands, and the third consist of the terminal ramifications of the artery (a'''). The latter form a network in the *stratum papillare*, from which loops pass into the papillæ, and small branches also pass to the hair follicles and sebaceous glands.

The **Veins** originate in a network in the *stratum papillare* by vessels coming from the loops in the papillæ and from the follicles and sebaceous glands. The small veins, descending close to the artery, receive branches from the sweat glands and from the adipose tissue. The papilla of the hair has an independent arterial branch.

8. The **Lymphatics** form two capillary networks—one, consisting of fine vessels forming narrow meshes, in the *stratum papillare*, below the blood capillary network; and the other, with wider meshes, lies in the subcutaneous tissue. Minute lymphatics are also found outside the hair follicles and the two sets of glands.

9. The Nerves, specially abundant in the palm of the hand and the sole of the foot, end partly in the subcutaneous tissue in the *corpuscles of Vater*, and partly in *touch corpuscles*, *touch cells*, and in intra-epithelial fine fibres. Touch cells are often present in the external sheath of the hair follicles.

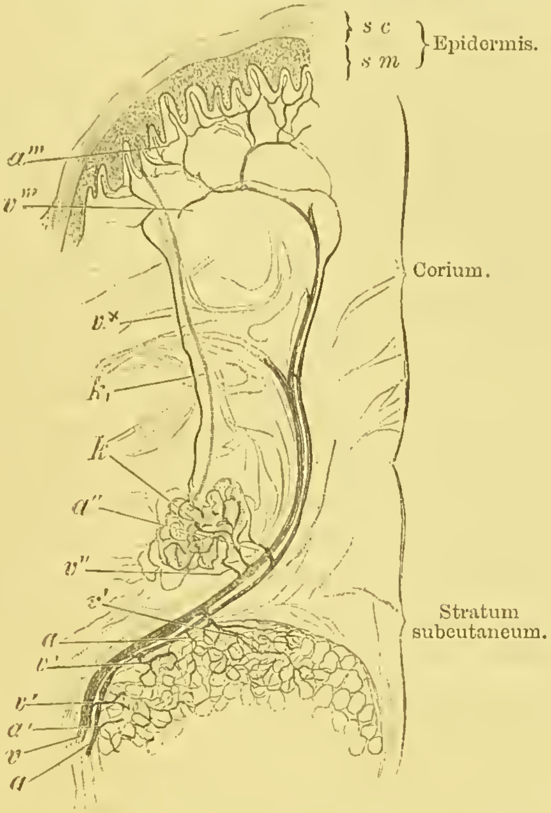

FIG. 208.—Perpendicular section of skin of the sole of the human foot. × 50 d. *s c*, *stratum corneum*; *s m*, *stratum mucosum*; *a*, artery; *v*, vein; *a'*, *v'*, branches of *a* and *v* for fat cells; *a''*, *v''*, for the sweat glands; and *a'''*, *v'''*, for the papillæ; *k*, sweat gland; *k'*, duct of sweat gland; $v^{\times}$, vein running along with the duct. (Method No. 75, Appendix.)

The Epidermic Appendages of the Skin.—In various classes of animals, the epidermis may be modified to form structures of diverse appearance, such as hairs, nails, horn, hoof, quills, feathers, and scales. All of these substances contain *keratin* (p. 80, Vol. I.). A considerable quantity of hairs falls off daily, and as their place is quickly occupied by new ones, the loss represents a certain amount of matter separated from the body. Thus Voit showed that a dog weighing 30 kilogs. lost daily a weight of hair of 1-2 grms., representing ·1 grm. of nitrogen. Beneke states that the amount of keratinous matter in the hair of the head daily formed by a man is about ·040 grm., and in the nails, according to Moleschott,

·005 to ·006 grm. In an observation on an ox, the animal lost daily from 2 to 20 grms. of hair, and Valentin showed that the currying of a horse caused a loss of about 5 to 6 grms. (Munk). The comparative study of these structures is of great interest, but the limits of this work will not permit of its discussion. The chief physiological points to be noted are : (1) each epidermic structure may be regarded as a permanent excretion from the blood ; (2) each epidermic structure has an individual existence—it is developed, grows, reaches maturity, declines, dies, and is removed from the body to be replaced by another of a similar kind ; (3) epidermic appendages of the most varied histological structure may serve purposes of beauty (hair, feathers, scales); of warmth (hair, wool, feathers); of defence (horn, hoofs, quills, or spines); or as aids to the sense of touch (whiskers of the cat and other felines, etc.) ; and (4) when epidermis is modified for purposes requiring strength and resistance, it assumes in structure a concentric arrangement of epidermic cells, simulating bone (contrast, for example, sections of bone with those of hoof, of whalebone, or of rhinoceros horn). Many feathers and scales produce beautiful iridescent tints of colour when seen by reflected light from the fine markings on their surface forming diffraction spectra. Such tints may be wholly independent of pigment, as may be seen in the hairs of the sea mouse (*Aphrodite*) and in mother of pearl.

CHAP. II.—THE EXCRETORY FUNCTIONS OF THE SKIN.

Man perspires readily, more especially on the skin of the forehead, the palms of the hand, the soles of the feet, and the armpits. The horse and the sheep also perspire, the ox to a less extent, and perspiration is absent from rats, rabbits, and goats. Felines, like the dog and cat, perspire only on the pads of the soles of the feet, and pigs perspire mostly on the snout.

(*a*) Sweat.

Sweat or *perspiration* is a transparent colourless liquid, having a peculiar odour, and salt taste, which varies in different parts of the skin. Its reaction in man is acid, but it is alkaline in the horse and cat, and also in man after very profuse sweating. The acidity is due to volatile sebaic acids originating from the decomposition, by some held to be fermentive, of the fatty matter of the sweat. Its specific gravity is 1,004. When examined under the microscope, it may show a few squamous epidermic cells, derived from the skin, and perhaps a few crystals and oil globules.

(1) *Chemical Characters.*—It contains from ·5 to 2·5 per cent. of solids, and 97·5 to 99·5 of water. One third of the solids consists of inorganic matter, in the form of salts, of which chloride of sodium constitutes one half. We also find phosphates of the alkalies and of the alkaline earths, and some oxide of iron.

Traces of urea have been detected to the amount of ·15 per cent., and this may decompose into ammonium carbonate, giving rise to salts of ammonia in the sweat. We also find minute quantities of volatile fatty acids, such as formic, acetic, butyric, propionic, caproic, and caprylic acids. The volatile fatty acids cause the odour of sweat, more especially that of the feet. The sweat also contains the neutral fats, palmitin and stearin, cholesterin, and very minute traces of albumin. The sweat of the horse frequently contains albumin.

The amount of sweat secreted per day varies much even in the same individual, and also among animals. Any circumstances favouring the determination of blood to the skin increases the secretion, and if more water is eliminated by the glands than can be evaporated from the surface of the skin in a given time, the sweat gathers in a fluid form on the surface. Hence exercise, copious drinking of water, warm baths, friction of the skin, and a high temperature excite the secretion. Certain active substances increase sweating, namely, pilocarpin, physostigmin, muscarin, strychnin, picrotoxin, nicotin, camphor, and salts of ammonia; on the other hand, morphin and atropin diminish or arrest it. The influence of psychical states, such as anxiety, anger, fear, or joyous excitement, increases the secretion. A compensating action exists between the kidneys and the skin as regards the excretion of water. Thus, if the function of the kidneys be partially suppressed, as occurs in various diseases of these organs, the skin may eliminate a fluid having a urinous odour and containing a considerable amount of urea.

From 800 to 1000 c.cm. of water are eliminated by the skin of an adult man in twenty-four hours, that is about $\cdot 01\dot{3}$ of the weight of the body, about the same amount as is separated by breathing. The amount of solid matter is very small.

The first portions of sweat secreted are richer in free volatile fatty acids and their salts, and contain less inorganic salts than the portions secreted after the glands have been for some time active, and, as already stated, the sweat may become alkaline. Profuse sweating also diminishes the amount of urea in the urine.

Many substances, such as iodine, iodide of potassium, alcohol, benzoic, cinnamic, tartaric, and succinic acids, and the odoriferous principles of certain plants, such as garlic, may be eliminated by the skin.

The secretion of sweat depends on the pressure of the blood in the cutaneous capillaries, the activity of growth of the epithelial cells in the sweat glands, and the innervation of the glands. Its excretion by the ducts will be facilitated by the contraction of the smooth muscular fibres of the sweat glands, already noticed (p. 386). The right side of the body perspires more freely than the left. Three classes of nerves may come into action in connection with sweating, namely, vaso-constrictors, vaso-dilators, and secretory or trophic nerves. The mere afflux of blood to the skin will not necessarily cause sweating, as we may see the surface bedewed with sweat in the pallor of fear and during the agony of death. In these circumstances, both the vaso-contrictors and the trophic secretory filaments are active. Claude Bernard and Dupuy saw profuse sweating on one side of the head and neck after section of the sympathetic in the neck, and electrical irritation of the nerve has been found to diminish such sweating, but in this case also, the secretory nerves were also involved. That special secretory nerves exist has been clearly proved, more especially by observations on cats, the hairless soles of the pads of the feet of these animals readily perspiring. If the sciatic nerve is divided and the peripheral end is stimulated, sweating takes place in the pads of the corresponding foot. Further, the important observation has been made that the normal sweating of the hind feet of this animal is due to nervous influences passing down fibres in the sciatic nerves, as a kitten in which the sciatic nerve had been cut on one side sweated profusely by the other three feet, when placed in a warm chamber, while the foot supplied by the divided sciatic nerve did not sweat. The secretory filaments in the sciatic nerve of the cat issue from the spinal cord by the anterior roots of the spinal nerves, from the ninth to the thirteenth dorsal vertebræ. In this region of the cord a sweat centre has been assumed to exist. The secretory fibres for the anterior limbs of the cat lie in the ulnar and median nerves, and they probably issue from the spinal cord in the lower part of the cervical region. The origin and route of the secretory fibres of the head and neck have not yet been clearly ascertained. Experiment indicates that such fibres exist in the cervical sympathetic, in the fifth cranial, and in the facial nerve, and no doubt they issue from a cerebral centre, as indicated by the effects of psychical excitement. It has been ascertained that stimulation of the facial, median, or tibial nerve in man causes a secretion of sweat not only on the area of skin supplied by the nerve, but also on the corresponding area on the opposite side of the body. This shows that the sweat centres may be stimulated in a reflex way. These *sweat centres*, like other centres, will be influenced by the kind of blood passing through them, and by peripheral impressions, but our knowledge of this subject is still vague.

Removal of Sweat from the Surface of the Skin.—If the secretion is limited in quantity, and if the surrounding atmosphere is not saturated with aqueous vapour, the watery portion of the sweat immediately passes into vapour, constituting what has been called *insensible perspiration.* But if the secretion is abundant, or if the atmosphere is already saturated, the sweat soon bedews the surface and trickles over the skin —*sensible perspiration.* It is evident that in both cases, the surface of the skin may become coated with solid matters, and if this state be allowed to continue, these may seal up the mouths of the sweat ducts and thus interfere with their functions.

(*b*) Sebaceous Matter.

This matter, secreted by the sebaceous glands, is oily, semi-fluid, and it has a peculiar odour. It contains about 1 per cent. of inorganic salts, 5 per cent of neutral fats and soaps, 61 per cent. of epithelial debris and albumin, and about 31 per cent. of water. The secretion of the glands of the prepuce contains a much greater amount of fat (that of the horse 50 per cent.) (Munk). The fats are olein and palmitin and the soaps are chiefly palmitate of soda. It also contains chlorides and phosphates of the alkalies and alkaline earths. The secretion of the *Meibomian glands* in the eyelid is sebaceous, and closely related to it in composition is the *cerumen* or wax formed by glands in the skin of the external auditory meatus. Ceruminous matter under the microscope (250 d.) shows fat globules and sometimes crystals of cholesterin. It also contains a peculiar bitter substance which has not been isolated by chemists. Sheep's wool contains a fatty acid united to potash to form a salt, and also a peculiar cholesterin-fat in which the fatty acid is in combination with cholesterin instead of with glycerine. This is the *lanolin* of Liebreich, existing also in horn, hairs, hoofs, feathers, and epidermis, and now used as the basis of various ointments.

No estimate can be given of the amount of sebaceous matter secreted daily. It is variable among animals and even among those of the same species. The amount is largest in the negro races of mankind. Although of no great importance quantitatively, as an excretion, the sebaceous matter plays a valuable rôle in many animals, covering the surface of the hairs and feathers with a fine film of oily matter through which moisture cannot penetrate. Water thus trickles off the surface of the hair or feathers and does not reach the skin.

(*c*) Gases.

The skin not only separates from the blood sweat, sebaceous matter and the substances forming epidermis and epidermic structures, but it is also concerned in gaseous exchanges. This constitutes its *respiratory* function. As the blood in the capillary network in the *stratum papillare* contains oxygen and carbonic acid, and as it is separated from the air by little more than the thickness of the epidermis, it is to be expected that gaseous exchanges take place according to the laws of diffusion, as in the lungs, although to a smaller extent,—oxygen passing in to unite with hæmoglobin, and carbonic acid passing out. Aqueous vapour, or strictly speaking, water gas, must also escape, when the external atmosphere is not saturated with water gas. By enclosing the body in a gas-tight bag, thus excluding the gases concerned in pulmonary respiration, the quantity of carbonic acid exhaled has been determined in man at from 4 to 8 grms. per twenty-four hours. From a horse, at rest, Gerlach thus collected from 15 to 23 grms., and, during active movement, about 82 grms. in twenty-four hours. The amount is also increased by raising the external temperature. From 4 to 7 grms. of oxygen are absorbed by the skin of a man. Thus the amount of carbonic acid exhaled is about ·0066 ($\frac{1}{150}$th) of that exhaled by the lungs, and the amount of oxygen absorbed about ·0071 ($\frac{1}{140}$th) of that absorbed by the lungs. Smaller animals seem to lose less carbonic acid by this channel than man, a dog losing only ·004 ($\frac{1}{250}$th) of that given off by the lungs. The amount of respiratory exchange by the skin is thus comparatively small, and we cannot suppose that its suppression is the cause of the well known occurrence of death after covering the skin with an impermeable varnish, or gilding the body of a child to cause it to resemble a golden Cupid. In these cases death resulted from an interference with the elimination of heat. Amphibians breath freely by the skin, so that a frog will live with the circulation active for many hours after removal or ligation of the lungs.

As to the amount of water separated in the form of invisible water gas (insensible perspiration), no estimate can be given, as it is impossible to collect it free from admixture with the water of the sweat. Röhrig collected from the skin of the arm enclosed in a gas-tight bag 1·6 grm. per hour.

The skin may also be regarded as a protective covering, and it is concerned in the regulation of temperature and in the sense of touch or pressure. (See ANIMAL HEAT AND TOUCH.)

B.—The Kidneys.

Chap. I.—THE STRUCTURE OF THE KIDNEYS.

On opening a kidney by a longitudinal section, from its outer to its inner border, the solid portion is seen to consist of a *cortical* and a *medullary* substance; the latter being in the form of conical masses named *pyramids* of *Malpighi*, the apices of which open into a space called the *sinus* (Fig. 209). The cortical part is of a light crimson brown colour and is soft and easily lacerated. The urine is secreted chiefly in the cortical part, and it is conveyed by the medullary part into the sinus, from there into the *pelvis*, or dilated extremity of the ureter, and by the ureter it passes into the bladder.

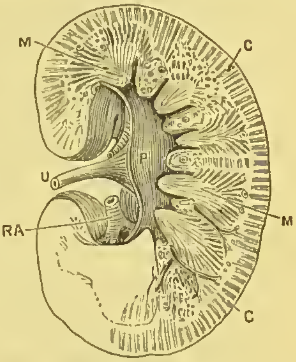

Fig. 209.—Section of a kidney. P, sinus; U, ureter; M, medullary; and C, cortical part.

The kidneys consist of numerous tubular glands intimately bound together. The tubes, termed *tubuli uriniferi*, pursue a tolerably straight course in the medullary portion of the kidney, and they are much convoluted in the cortical portion. Each small tubule begins in the cortex as a capsule surrounding a small spherical body known as a *Malpighian body*, after its discoverer (Fig. 210, *a*). The capsule is constricted at the neck, and the tube forming it is then much convoluted, *tubulus contortus* (*b*). This passes into a portion of the tube which runs at first towards and into the medullary portion, and then forming a loop, passes back to the cortical part, thus forming the *loop of Henle.* In this loop we notice a descending (*c*) and an ascending (*d*) portion. The ascending part of the loop, when it reaches the cortex, becomes slightly spiral, and forms the *intercalary portion* of the tube (*e*), and this finally pursues a straight course, and is termed a *collecting tube* (*f*). These collecting tubes, as they run towards the medulla of the kidney, unite with other intercalary tubes; they also unite, at acute angles, with adjacent collecting tubes (*f*), and, finally, they pass to the papillæ. In and near the papillæ they are few in number, but as they have strong walls, they are now termed the *ducti papillares.* The loops of Henle and the collecting tubes constitute the *tubuli recti* of older writers. Each uriniferous tubule is thus completely isolated as far as the junction of the intercalary with the collecting tube. A portion of the loops of Henle and the upper part of the collecting tubes form little formations in the cortex, visible to the eye, known as the *pyramids of Ferrein*.

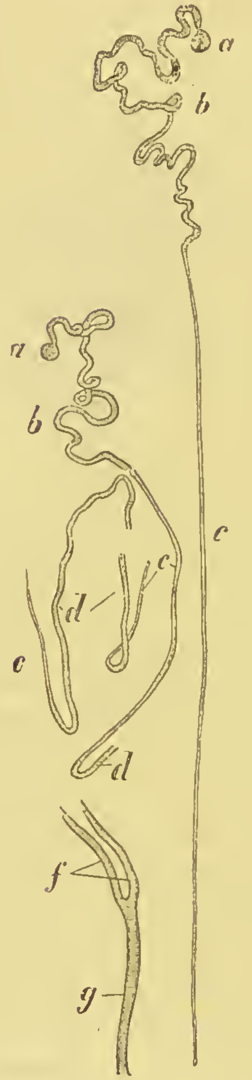

FIG. 210.—Small uriniferous tubule from rabbit four weeks old. × 30 d. *a*, Malpighian corpuscle; *b*, convoluted tube; *c*, descending limb of Henle's loop; *d*, ascending limb; *f*, collecting tube; *g*, *ductus papillaris*. (Method No. 76, Appendix.)

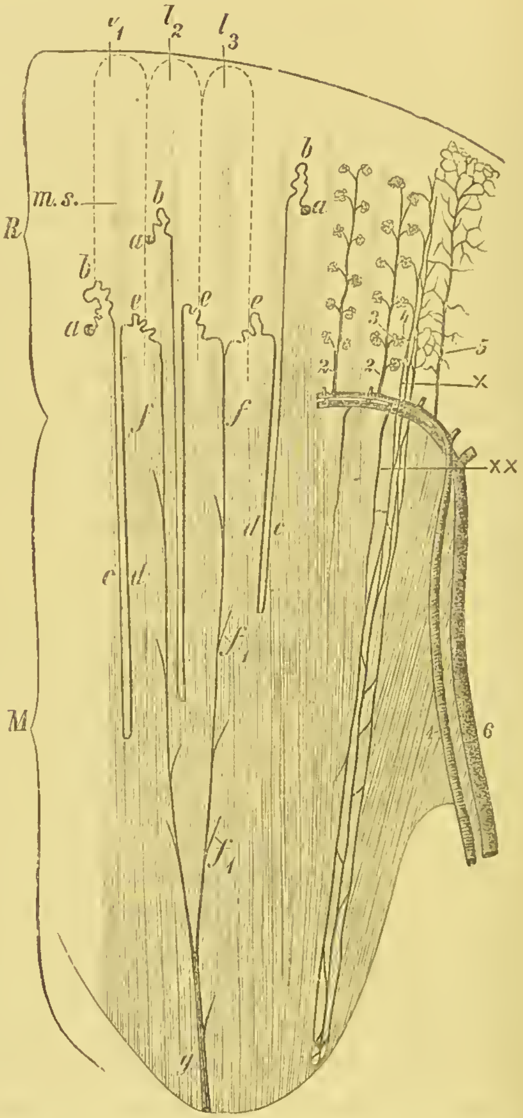

FIG. 211.—Diagram showing the course of a uriniferous tubule on the left, and the arrangement of the vessels of the kidney on the right. *R*, cortex; *M*, medullary substance; *m s*, pyramids of Ferrein; l_1, l_2, l_3, small lobules of kidney; *a*, Malpighian corpuscle; *b*, convoluted tube; *c*, descending, *d*, ascending, limb of loop of Henle; *e*, intercalary portion of tube; *f*, collecting tube; f_1, portions of collecting tubes; *g*, ductus papillaris; 1, branch of renal artery; 2, interlobular artery; 3, vas afferens; 4, vas efferens; 5, interlobular vein; × × ×, *arteriæ rectæ*, p. 398. From transverse section of kidney of a child seven weeks old. × 10 d.

The minute structure of these small canals varies at different parts of their course. The Malpighian corpuscle, from ·13 to ·22 mm. in breadth, consists of a spherical plexus or knot of blood-vessels, termed the *glomerulus*, which is enclosed in the dilated end of the uriniferous tubule, known as the *capsule of Bowman.* As the end of the capsule has been infolded by the glomerulus being pushed into it (as one would infold the end of the finger of a glove by the tip of the finger), it follows that the capsule consists of two layers, an internal, covering the glomerulus closely, and formed in young animals of cubical cells, more flattened in adults, and an external, built of flat polygonal cells (Fig. 214). The

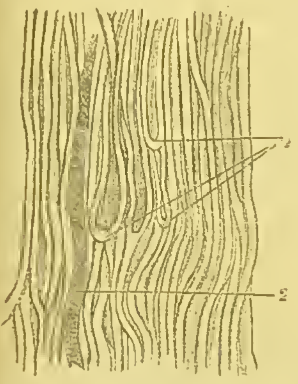

FIG. 212.—Longitudinal section through the medullary portion of human kidney. × 20 d. Observe Henle's loops 1, and below the loops the union of two small collecting tubes to form a larger one. (Method No. 77, Appendix.)

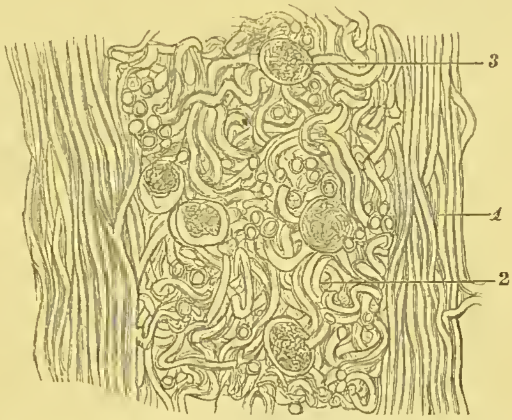

FIG. 213.—Section of cortical substance of human kidney. 1, tubuli recti, forming the medullary rays or pyramids of Ferrein; 2, convoluted tubes; 3, Malpighian corpuscle. (Method No. 78, Appendix.)

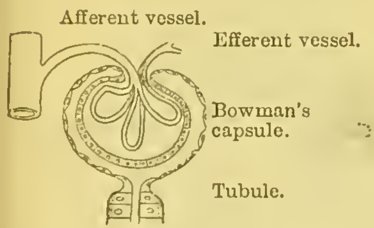

FIG. 214.—Diagram showing the artery on the left giving off an afferent vessel, which breaks up into branches, from which originates the efferent vessel. The three loops represent the glomerulus. This is surrounded by Bowman's capsule, both portions of which are seen. Observe the external layer passing into the wall of the tubule.

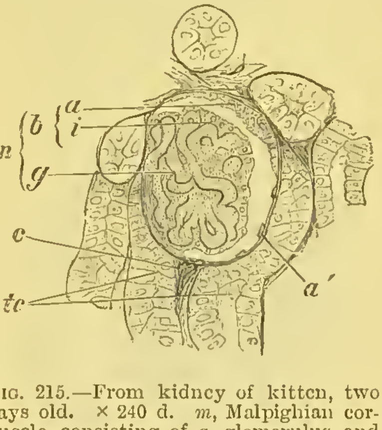

FIG. 215.—From kidney of kitten, two days old. × 240 d. *m*, Malpighian corpuscle, consisting of *g*, glomerulus, and *b*, Bowman's capsule; *a*, outer layer of capsule showing flat cells, *i*, and the inner cubical cells. At *a*, flat cells seen from surface, and at *a′* from the side; *t c*, convoluted tube; *c*, interstitial connective tissue.

outer layer of the capsule passes on into the neck, and thence forms the wall of the convoluted tube, which has a narrow lumen, as the wall is from ·04 to ·06 mm. in thickness.

The cells in this portion of the tube are shaped like a truncated cone, the narrow end being directed to the lumen, and fine longitudinal lines may be seen on each cell, giving a rod-like appearance (Fig. 216, A, B.).

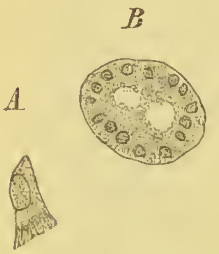

Fig 216.—*A*, isolated cell from convoluted tube. Observe the rod-like appearance at the broad end. *B*, transverse section of convoluted tube. Observe the fine striæ. (Method No. 79, Appendix.)

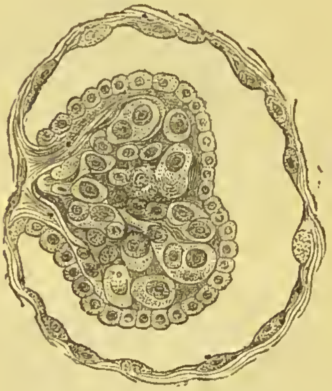

Fig. 217.—Another view of the structure of Bowman's capsule, showing the two kinds of epithelium.

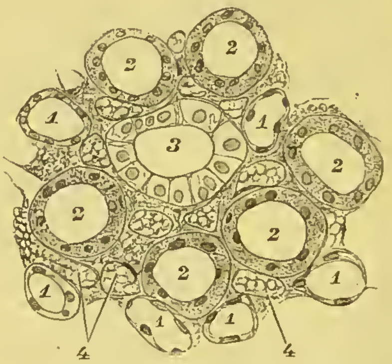

Fig. 218.—Portion of a transverse section of the medullary part of human kidney. × 24 d. The section passed through the base of the papillæ, 1, descending, and 2, ascending, portions of Henle's loop; 3, small collecting tubes; 4, blood-vessels filled with corpuscles. (Method No. 80, Appendix).

The descending portion of Henle's loop is from 9 to 15 μ in diameter, and the lumen is wide. The epithelial cells are flat, with a nucleus prominent towards the lumen (Fig. 218, 1). The ascending loop is from 23 to 28 μ in diameter, and the lumen is relatively narrower than in the descending loop. The epithelial cells here resemble those of the convoluted tubes, but they are somewhat smaller (Fig. 218, 2). The intercalary ducts are 39 to 46 μ in diameter, and their epithelial cells are cylindrical or slightly conical and very brilliant. The collecting tubes become wider as we approach the papillæ, the narrowest being about 45 μ, and the widest 200 to 300 μ in diameter. The cylindrical epithelial cells are clear or dark (Fig. 218, 3), and their height increases with the diameter of the tube. The small uriniferous tubes have a structureless *membrana propria,* outside the epithelium, and this is thickest in the descending portion of Henle's loop. A small amount of loose interstitial connective tissue exists between the tubes (Fig. 215, *c*), and this is condensed on the surface of the kidney to form a capsule, the *tunica albuginea.* In the capsule we find smooth muscular fibres. Blood-vessels course in the interstitial connective tissue.

The **Vessels.**—The renal artery divides in the hilum into branches which, after giving off minute twigs to the *tunica albuginea* and the *pelvis,* pass into the parenchyma of the organ (Fig. 219, 1). They enter the medullary substance and run up to the boundary between the medulla and cortex. Here the vessels bend at right angles and form a series of loops or arches, the convexity being towards the cortex. From the convex sides of the arches, vessels spring at regular intervals, termed the *interlobular arteries* (Fig. 211, 2). They sometimes run up so as to divide the cortex into small lobules, not well differentiated, and represented diagrammatically in Fig. 211, l_1, l_2, l_3. The interlobular arteries give off small branches here and there, and a single branch passes to each glomerulus. The branch termed the *afferent artery* or *vessel* (Fig.

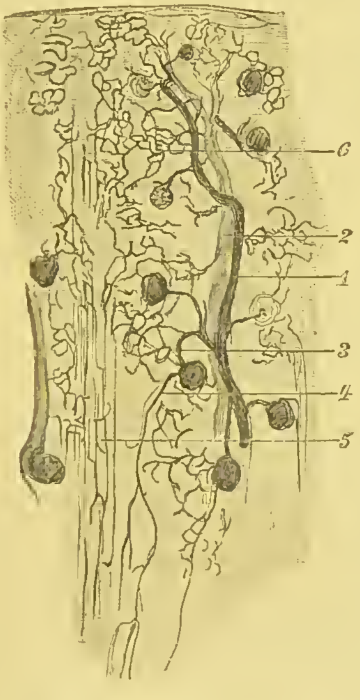

FIG. 219.—Longitudinal section of injected kidney of a guinea-pig. × 30 d. 1, interlobular artery; 2, interlobular veins; 3, afferent vessel; 4, efferent vessel; 5, long capillary meshes in cortex. (Method No. 81, Appendix).

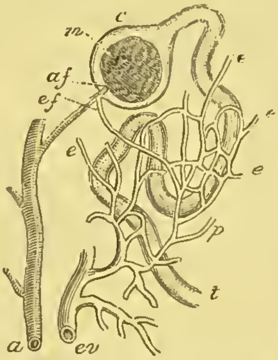

FIG. 220.—Diagram showing the relation of the Malpighian body to the uriniferous tubules and blood-vessels. *a*, interlobular artery; *c*, expansion of the end of the tubule; *m*, tuft of vessels forming glomerulus; *a f*, afferent vessel, conveying blood to, and *e f*, efferent vessel, conveying blood from *m*; the efferent vessel, *e f*, splits up into capillaries *e*, *e*, *e*, *e*, which ramify on the uriniferous tubule; *e v*, interlobular vein.

211, 3, 219, 3), passes into the glomerulus, at once breaks up into fine vessels, forming the glomerulus, and these combine to form the *efferent vein* or *vessel* (Fig. 211, 4, 219, 4). The efferent vessel also divides to form a second capillary network, with elongated meshes, in the situation of the pyramids of Ferrein (Fig. 220, *e*, *e*, *e*), and from these arise the inter-lobular veins (Fig. 211, 5, 219, 2, and 220 *ev*). These run close to the interlobular arteries. The veins in the outer part of the cortex form a peculiar stellate meshwork (*stellulæ Verheynii*), but they ultimately anastomose with the interlobular veins. The medullary part of the kidney is supplied by the *arteriæ rectæ*, vessels which spring either from the arterial arches already described, or from the interlobular arteries, and, according to some, from the efferent vessels of the deepest and largest glomeruli. The veins of the medulla run spirally round the *ducti papillares*, and open into a venous arch at the boundary between the medulla and cortex.

The *Lymphatics* of the kidney lie partly in the capsule, and they partly accompany the arterioles passing into the parenchyma. *Nerves* also accompany the vessels, but the mode of their termination is unknown.

CHAP. II.—GENERAL CHARACTERS AND THE SPECIAL CONSTITUENTS OF THE URINE.

Normal urine is a clear, transparent fluid, of an amber colour, peculiar odour, and a saltish taste. It gives an acid reaction with blue litmus paper, from the presence of the acid phosphate of soda, NaH_2PO_4. The temperature of the urine when passed is about 39° C. After standing for a short time, a light cloud gathers in the bottom of the vessel, consisting of mucus. The mucus shows under the microscope a few large mucus corpuscles, like swollen leucocytes, and usually a few flattened epithelial cells from the bladder and passages. A little later, in the mucus cloud we may see dark reddish-brown specks and these will will be found, on microscopic examination, to be crystals of uric acid, of the whetstone form. If the urine is allowed to stand in a cold room, it may become muddy owing to the precipitation of urates which are much less soluble in cold than in hot water. By and bye the urine may again become clear and a deposit falls to the bottom consisting chiefly of the acid urate of soda (Vol. I. Fig. 36, p. 101). In a clean vessel, and in cold weather, the urine may then remain clear and acid for several days, but the acidity slowly diminishes, or it becomes neutral, and then becomes alkaline. It now becomes paler in colour, a whitish iridescent pellicle gathers on the surface, and it has an ammoniacal and foetid smell. This is owing to a fermentation having been set up by a specific organism derived from the air termed *micrococcus ureæ*. If a little urine is boiled in a flask, and the neck of the flask is then hermetically sealed or plugged with cotton or wool, the urine will remain as when passed and retain its acid reaction for an indefinite period of time. The micro-organisms convert urea into carbonate of ammonia, the reaction being represented thus: $CN_2H_4O + 2H_2O = (NH_4)_2CO_3$. (The same change occurs when a pure aqueous solution of urea is heated for 4-6 hours in a hermetically sealed tube at a temperature of 180°-200° C.) A deposit is also thrown down, consisting of the ammoniaco-magnesian or triple phosphate ($MgNH_4PO_4 + 6H_2O$), phosphate of lime $Ca_3 2(PO_4)$, and urate of ammonia, $C_5H_2(NH_4)_2N_4O_3$. The microscopical examination of such urine shows bacteria, micrococci, crystals of triple phosphate (Vol. I. Fig. 18, p. 42), amorphous masses of phosphate of lime, and spiny balls ("thorn apple crystals") of urate of ammonia (Vol. I. Fig. 37, p. 101). The urine may also be alkaline from the presence of fixed alkalies, as occurs after the ingestion of acetates, malates, tartrates, citrates, and phosphates in the food, and hence the urine of herbivora is alkaline. To determine whether the alkali is fixed or volatile, dip a bit of sensitive red litmus paper into the fluid and a blue reaction is obtained. Dry this gently over a flame; if the red colour of the paper reappears, the alkali is volatile, and if not, it is fixed.

To determine the acidity of urine, prepare a solution of caustic soda so that 1 c.cm. = ·0031 grm. of caustic soda, and 1 c.cm. will exactly neutralize ·0063 grm. of oxalic acid. Place 100 c.cm. of urine in a beaker and add the soda drop by drop from a burette until an exactly neutral reaction is obtained with sensitive litmus. Read off the number of c.cm. of solution of soda required, and as 1 c.cm. = ·0063 grm. of oxalic acid, calculate the quantity of oxalic acid represented. Thus suppose 20 c.c. employed, then ·0063 × 20 = ·126 grm. of oxalic acid in 100 c.cm. would be the degree of acidity. Suppose 1500 c.cm. passed in twenty-four hours, then ·126 × 15 = 1·89 grm. of oxalic acid.

The *colour* of urine varies considerably. It may be almost colourless, like water, pale yellow, orange, reddish, or brownish red. In cases of disease, the colour may be much altered. Thus it is usually pale in diabetes, milky from admixture with chyle, dark red and smoky from the presence of blood, or blood pigment, or it may have a greenish hue from the presence of bile. The varying colours of normal urine do not depend on different pigments, but on different degrees of dilution of the one pigment, urobilin, derived from the alimentary canal and identical with bilirubin (see Vol. I. p. 134). Urine may also have a bluish tint from the presence of indigo-blue, derived from indican (Vol. I. p. 135, and p. 109-10).

To determine the composition of the urine, all that is passed in twenty-four hours must be collected and mixed and an analysis made of the mixed urine. This proceeding is necessary because the composition of the urine, as will be seen, is subject to considerable variations during twenty-four hours. The *quantity* secreted by a healthy adult man varies from 1500 to 2000 c.cm., and by an adult woman about 400 or 500 c.cm. less. The specific gravity, as determined by a urinometer, Fig. 221, varies from 1015 to 1025, taking distilled water as 1000, and it rises in proportion to the amount of solid matter dissolved in it. Each degree of the urinometer represents about 2·33 of solid matter in 1000 parts. Hence if we multiply the last two figures of the sp. gr. by 2·33 we obtain the total amount in 1000 parts (*Christison's formula*). For example, if the sp. gr. be 1017, then $17 \times 2\cdot33 = 39\cdot61$ grms. in 1000 parts, and if the amount passed in twenty-four hours be 1700 c.cm., then $\frac{1700 \times 39\cdot61}{1000} = 67\cdot33$ grms. The formula may be made still more simple; thus, in the example given:—$17 \times 2\cdot33 \times \cdot1700 = 67\cdot33$—that is to say, multiply the last two figures of the specific gravity by 2·33 and the quotient by the figures expressing the total quantity with a decimal point *before* the first figure.

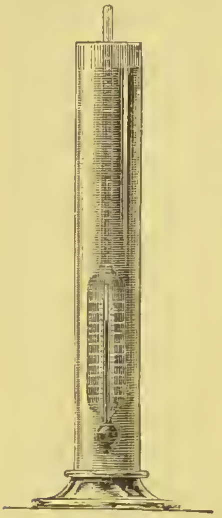

Fig. 221.—Urinometer floating in a testing glass.

The student is recommended to make himself practically acquainted in the laboratory with the analysis of urine. For this purpose he will require: (1) test tubes; (2) spirit lamp or gas flame; (3) filter paper; (4) funnels and stands; (5) litmus paper, red and blue; (6) turmeric paper; (7) nitric acid; (8) fuming nitric acid; (9) strong acetic acid; (10) strong solution of caustic potash; (11) solution of ferrocyanide of potassium; (12) Fehling's solution (Vol. I. p. 152); (13) Nylander's solution, consisting of 2 parts of basic nitrate of bismuth and 4 parts of Rochelle salts, dissolved in 100 parts of an 8 per cent. solution of caustic soda; (14) chloroform; (15) ether; (16) alcohol; (17) solution of perchloride of iron; (18) strong sulphuric acid; (19) cane sugar; (20) solution of nitrate of mercury; (21) solution of sulphate of copper; (22) strong solution of ammonia; (23) a few porcelain lids; (24) a few beakers; (25) glass rods; (26) a 10 c.cm. pipette.

It is convenient to estimate the amount of certain constituents of the urine by volumetric processes. These consist in submitting the substance to be estimated to certain well-known reactions, using for such reactions solutions of known strength, and, from the quantity of solution employed, calculating the weight of the substance to be estimated according to the laws of equivalence.

We require in every volumetric process:

1. A solution of the re-agent, the chemical equivalence of which is accurately known. This is the standard solution (symbol S.S.).

2. A graduated vessel from which portions of the fluid contained in it may be accurately delivered—the burette.

3. The decomposition which the solution produces with any given substance is usually of such a character that its termination is unmistakable to the eye, and thereby the quantity of the substance with which it has combined accurately determined. Occasionally, however, we use another solution, which produces a characteristic reaction with the standard solution, and which thus informs us when we have added excess of the standard solution. This is termed the *indicator.*

Apparatus required: 1. *Graduated Pipettes.*—Containing 50, 20, 15, 10, 4, 3 c.cm.

2. *Flasks and Jars.*—Graduated from ·1 litre to 5 litres.

3. *Mohr's Burette.*—This instrument consists of a glass tube, graduated into tenths of a c.cm. and provided below with a caoutchouc tube, is closed by a spring clamp, or with a glass stopcock. Two or more of these may be fixed into a wooden or iron frame.

In use, the burette is filled up to zero with the S.S., the urine to be tested measured out into the glass beaker, and the S.S. allowed to run out into the glass beaker by pressing on the clip, and towards the end of the experiment to drop into it, until the proper quantity has been added. (The volumetrical fluid is usually placed in the burette, and the urine in a beaker or porcelain capsule, but occasionally, as in the diabetic sugar process, the reverse is the case.)

When the urine to be tested has been measured, and the burette filled with the S.S., we first of all allow the solution to run slowly out, and at last to pass drop by drop into the urine, until the operation is completed. When the point of completion is shown in all parts of the fluid, by some distinct reaction, or by the use of an *indicator*, we are sure that the experiment is complete; but if this be not the case, then we must test the mixture again and again until the right point has been attained.

The constituents of the urine may be classified as follows:—(1) nitrogenous, (2) non-nitrogenous, (3) pigments, (4) salts, and (5) gases.

(1) Nitrogenous.

a. Urea, CH_4N_2O, is the nitrogenous matter most abundant in the urine, varying from 2·5 to 3·2 per cent. The amount eliminated daily is from 25 to 30 grms. For each kilog. of body weight the following quantities are formed in children: From 3 to 6 years, 1 grm.; from 8 to 11 years, ·8 grm.; from 13 to 16 years, ·04 to ·6 grm. The general characters of the substance have already been described, Vol. I. p. 84.

If a dilute solution of mercuric nitrate is added to an alkaline solution of urea, a white amorphous precipitate is formed, having a composition represented by the formula $2CON_2H_4.4HgO.2NO_3$, and a slight yellow tinge indicates the formation

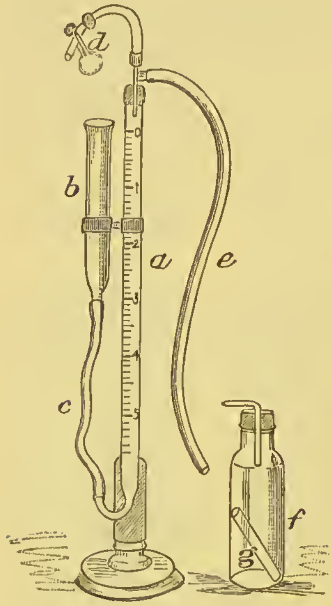

FIG. 222.

of mercuric subnitrate, after all the urea has been precipitated. This is the reaction on which Liebig's volumetric method for the estimation of urea is based, but, as it yields only approximately accurate results after the elimination, as far as possible, of several sources of error, it is not of much service to the physiologist. The most efficient method is by the hypobromite of soda process, devised by Knop and Hüfner, and depending on the reaction $CON_2H_4+3NaBrO=CO_2+N_2+2H_2O+3NaBr$. The carbonic acid set free is absorbed by the excess of caustic soda, and from the volume of nitrogen liberated the amount of urea is calculated. A convenient form of the apparatus is shown in Fig. 222. It consists of a burette of 50 c.cm. capacity. The upper end of the burette, guarded by a stopcock, communicates by an india-rubber tube with the evolution bottle, *f*, the capacity of which is about 75 c.cm. The re-agent is prepared by dissolving 100 grms. of caustic soda in 250 c.cm. of water, 27 c.cm. of this solution are placed in a glass-stoppered bottle, 2·5 c.cm. of bromine added, and the mixture diluted to 150 c.cm. The latter constitutes a solution of hypobromite of soda. Into the evolution flask we now place a small tube, *g*, containing 5 c.cm. of the urine, and 20 c.cm. of the hypobromite solution are poured round it in *f*. The cork is pressed into the evolution bottle, and, by opening the stopcock at the top of the burette, the latter is so adjusted that the level of water in the burette is the same as that in the tube *b*, communicating with the bottom of the burette by the tube *c*. The evolution bottle is then tilted, so that the urine mixes with the hypobromite solution; brisk action takes place, carbonic acid and nitrogen coming off, and the cylinder (*b*) is lowered from time to time, so as to keep the level in the burette and in the cylinder (*b*) the same. The carbonic acid is absorbed by the caustic soda, and the nitrogen collects in the burette. At the end of an hour the adjustment of levels is again made, the amount of nitrogen in c.cm. is read off, and the height of the barometer and the temperature are also noted. If the latter precaution is not used there may be an error of ·1 per cent.

Let V′ be the volume of nitrogen at standard temperature, 0° C., and standard pressure, 760 mm., V be the volume of the gas observed, B, the barometric pressure at the time of the experiment, W, the tension of the aqueous vapour in mm. at the temperature of the experiment, δ, the co-efficient of the expansion of a gas for each degree C. (·00366), t, the observed temperature. Then $V'=\frac{V\,(B-W)}{760.\;(1+\delta t).}$

For example, suppose 30 c.cm. of N were collected at 15° C. and 740 B.P. the volume of the gas at 0° C. and 760 mm. pressure will be

$$\frac{30\,(740-12{\cdot}677)}{760\,(1+{\cdot}00366\times15)}=\frac{30\times727{\cdot}323}{760\times1{\cdot}0549}=\frac{21819{\cdot}690}{801{\cdot}724}=V'=27{\cdot}23\text{ c.cm.}$$ [1]

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[1] To make the above calculation, it is necessary to know the tension of aqueous

(*b*) *Uric acid*, $C_5H_4N_4O_3$, the general characters of which have been described in Vol. I. p. 97, *et. seq.*, exists in urine to the extent of ·05 per cent., and about ·7 grm. are eliminated in twenty-four hours.

It is chiefly in combination with bases forming neutral urate of soda, dissolved in the urine, or acid urates of soda and potash (chiefly the first), which fall as a precipitate in the cold in acid urine. By the uric acid uniting with ammonia in alkaline urine, urate of ammonia falls as a precipitate. Urate of lime may be deposited from an alkaline urine. Uric acid may also exist in a free condition and is deposited in acid urine. Uric acid may be readily demonstrated in urine by adding a few drops of hydrochloric acid to the urine, and in a few hours it appears in the crystalline forms seen in Vol. I. Fig. 35, p. 100. Uric acid is soluble in cold water to the extent of only 1 in 1100, and in hot water of 1 in 125. Consequently when the urine cools it is deposited, if present in the free state beyond the amount soluble in the cold, in a given volume of urine. It is not often important to estimate the quantity of uric acid, but various methods have been employed, of which the following is the best. The following solution is prepared: 1 part of sulphate of magnesia, 2 parts of sal ammoniac, 4 parts of ammonia (sp. gr. ·924), and 8 parts of water. Mix 250 c.cm. of urine with 50 c.cm. of this mixture and filter. Add to the filtrate a 3 per cent. solution of nitrate of silver till a precipitate ceases to be formed. The precipitate thus formed contains all the uric and phosphoric acids (the chlorides being kept in solution by the ammonia). It is collected and washed with dilute ammonia. A warm solution of potassic sulphide is added, forming urate of potash which passes into solution. Filter, add a little hydrochloric acid to the filtrate, and evaporate in a warm bath. The uric acid crystallizes out on cooling. The crystals are washed with water, dried at 40° C., and then treated with bisulphide of carbon to remove adhering sulphur, and lastly, treated with ether. They are thus obtained pure, and they may then be weighed.

(*c*) *Kreatinin*, $C_4H_7N_3O$ (anhydrous), or $C_4H_7N_3O.2H_2O$ (efflorescing), (Vol. I. p. 94) may be found in urine to the amount of ·1 per cent. and from 1·7 to 2·1 grms. are excreted daily.[1]

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vapour at temperatures varying from 10° C. to 25° C. This is given in mm. of mercury in the following table:—

10° C.,	9·126	14° C.,	11·882	18° C.,	15·351	22° C.,	19·675
11 ,,	9·751	15 ,,	12·677	19 ,,	16·345	23 ,,	20·909
12 ,,	10·421	16 ,,	13·519	20 ,,	17·396	24 ,,	22·211
13 ,,	11·130	17 ,,	14·409	21 ,,	18·505	25 ,,	23·582

Then 1 grm. of urea contains ·46666 grm. of N, and the volume of this gas is 372·7 c.cm. at 0° C. and 760 mm. pressure; but as the whole of the N is never set free, we may take the volume of N in 1 grm. of urea as 343·3 c.cm.; and 27·23 c.cm. will represent of urea $\frac{27{\cdot}23}{343{\cdot}3} = {\cdot}0793$ grm. of urea in 5 c.cm. of urine. Suppose the total quantity of urine in twenty-four hours to be 1500 c.cm. then $\cdot 0793 \times 300 = 23{\cdot}79$ grms., the total quantity, or about 1·586 per cent.

[1] G. S. Johnson on "Kreatinins." *Proceed. Roy. Soc.* vol. xlii. p. 368.

This substance has a reducing action on cupric oxide, a fact to be kept in mind in testing for sugar. Thus Johnson states that the amount of kreatinin in normal urine will reduce cupric oxide to an extent equivalent to the reduction effected by ·43 to ·51 grain of glucose per fluid ounce. In this reducing action the uric acid also takes part. Complete precipitation of the reducing substances is effected in forty-eight hours by adding to fresh urine $\frac{1}{20}$th of its volume of a cold saturated solution of acetate of soda and then $\frac{1}{4}$th of its volume of a cold saturated solution of mercuric chloride. The precipitate, which contains no reducing agent except uric acid, is filtered off, and then the mercury salt of the reducing base begins to be deposited from the filtrate in about half an hour. This also is filtered off, suspended in cold water, and treated with hydrogen sulphide. The compound is thus dissolved, mercuric sulphide being formed, and the fluid becomes acid. The hydrochloride of kreatinin may thus be obtained by evaporation. The kreatinin is obtained by decomposing the hydrochloride with excess of lead hydrate without heat, depositing in the alkaline filtrate in large square plates, with bevelled edges. (Johnson's process.) To detect kreatinin, add to the urine a few drops of a solution of nitro-prusside of soda, and afterwards a little of a weak solution of caustic soda till a reddish hue appear. The red colour is soon lost, but if the solution is now treated with glacial acetic acid a greenish tinge appears, which changes to blue. (Weyl's test.)

(*d*) *Oxaluric acid*, $C_3H_4N_2O_4$, is an oxidation product of uric acid, and it may exist in minute quantity in urine (Vol. I. p. 88).

(*e*) *Sulphocyanic acid*, CNHS, or rather sulphocyanides, have been found to the amount of from ·003 to ·01 per cent. (Vol. I. p. 97).

(*f*) *Hippuric acid*, $C_9H_9NO_3$ (Vol. I. p. 104), exists in human urine if the individual has taken benzoic acid either in food or as a drug, and it may then be found to the extent of ·02 to ·06 per cent. Salkowski obtained ·087 to ·204 grm. per day from dogs weighing from 15 to 24 kilogs. It may be readily prepared from the urine of a horse or cow.

Boil the urine with excess of milk of lime, filter and evaporate to $\frac{1}{10}$th of its bulk, and when cold acidulate with hydrochloric acid. Brownish yellow crystals separate, having the form seen in Fig. 38, p. 105, Vol. I. Hippurate of zinc is obtained by treating fresh urine with excess of sulphate of zinc, evaporating and filtrating. The amount can be determined by weighing. For tests see Vol. I. p. 105.

(*g*) *Xanthin bodies.*—Certain bodies related to xanthin may appear in urine to the extent of ·01 to ·1 per cent.

These are: hypoxanthin, or sarcin, $C_5H_4N_4O$; xanthin, $C_5H_4N_4O_2$; methylxanthin, or heteroxanthin, $C_6H_6N_4O_2$; paraxanthin, or dimethylxanthin, $C_7H_8N_4O_2$; and guanin, $C_5H_5N_5O$. They are all colourless, crystalline bodies, slightly soluble in water and insoluble in alcohol and ether. Weidel's reaction is as follows:—Add to the fluid a few drops of chlorine water and nitric acid, place under a glass cover containing vapour of ammonia, and a beautiful rose-red colour is produced.

(*h*) *Kyanuric acid*, or *oxychinolincarbonic acid*, $C_9H_6O.COOH.N$, occurs in the urine of the dog, and separates in the form of needle-like crystals (or prisms) after the addition to the urine of a few drops of nitric acid.

(2) Non-Nitrogenous.

(*a*) *Oxalic acid*, $C_2H_2O_4$ (Vol. I. p. 166), occurs in urine as oxalate of lime after the ingestion of articles of food containing it, such as rhubarb, spinage, apples, tomatoes, etc., and it is usually abundant in the urine of herbivora, even to the extent of 10 to 14 per cent. It may also be found in urine in small amount, even when no articles of food containing it have formed part of the diet. In these circumstances, the urine of a dog fed entirely on flesh yielded ·02 grms. per day (Auerbach). It is easily detected by the octahedral or dumb-bell-shaped crystals (Fig. 65, p. 166, Vol. I.).

It may be estimated quantitatively by precipitation with chloride of calcium, but the following process by Lehmann is readily carried out. Filter and evaporate 100 c.cm. of urine, add 60 per cent. alcohol to the residue, and shake up with ether. The extract of alcohol and ether deposits a sediment, insoluble in water, which consists of oxalate of lime.

(*b*) *Glycerine-phosphoric acid*, $C_3H_9.PO_6$ (Vol. I. p. 82), has been found in very small amount in urine.

(*c*) *Lactic acids*, $C_3H_6O_3$, belonging to the ethylidene division, have been found in urine in small quantities. (See Vol. I. p. 165.)

(*d*) *Phenolsulphuric acid*, $C_6H_5O.SO_2.OH$, united to potassium, forming phenol-sulphate of potassium, also may exist in urine in very small amount, – ·001 grm. in twenty-four hours. The quantity may be much increased by a rich vegetable diet, or by the ingestion of phenol (carbolic acid)—even to the extent of ·17 to ·34 grm. in twenty-four hours.

(*e*) *Kresolsulphuric acid*, $C_7H_7O.SO_2.OH$, united to potassium, exists in human urine in traces, but it is found in larger quantities in the urine of herbivora.

(*f*) *Brenzcatechinsulphuric acid*, $C_6H_4.(HO)_2.O.SO_2$, has been found in a child's urine and in the urine of the horse. The surface layers of the urine containing it become very dark in decomposing. It reduces cupric oxide. The ingestion of pyrogallic acid, salicin, and hydrochinon, increases the amount. Traces of *paroxyphenylacetic acid*, $C_6H_4.OH.CH_2.COOH$, have been found in human urine (Vol. I. p. 149).

(*g*) *Volatile fatty acids*, formic, acetic, butyric, etc., are found in very small amount in urine (·02 per cent.), especially if slightly fœtid. They probably arise from the decomposition of albuminous matters. They have been found in most cases of leukæmia and in many of diabetes.

(3) Pigments.

These have already been described in Vol. I. p. 134, and it is only necessary here to refer to a few points of practical importance.

(*a*) *Urobilin, or hydrobilirubin*, $C_{32}H_{44}N_4O_7$, may be prepared from urine by the following process devised by Jaffe[1]—

Render 20 litres of high coloured urine alkaline with ammonia, filter, add to filtrate a strong solution of chloride of zinc, and again filter. Wash the zinc precipitate with cold water then with hot water, then boil in absolute alcohol and dry at a low heat. Powder the precipitate, dissolve it in ammonia, and precipitate with a solution of neutral acetate of lead. Collect the precipitate, add a few drops of sulphuric acid, rub it up with alcohol, let it stand for twenty-four hours and filter. Shake up the alcoholic solution with its own volume of chloroform, then add an equal bulk of water. Draw off the chloroform solution of urobilin with a pipette, shake up with water, distil off the chloroform, and the resinous mass obtained is urobilin. As to its spectroscopic characters, see Vol. I. p. 135, and Frontispiece Plate, Vol. I. spectrum No. 15. The average amount of urobilin separated in twenty-four hours has not been estimated.

(*b*) *Indican*, or *indoloxylsulphate of potassium*, $C_8H_6NKSO_4$, as it exists in urine (Vol. I. p. 135), may be readily prepared from the urine of the horse. It is sometimes called *uroglaucin.*

Concentrate 300 c.cm. to a syrup, extract the syrup with alcohol, distil off the alcohol, and shake up residue with ether. Remove the crystals of hippuric acid that have formed, dissolve the residue in water. Add to the fluid a strong solution first of neutral and then of basic acetate of lead, then add ammonia and set it aside for twenty-four hours. Collect the precipitate, suspend in water, and pass carbonic acid through the fluid for half an hour. Filter, evaporate the filtrate to dryness, extract the residue with alcohol, pass through the alcoholic solution a current of sulphuretted hydrogen to separate the lead, filter, evaporate to dryness, and impure indican is obtained.

It may be readily demonstrated either in the urine of the dog or of the horse by mixing the urine with an equal volume of strong hydrochloric acid, and then adding a solution of hypochlorite of calcium till a blue colour appears, and lastly, shaking up with chloroform. A chloroform solution of indigo blue is thus obtained. The rationale of the process is that in the reaction an oxidation occurs and indoloxylsulphate of potash splits up into oxindol (which becomes indigo blue) and sulphuric acid, the latter uniting with the potassium present. $2C_8H_6NKSO_4 + O_2 = C_{16}H_{10}N_2O_2 + 2(KHSO_4)$.

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[1] Salkowski, *op. cit.* s. 157.

(*c*) *Skatoloxylsulphate of potassium*, $C_9H_8NKSO_4$, may also exist in urine. It gives a violet instead of a blue with the indican test above described.

(*d*) *Urohœmatin* is a pigment found by MacMunn in cases of Addison's disease and in rheumatic fever. (See Vol. I. p. 136. See also present volume p. 177.)

(*e*) *Urochrome*, *uromelanin*, etc., are pigmentary matters obtained by Thudichum from urine, but there is no evidence that they constitute *normal* pigments. They are probably derivatives of urobilin.

(4) Salts.

Under this head we shall include chlorides, sulphates, phosphates, iron, ammonia, and silicic acid.

(*a*) *Chlorides* (see Vol. I. p. 83).—The hydrochloric acid in the urine is chiefly united to the base sodium, so that an adult man excretes in twenty-four hours from 15 to 20 grms. of chloride of sodium, the amount being determined chiefly by the quantity introduced in food. The amount in urine may be taken as 1 per cent. The amount diminishes in certain inflammatory conditions, increasing about the period of crisis, and then increasing to even beyond the normal amount after the crisis is over. Thus, in a case of pneumonia the amount fell to about 1 to 1·6 grm. in twenty-four hours, on the day of the crisis it rose to 7·87 grms., and in the two following days it rose to 16·18 grms. Chloride of calcium also exists, inasmuch as there is more chlorine in the urine than can be saturated by the sodium. There is no proof of the existence of chloride of potassium.

Nitrate of silver gives a white curdy precipitate when added to urine. This consists chiefly of chloride of silver, which is soluble in ammonia, but it also contains phosphate of silver. To prevent the precipitation of the latter, make the urine strongly acid by the addition of a few drops of nitric acid. The existence of sodium in the urine is shown by a few drops on a platinum wire giving a yellow colour to the inner blowpipe flame, and potassium by giving a yellow precipitate of octahedral crystals of the double chloride of potassium and platinum on adding a solution of the tetrachloride of platinum to an acid solution of the ash of urine. To determine the quantity of chlorides, the following process by Volhard may be followed. (1) The S.S. is prepared by dissolving 29·075 grms. of pure nitrate of silver in sufficient distilled water to make 1,000 c.cm. Triturate this with a solution of pure chloride of sodium of 10 grms. of the salt to 1,000 c.cm. of distilled water, so as to find the volume of the S.S. of nitrate of silver required to precipitate a certain amount of chloride of silver from the chloride of sodium solution, and add, if necessary, a sufficient amount of distilled water to the S.S. to make its value such that 1 c.cm. = ·010 grm. of NaCl or ·006 of Cl. (2) Next prepare a solution of yellow neutral chromate of potassium, 10 grms. in 90 grms. of distilled water. Place 2 c.cm. of the urine in a small glass, add a few drops of solution (2), and drop in S.S. from a burette. When a drop falls in, a red precipitate of chromate of silver is formed, which disappears on agitation, and is replaced by a white precipitate of chloride of silver. Add drops of S.S. from burette till all the chlorine has been precipitated, and this is indicated by the red colour of the chromate of silver persisting, so that the fluid becomes red. So long as any chlorine exists in the fluid, the red chromate of silver disappears, but when all the chlorine has been precipitated, the red colour persists. On the appearance of the faintest orange red, stop. Test the colour by daylight, and not by lamp or gaslight. If the amount of chlorides is very small, use 8 or 10 c.cm. of urine. Read off the number of c.cm. of S.S. used, and make the following calculation : 1 c.cm. of S.S. = ·010 grm. of NaCl. If 1 c.cm. of S.S. had been used to precipitate all the chloride in 2 c.cm. of urine, these 2 c.cm. would contain ·010 of chloride, $\therefore$ 1 c.cm. of urine = ·005 and n c.cm. of urine would contain ·005 n. Let b = number of c.cm. of S.S. used, then $\cdot005 \times n \times b$ = amount of NaCl, that is $\frac{5}{1000} \times nb = \frac{1}{200} \times nb = \frac{nb}{200}$, or multiply the number of c.cm. of urine passed by the number of c.cm. of S.S. and divide by 200. Suppose a person passed 2000 c.cm. of urine in twenty-four hours, and that 2 c.cm. of S.S. were required to obtain the reaction ; then, $\frac{2000 \times 2}{200} = 20$ grms. of NaCl.

(*b*) *Phosphates.*—The phosphoric acid of the urine is in combination with the alkalies and with the alkaline earths. Thus we find the acid and basic phosphates of sodium and potassium (Na_2HPO_4, NaH_2PO_4, K_2HPO_4, and KH_2PO_4), and the phosphates of lime (Ca_32PO_4), and of magnesia (Mg_32PO_4), and the ammoniaco-magnesian phosphate in alkaline urine ($NH_4Mg_2PO_4 + 6H_2O$) (see Vol. I. p. 42). From 2·5 to 3 grms. of phosphoric acid are excreted daily by an adult. In four researches on the amount passed by an adult, it was found to be 2·857 grms. in twenty-four hours, and it was distributed as follows :—1·937 grm. to the alkalies, and ·937 grm. to the alkaline earths. Of the ·937 grm., about ·627 was combined with magnesia, and ·310 with lime.

Phosphates are precipitated by chloride of barium, or nitrate of baryta, by ammonia, by caustic potash, by caustic soda, by a solution of perchloride of iron (yellowish white), and by molybdate of ammonia and nitric acid (canary yellow). If we add a few drops of acetic acid and then a little of a solution of nitrate of uranium to urine, a lemon yellow precipitate is formed as follows : $UrO(NO_3)_2 + Na_2HPO_4 = UrOHPO_4 + 2\,(NaNO_3)$. The precipitate of phosphate of uranium has a molecular weight of 368, of which 71 consist of phosphoric anhydride, P_2O_5, or 98 of phosphoric acid, H_3PO_4. Upon this reaction, the best process for the estimation of phosphates is founded. The phosphate of uranium thrown down appears as a whitish-yellow precipitate ; it is insoluble in water and acetic acid, but soluble in mineral acids. The exact point of the completion of the reaction cannot be ascertained in the fluid ; consequently, to determine whether or not the whole of the phosphoric acid has been precipitated, a small excess of uranic oxide must be added, the presence of this salt being shown by the sensitive reaction of the salts of uranic oxide with ferrocyanide of potassium, which gives a reddish-brown precipitate. The ferrocyanide of potassium thus serves as an *indicator*.

(*a*) *Standard Phosphoric Acid Solution.*—50 c.cm. of it should contain 0·1 grm. of phosphoric acid. Crystals of pure sodium phosphate are rubbed down fine, dried between folds of bibulous paper, and 10·085 grms. dissolved in 1000 c.cm. of water. 50 c.cm. of this solution contain 0·1 grm. of phosphoric acid.

(*b*) *Acetate of Soda Solution.*—It has been found that 0·5 grm. of acetate of soda is sufficient for 50 c.cm. of urine. Consequently, 100 grms. of acetate of soda are dissolved in 900 c.cm. of water, and the solution brought up to 1000 c.cm. by the addition of 100 c.cm. of concentrated acetic acid. In the volumetrical process, 50 c.cm. of urine are treated with 5 c.cm. of this acid solution of acetate of soda.

(*c*) *Solution of Uranic Oxide.*—Uranic oxide is dissolved in acetic acid, the solution diluted, and its strength tested with the standard phosphate of soda solution (*a*). 1 c.cm. should precipitate 0·005 grm. of phosphoric acid. 50 c.cm. of the phosphoric acid solution (*a*) = 0·1 grm. of phosphoric acid, would consequently require 20 c.cm. of the uranic oxide solution; this solution, therefore, contains 0·4023 grm. of uranic oxide for the precipitation of the phosphoric acid, and, secondly, a slight excess of uranic oxide for the indication of the completion of the reaction.

50 c.cm. of the solution of phosphoric acid require 20 c.cm. of the uranic oxide solution, which, again, must indicate and precipitate 0·005 grm. of phosphoric acid. If, for example, we employ 18·0 c.cm. of the uranic oxide solution to 50 c.cm. of phosphoric acid solution, we must add to each 180 c.cm. of the same 20 c.cm. of water. For this purpose, measure off 1 litre of the uranic oxide solution, and add the quantity of water required. In the case supposed, 111·2 c.cm. of water must be added to 1000 c.cm. of uranic oxide solution to produce the required degree of strength.

Thus, if we have a second time used 19·8 c.cm. of uranic oxide solution to 50 c.cm. of phosphoric acid solution (0·1 grm. of phosphoric acid), we add to each 198 c.cm. of the same, 2 c.cm. of water, and make a new and final test with the phosphate of soda solution.

The uranic oxide solution, each c.cm. of which precipitates ·005 grm. of phosphoric acid, and which also contains a small excess of uranic oxide for the final reaction, must contain 20·3 grms. of pure uranic oxide in a litre.

Place 50 c.cm. of filtered urine in a beaker; add to it 5 c.cm. of a solution of sodium acetate; drop in standard solution of uranium acetate, until a drop gives a faint brown colour when mixed with a drop of ferrocyanide of potassium, on a porcelain plate; boil and test again. If necessary, add a few drops more of the S.S., until the brown colour again appears immediately on testing. Then, if to precipitate all the phosphates in 50 c.cm. of urine, we used 1 c.cm. of S.S., the 50 c.cm. would contain ·005 grm. of phosphoric acid. 1 c.cm. of urine would contain $\frac{\cdot 005}{50}$, and n c.cm. of urine would contain $\frac{\cdot 005 \times n}{50}$. If, in place of one, x number of c.cm. of S.S. were used, then $\frac{\cdot 005 \times n \times x}{50} = \text{phosphoric acid} = \frac{5 \times n \times x}{50{,}000} = \frac{nx}{10{,}000}$, or multiply the total amount of urine by the number of c.cm. of S.S. used, and divide by

10,000. Suppose a person passed 1800 c.cm. of urine, and that 20 c.cm. of S.S. were used. $\frac{1800 \times 20}{10,000} = 3\cdot6$ grms. of phosphoric acid.

The following is the process for estimating the amount of phosphoric acid united with the alkaline earths. Take 100 c.cm. of filtered urine, and make it alkaline with ammonia. The earthy phosphates are thus precipitated. Let the urine stand for twelve hours. Collect the earthy phosphates on a filter, and wash with ammonia water. Wash precipitate into a beaker; heat and dissolve in a few drops of acetic acid. Add 5 c.cm. of acetate of sodium solution, and add water to make up volume to 50 c.cm. Proceed with acetate of uranium solution as before, and make the necessary calculation.

Taking the previous example, we find that the whole of the phosphoric acid is 3·6 grms. The phosphoric acid with the earths required 10 c.cm. of S.S. Therefore, $\cdot010 \times 5 = \cdot05$ grms. in 100 c.cm. of urine. The patient passed 1800 c.cm. Therefore, in 1800 c.cm. we find, of phosphoric acid united to the alkaline earths, ·9, and of phosphoric acid with alkalies, 2·7 grms.

(*c*) *Sulphates* (Vol. I. p. 43).—The sulphuric acid of the urine exists partly in combination with potassium and sodium forming sulphates, and it is partly in combination in such bodies as phenolsulphates and indoloxylsulphates of potassium, and probably also in other aromatic substances met with in small quantities in the urine.

The larger proportion is in combination with the alkalies. From 2 to 2·5 grms. of sulphuric acid are eliminated daily by a healthy man. Sulphuric acid is precipitated as sulphate of barium on the addition of chloride of barium or nitrate of baryta to urine. To estimate the total amount of sulphuric acid, proceed as follows: mix 100 c.cm. of filtered urine with 5 c.cm. of hydrochloric acid (sp. gr. 1·12), add a solution of chloride of barium until a precipitate ceases to be formed. Warm over a water bath and allow the precipitate to settle. Filter through many layers of filter paper, and wash the precipitate thoroughly with water and with alcohol and ether. Collect the sulphate of barium carefully from the filter with a glass rod into a platinum capsule; heat this to redness till quite hot; cool and weigh. The weight will give the amount of sulphate of baryta. To estimate the amount of sulphuric acid combined with organic bodies, the following method by Salkowski is the best. Mix 100 c.cm. of urine with 100 c.cm. of an alkaline barium solution, consisting of 2 vols. of a saturated solution of barium hydrate and 1 vol. of a cold saturated solution of barium chloride, and filter. Take 100 c.cm. of the clear filtrate (containing 50 c.cm. of urine), acidify with hydrochloric acid, and keep the fluid over a water bath for several hours. Then collect the filtrate and proceed as above described for the estimation of the total sulphuric acid. As 233 parts of barium sulphate contain 98 parts of H_2SO_4, or 80 parts of SO_3, or 32 parts of S, the quantity of each of these in the precipitate of sulphate of barium is readily calculated. Thus $\frac{98}{233} = \cdot4206$ for H_2SO_4, $\frac{80}{233} = \cdot34335$ for SO_3, and $\frac{32}{233} = \cdot13734$ for S. For example: 100 c.cm. of urine gave ·487 grm. of $BaSO_4$, then the $H_2SO_4 = \cdot4206 \times \cdot487 = \cdot2048$ per cent., and the $S = \cdot13734 \times \cdot487 = \cdot0669$ per cent.[1]

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[1] Salkowski, *op. cit.* s. 177.

(*d*) *Carbonic acid* exists occasionally in urine in the form of carbonate of soda, more especially in the urine of herbivora. It may also exist, combined with lime ($CaCO_3$), and magnesia ($MgCO_3$). Such a urine may effervesce on the addition of a few drops of nitric acid. If effervescence occurs, it can readily be proved that it is due to carbonic acid, by holding above the tube during effervescence a bit of glass wetted with baryta water, when a white milky appearance is produced. Urine that has undergone the alkaline fermentation contains carbonate of ammonia.

(*e*) *Calcium* exists in urine almost wholly in combination with phosphoric acid, a very small portion being in combination with oxalic acid. The amount excreted daily has been found to vary considerably from ·216 grm. to ·407 grm., the mean of many observations being ·290 grm. (Vol. I. p. 40).

(*f*) *Magnesium* exists as phosphates (Vol. I. p. 41).—From ·4 to ·5 grm. are excreted daily by an adult.

(*g*) *Ammonium* (Vol. I. p. 40).—Ammonia exists in urine in the form of various nitrogenous substances, which may be regarded as ammonias, and which readily yield ammonia. This is not to be confounded with the carbonate of ammonia resulting from the decomposition of urea in fœtid urine. The quantity of combined ammonia eliminated in twenty-four hours is about ·7 grm. Its amount appears to be largely influenced by the nature of the diet. Thus with a vegetable diet an adult excreted ·3998 grm., with a mixed diet ·6422 grm., and with a flesh diet ·875 grm.

(*h*) *Iron* exists in the urine to the extent of ·003 to ·011 grm. per 1000 c.cm. Evaporate 50 c.cm. of urine in a platinum capsule, heat to redness, and dissolve the ash in a little hydrochloric acid; the fluid may then give a blue colour with ferrocyanide of potassium or a red with chromate of potash.

(*i*) *Nitric Acid and Nitrates.*—Minute traces of these substances have been found in urine. Thus Röhmann found ·004 to ·005 grm. of nitric acid in 100 c.cm. of urine.

(5) Gases.

When urine is introduced into the vacuum of a mercurial air pump (p. 328), a considerable amount of gas is evolved, from 18 to 20 vols. per cent. These consist of 17 to 18 vols. of CO_2, ·09 to ·1 vol. of O, and 1 to 1·25 vol. of N, measured at 0° C. and 760 B.P. The carbonic acid is in loose combination with the acid phosphate of soda.

(6) Abnormal Constituents.

(*a*) *Albuminous substances.*—We may find in the urine the following :—

(1) *Albumin.*—The substances classed under this term are serum-albumin an serum-globulin. They give the following reactions :—(*a*) Add a few drops of nitric acid, boil, and a precipitate appears, and if much albumin and nitric acid be present, the precipitate may have a reddish colour, which becomes yellow on adding ammonia in the cold (xantho-proteid reaction). (β) Heat a little of the urine in a test tube, and the albumin will coagulate ; if a turbidity appear, it may be due also to the presence of carbonates or of earthy phosphates, but on adding a drop of nitric acid, the turbidity disappears if due to these salts, and it will remain if it be due to albumin. (γ) Albumin is precipitated in the cold by acetic acid and ferrocyanide of potassium. This is a good test if the urine is clear. (δ) Add 5 drops of acetic acid and ⅓rd of the vol. of the urine of a saturated solution of common salt ; boil, and the albumin is thrown down as a white flocculent mass.

(2) *Hemialbumose.*—This substance, which is intermediate in character between albumin and peptone, is not precipitated by heat, but it is precipitated by nitric acid, acetic acid, and ferrocyanide of potassium, and acetic acid and common salt, and all the precipitates are dissolved on heating. It may be discovered readily by adding to the urine common salt solution and a few drops of acetic acid ; this precipitates any albumin present. Filter while warm, and allow the filtrate to cool, and if this substance be present the urine will become turbid.

(3) *Peptone.*—This substance is rarely in urine. It is not precipitated by any of the reactions above noted. Remove the two substances, albumin and hemialbumose, and test the filtrate by the biuret reaction. Add caustic soda and then a few drops of sulphate of copper, and if peptone is present a rose-red colour is produced. The ferment pepsin has also been found in traces.

(4) *Fibrin* may appear in urine if a small blood clot has been formed in the fluid. It is recognized by the microscope as fine fibres.

(5) *Hæmoglobin* is detected by its characteristic spectrum.

The quantity of albuminous matter is quickly determined by Esbach's method. A small tube has in the middle a horizontal line, in the upper part another line, and in the lower part it is graduated from 1 to 7. The scale is such that each degree (it will be observed they are unequal) represents 1 grm. of albumin for 1,000 c.cm. of urine. Fill the tube to the middle line with urine (filtered, if necessary), add to upper line a solution of picric acid consisting of 1 part of pure picric acid, 2 of citric acid, and of distilled water enough to dilute to 100 c.cm. Stop the upper end of the tube, turn it up and down a dozen times to secure thorough mixing of the fluids, and allow it to stand in a vertical position for twenty-four hours. The deposit of albumin sinks to the bottom, and the amount is read off on the scale. Suppose the deposit reaches 4 on the scale, and that the patient passes 1,600 c.cm. in twenty-four hours, the amount of albumin is $4 \times 1{\cdot}6 = 6{\cdot}4$ grms. in the twenty-four hours. That is, 4 grms. in 1,000 c.cm. $\therefore \frac{1{,}600 \times 4}{1{,}000} = 6{\cdot}4$.

(*b*) *Sugar.*—The reactions for this substance have already been given in Vol I. pp. 152-156, and special attention is directed to the spectro-polarimeter of Von

Fleischl (Fig. 63, p. 154) as a most convenient instrument for determining the amount of sugar.

(*c*) *Bile Pigments.*—The reaction of the pigments, known as Gmelin's test, has been given in Vol. I. p. 130. It depends on the oxidation of bilirubin into biliverdin and other derivative pigments. Place a few drops of the urine on a white plate, add to the centre of the fluid a few drops of fuming nitric acid (that is, nitric acid containing nitrous acid), and a series of coloured rings appear—green, violet, red, orange. The green is the characteristic tint, as the other colours may be produced by the action of the nitric acid on urobilin and indican. If the reaction is doubtful, add to the urine in a test tube a little chloroform, and then proceed as before.

(*d*) The *Bile Salts*, glycocholate and taurocholate of soda, are detected by Pettenkofer's reaction, which is strictly a test for cholalic acid. Add to the urine in a test tube a strong solution of sugar, or a bit of white lump sugar, and allow a few drops of strong sulphuric acid to trickle down the side of the tube. A purple colour appears at the junction of the fluids. (See Vol. I. p. 108.)

(*e*) *Fat.*—Urine may be milky in appearance from admixture with the fatty globules of the chyle, or it may contain fat globules in cases of fatty disease of the kidney. Chylous urine is not uncommon in hot climates, and is said to be due to the presence in the blood of the parasitic worm, *Filaria sanguinis hominis.* Fat is readily discovered in urine by shaking up a few c.cm. with ether or chloroform, and the solution thus obtained leaves a fatty stain on white paper.

(*f*) *Mucus*, containing *mucin.* This gives a viscous mass with caustic potash.

(*g*) *Pus.*—If present in large quantity, it gives a viscous mass with caustic potash, and if it is present only in small amount the pus cells, somewhat swollen and transparent, are seen under the microscope.

(*h*) *Blood.*—In hæmaturia we find red corpuscles in the urine, and in hæmoglobinuria we find hæmoglobin. To detect the corpuscles, use the microscope, or if the blood be present in considerable quantity, giving often a smoky appearance to the urine, the guaiacum reaction may be obtained. Add to the urine its volume of tincture of guaiacum and peroxide of hydrogen, and a blue colour appears. As already pointed out, hæmoglobin is detected by the spectroscope. If we boil urine containing blood with strong caustic potash, the corpuscles are dissolved and hæmatin is precipitated with the phosphates, which have a characteristic red appearance (Heller).

(*i*) *Chrysophanic Acid*, from rhubarb or senna, and *santonin* give the urine a yellow colour. In the case of the former, the urine becomes of a red carmine colour on the addition of caustic potash. Ether will dissolve out the chrysophanic acid, whilst the colour of santonin is not soluble in ether. *Carbolic acid* gives a greenish brown colour to urine. If *salicylic acid* is present, perchloride of iron produces an intense violet. We detect *iodine* (as KI) by dipping into the urine a blotting paper moistened with starch, and adding to this a drop of weak nitric acid, and a blue colour appears; or add a few drops of strong-fuming nitric acid, and then a little chloroform, and we obtain a red-violet colour. *Bromine* may be detected by adding fresh chlorine water, and chloroform or carbon disulphide, and the chloroform solution becomes yellow. If *tannin* is present, perchloride of iron gives a bluish-black. *Turpentine* gives urine the odour of violets, and, as also happens if the resin of *copaiba* be present, nitric acid causes turbidity. Urine containing copaiba gives a red with hydrochloric acid, becoming violet on heating. The addition of a little chloride of calcium, or tincture of iodine, furthers the reaction, and there is a very disagreeable smell on boiling. *Antipyrin* causes the urine to have a yellow or blood-red colour, and it may be readily mistaken for the presence of blood, especially as the solution of both is dichroic, that is, red by transmitted, and greenish by reflected, light. Add a few drops of dilute solution of perchloride of iron; this changes the reddish-yellow into dark red. It may also give a colour to a precipitate of phosphates in such urine. In like manner, *thallin* gives a greenish-yellow, or green, or greenish-black tint to urine, and perchloride of iron strikes a red with such urine. An etherial solution of this pigment gives an intense dark-green with perchloride of iron. *Naphthalin,* in large doses for several days causes the urine to be dark brown; add to a drop or two of such urine 1 c.cm. of strong sulphuric acid, and, at the junction of the two fluids, a beautiful dark green makes its appearance.

(*k*) *Aceton,* $CH_3.CO.CH_3$, is found in diabetic urine. Lieben's test is as follows:—Dissolve 1 grm. of iodide of potassium in 2 c.cm. of caustic potash solution and boil. Pour the urine on the surface of this fluid. A ring of phosphates is precipitated, and if aceton is present, the deposit becomes yellow and yellow particles of iodoform fall to the bottom of the fluid.

The *sediments* appearing in urine are readily distinguished by the microscope (Fig. 223), and they may be divided into :—

1. **Deposits found occasionally in Acid or Alkaline Urine, usually in the former.**—(1) *Uric Acid* (Vol. I. Fig. 35, p. 100).—Yellow, reddish, or brown coloured sediment, consisting of little masses of crystals. It assumes various crystalline forms : (*a*) lozenge-shaped rhombs ; (*b*) rectangular tables or prisms ; (*c*) dumb-bell crystals ; and (*d*) spindle or barrel-shaped forms.

(2) *Urates.*—Appear when the urine is cold, if the salts are present in excess, because they are much more soluble in hot water than in cold. Consequently, every deposit which disappears on heating consists of urates. They usually form a heavy precipitate at the bottom of the glass, presenting an ill-defined upper border. The deposit may be white, or deeply tinted by the colouring matter of the urine. Such deposits have been termed "lateritious deposit," "brick-dust deposit," "critical deposit," and "purpurates." (*a*) *Urate of soda* is amorphous in urine, but when prepared artificially, by acting with uric acid on sodium phosphate, it forms acicular crystals (Vol. I. Fig. 36, p. 101). (*b*) *Urate of ammonia* appears as an amorphous granular sediment, or in the form of brown round balls covered with spines (Vol. I. Fig. 37, p. 101). (*c*) *Urate of lime* is very rare, and appears as a white amorphous powder.

(3) *Phosphates.*—In acid urine, phosphates may be present in excess, when they appear as a cloudy precipitate, at once soluble in a drop of nitric or hydrochloric acids.

(4) *Oxalate of Lime* (Vol. I. Fig. 65, p. 166).—This salt is easily detected by its characteristic crystals, which are octohedra (*a*) or dumb-bells (*b*). It is not found as a distinct sediment, but exists as isolated crystals entangled in the mucous cloud with which it is usually associated.

(5) *Cystin* (Vol. I. Fig. 34, p. 97).—This is occasionally found as a sediment mixed with amorphous urates. Under the microscope its transparent, colourless,

six-sided plates can scarcely be mistaken. If it exist in large quantity along with urates or phosphates, or both, it may be distinguished from them by heating and adding acetic acid. The heating dissolves the urates and the acid dissolves the phosphates, but neither has any effect on cystin.

(6) *Tyrosin* crystallizes in long, white, silky needles, forming stars or crosses. They are scarcely soluble in boiling water, and they are insoluble in ether (Vol. I. Fig. 30, p. 93).

Fig. 223.—The more common substances that may be detected in the urine by the microscope; 1. Uric acid.—*a*, lozenge; *b*, barrel; *c*, group of lozenges seen sideways; *d*, dumb-bell form; near *d*, a rosette is seen. 2. Oxalate of lime.—*d*, octohedra; *b*, dumb-bell. 3. Leucin. 4. Tyrosin. 5. Pus corpuscles. 6. Pus, after acetic acid. 7. Epithelium. 8. Triple phosphate.—*a*, knife rest; *b*, same with bevelled edge; *c*, feathery semilunar form. 9. Urates.—*a*, acid urate of soda; *b*, urate of ammonia. 10. Cystin. 11. Epithelial cells, *a*, showing fat globules; *b*, fat globules. 12. Epithelium from uriniferous tubule. 13. Epithelium from bladder. 14. Epithelium from ureter. 15. Epithelium from ureter. 16. Leucocytes. 17. Spermatozoids. 18. Slightly granular casts. 19. Cast with blood corpuscles and fat globules. 20. Blood cast. 21. Red blood discs. 22. Leucocytes. 23. Granular cast. 24. Highly granular cast. 25. Hyaline casts.

(7) *Leucin* occurs as yellowish-brown balls, or highly refractive spheres, composed of needle-shaped crystals (Vol. I. Fig. 29, p. 92).

2. **Deposits found occasionally in Alkaline Urine only.**—They are all dissolved on adding a few drops of nitric or hydrochloric acids. They are:—

(1) *Ammoniaco-Magnesian, or Triple Phosphate* (Vol. I. Fig. 18, p. 42).—This salt always exists in ammoniacal urine, and is recognized by its well-known crystalline forms. It is found in variously modified six-sided crystals, some elongated, others nearly square; some having sharp angles, while others have broad facets, and in very alkaline urine they appear as feathery crystals.

(2) *Phosphate of Lime.*—It is usually an amorphous white powder, but occasionally it appears aggregated into rosette-like crystals.

(3) *Urate of Ammonia* is always present in alkaline, and rarely in acid urine. It has been described above.

(4) *Urate of Lime* is also occasionally found in alkaline urine.

3. **Organized Deposits.**—(1) *Mucus.*—When urine is left at rest, cloudy transparent flocculi are seen, which consist of mucus entangling various forms of epithelial cells, derived from the urinary passages. If the supernatant liquid is carefully poured off, and acetic acid added to the mucus, it coagulates, forming delicate molecular fibres.

(2) *Blood.*—Urine containing blood has a smoky appearance that the practised eye can detect. Identify the blood corpuscles by means of the microscope, or use the spectroscope. As a rule, the blood corpuscles are colourless and have lost their biconcave form, and are globular from the imbibition of water. Urine containing blood always contains a trace of albumin.

(3) *Pus.*—If there be a thickish yellow deposit at the bottom of the vessel, which has a stringy consistence, it usually consists of mucus containing pus. Pour off the supernatant fluid, and add to the deposit an equal bulk of caustic potash. It gelatinizes, becoming so thick and tough that it cannot be poured from the test tube. When pus is present in small quantity, by means of the microscope detect the pus corpuscles.

(4) *Tube Casts.*—These bodies are detected by allowing any sediment to fall to the bottom of a conical glass, removing a small portion of it with a fine pipette, placing a drop on a slide, covering it with a thin glass, and examining it with a power of 250 diam. linear. Tube casts are of various kinds, but they may be conveniently classified under the following: (*a*) *Fibrinous* casts, often containing blood corpuscles; (*b*) *Desquamative* casts, containing epithelial cells; (*c*) *Granular* or *fatty* casts, containing numerous oil globules, free, or in the epithelial cells; (*d*) *Hyaline* or *waxy* casts, solid and transparent, or containing epithelial cells, granules, corpuscles, leucocytes, and fat globules. These may be stained by osmic acid or carmine.

(5) *Epithelium*—(*a*) *renal epithelium from the tubuli uriniferi*, polyhedral cells, usually granular, and showing an oval nucleus. They are much smaller than the cells of the ureter and bladder. (*b*) *Epithelium from urinary passages*, including those from pelvis, ureter, and bladder. Flat polygonal cells, often showing several nuclei, or pear-shaped cells, may be found. The epithelium of the ureter is cylindrical and has a *single* nucleus. Flat polygonal cells with a single nucleus, in the urine of a female, may be derived from the vulvo-vaginal region.

(6) *Spermatozoids, Torulæ, Sarcinæ, Bacteria, Micrococci, Vibriones, etc.*—These, occasionally found in urine, may all be readily detected by their characteristic microscopical appearances.

The following table shows approximately the quantities in grms. of the various substances eliminated by the kidneys of a healthy adult man in twenty-four hours.[1]

	Total amount in grms.	Percentage amount in grms.
Water,	1436-1444	96
Solids,	57-63	4

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[1] I have placed queries where reliable information was not available.

		Total amount in grms.	Percentage amount in grms.
Organic	Urea,	25-30	2·5-3·2
	Uric acid,	·7	·05
	Kreatinin,	1·7-2·1	·1
	Xanthin, hypoxanthin,	·5	·003
	Oxaluric acid,	?	Traces.
	Allantoin (in pregnancy and in newly-born children),	?	?
	Sulphocyanic acid,	?	·003-·01
	Hippuric acid,	?	·02-·06
	Oxalic acid,	?	10-14 (Herbivora).
	Glycerin-phosphoric acid, lactic acid, phenolsulphuric acid, kresolsuphuric acid, brenzcatechin-sulphuric acid, paroxyphenylacetic acid,	?	Traces.
	Urobilin,	?	?
	Indican,	?	1·8 (?)
Inorganic	Chloride of sodium,	15-20	1-1·5
	Chloride of potassium,	?	?
	Phosphoric acid (with alkalies 1·6, with magnesia ·6, with lime ·3),	2·5-3	·16
	Sulphuric acid,	2-2·5	·16
	Carbonic acid,	?	?
	Nitric acid and nitrates,		Traces.
	Sodium,	5-7·5	·4
	Potassium,	3-4	·23
	Calcium,	·29	·019
	Magnesium,	·4-·5	·03
	Ferrum,	·45	·03

The sum of the averages of the above quantities of solids is 63·2 *grms. ; and about ⅔rds of this quantity are organic and ⅓rd inorganic.*

Chap. III.—THE PHYSIOLOGICAL CHARACTERS OF THE URINE.

The kidneys separate a considerable quantity of water, inorganic salts, and nitrogenous matters. A diet rich in alkaline salts introduces a large quantity of these into the blood. The plasma of a herbivorous animal therefore contains more alkaline salts than that of a carnivorous animal. We find a corresponding difference in the urine of the two classes. The urine of an animal fed largely on flesh is clear, acid, is rich in urea and phosphates, and often deposits crystals of uric acid, while that of a herbivorous animal is usually muddy when cold, has an alkaline reaction, is so rich in carbonates that it effervesces on adding an acid, but is poor in phosphates, and, finally, it contains hippuric, instead of uric, acid. The proof that the nature of the food is the chief cause of these differences is, that if a herbivorous animal is starved, its urine becomes like that of a carnivorous creature, or, in other words, it becomes carnivorous by living on its own tissues. A mixed diet, as used by man, produces a urine of intermediate character, and the urine may be caused to lean in characters to the side of the carnivor or of the herbivor by adding to the diet an excess of flesh or an excess of vegetable substances.

In man, about 60 per cent. of the total water eliminated from the body escape by the kidneys, and 40 per cent. by the lungs and skin. Munk points out the remarkable circumstance that in carnivora 70 per cent. of water escape in the urine, and 30 per cent. by the lungs and skin, while in herbivora the proportions are 30 per cent. in the urine and 70 per cent. by the lungs and skin. Thus, in herbivora much more water is eliminated by the lungs and skin than by the kidneys, and in carnivora the reverse is the case. If a large quantity of urine be passed, or, in other words, if the elimination of water be increased, the total quantity of solids eliminated in twenty-four hours will be probably increased, although the specific gravity of the urine may be low. Thus the amount of urea may be increased by 3 to 5 per cent. On the other hand, if the body loses water largely by other channels, as by the skin and lungs, the urine becomes concentrated. The total deprivation of water causes a fall of $\frac{1}{5}$th or $\frac{1}{6}$th of the normal amount. Substances readily soluble quickly appear in the urine. Thus iodide of potassium may be detected in from five to ten minutes after it has been swallowed, the pigment alizarine has been found in the urine after fifteen minutes, and that of rhubarb after twenty minutes.

The most important organic constituent is *urea*. It is the chief nitrogenous waste product eliminated from the body, containing 46·7 per cent. of nitrogen, or, in other words, it is the organic substance which contains the smallest amount of carbon in proportion to the amount of nitrogen. Thus albumin contains 1 part of N to 4 of C, while in urea the ratio of C to N is 1 : $\frac{1}{2}$. The amount of urea eliminated is influenced largely by the amount of albumin or proteid matter in the food. During starvation the daily amount eliminated by an adult man falls from 30 grms. to 6 or 9 grms., and the minimum quantity is eliminated daily until shortly before death. The chief locality in which urea is formed is the liver. It is not formed by the kidneys, as is proved by the fact that urea exists in large quantity in the blood after removal of the kidneys. It can also be shown that there is less urea in the blood of the renal vein than in the blood of the renal artery. Liebig supported the view that urea was formed at the expense of muscular tissue. He supposed that muscular activity was carried on at the expense of nitrogenous matters obtained either from the muscles themselves or from the food. According to this view, he divided foods into *tissue-forming*, such as albuminates, and *heat-pro-*

ducing, such as carbohydrates and fats. The first he supposed were used for the construction of the tissues, and for the production of muscular work; whilst the second, by oxidation into carbonic acid and water, were regarded as the producers of heat. It is well known that the chief products of the decomposition of nitrogenous matters are urea and uric acid, whilst those resulting from non-nitrogenous matters are carbonic acid and water. If, therefore, the theory of Liebig were true, we would expect to find that prolonged muscular exercise would cause an increase in the amount of urea and uric acid separated by the kidneys. This question has repeatedly been put to the test of experiment, more especially by Voit, Parkes, Flint, and Fick and Wislicenus.

The observations made by the latter, Fick and Wislicenus, both expert physiological chemists, are generally regarded as conclusive. These two observers, in 1866, ascended the Faulhorn, one of the Swiss alps, about 1,956 metres high. For seventeen hours previous to the ascent they took no nitrogenous food, and the ascent occupied six hours. The urine passed was collected and examined. It was collected in four portions, each of which was separately examined :—(1) before the ascent; (2) during the ascent; (3) during six hours of repose after the ascent, at the end of which time they had a meal rich in nitrogenous matter; and (4) during the night passed on the mountain after this meal. It will be observed that the amount of work produced during the ascent must have resulted either from changes in their albuminous tissues, or been derived from the non-nitrogenous matter used in their food. By thus collecting and estimating the urea formed, and assuming that it was all produced from albuminous matter, it was not difficult to calculate the amount of albuminous matter represented by this quantity of urea, and the amount of energy liberated by the oxidation processes. The actual amount of energy, in the form of muscular movement, expended during the ascent was ascertained by multiplying the body-weight by the height. Thus, the work done by Fick was 66 kilos. × 1,956 = 129,096 kilogrammetres, and that of Wislicenus was 76 × 1,956 = 148,656 kilogrammetres. But the amount of energy liberated by the presumed decomposition of albuminous matters was found in the case of Fick to be only 66,690 kilogrammetres, and of Wislicenus only 68,376 kilogrammetres—both little more than one-half of the energy actually expended. It was evident, therefore, that the energy expended could not have been entirely obtained from the decomposition of nitrogenous matters, and that the amount of urea was not, as Liebig had supposed, any measure of the muscular waste. The following table gives the amount of nitrogen in the urea excreted in the different periods :—

URINE.	FICK. Grammes of Nitrogen in the Urea.		WISLICENUS.
1. During period of seventeen hours previous to the ascent,	6·9	...	6·6
2. During six hours occupied by ascent,	3·3	...	3·1
3. During six hours of repose after ascent,	2·4	...	2·4
FULL NITROGENOUS MEAL.			
4. During the night spent on the mountain after the meal,	4·1	...	5·3

On studying these facts, it will be observed (1) that the amount of nitrogen excreted was very much lessened by the non-nitrogenous diet, even during the ascent and during the period of repose, when muscular waste might be supposed to have been going on; (2) that the amount of nitrogen was increased immediately after a nitrogenous diet; and (3) that the energy actually liberated during the ascent was much greater than could be accounted for by presumed changes in nitrogenous matter, estimated from the amount of urea excreted. The inference is that muscular energy is at least partly derived from changes occurring in carbohydrates and fats, and not, as Liebig supposed, from changes in nitrogenous tissues alone. These researches have been corroborated by Pettenkofer and Voit, and by Parkes, who have shown that the amount of carbonic acid is largely increased during muscular exercise, exactly what would be expected if we assume that, during muscular work, carbohydrates and fats are chiefly used. Slightly different results as regards the amount of urea excreted have been obtained by Flint and B. W. Richardson in observations on Weston, a famous pedestrian; and it would appear that in some cases the amount of nitrogen eliminated may not be diminished, but remain merely normal, or even be slightly increased.

The theory of Liebig is also conclusively negatived by the observation, made by Haycraft, that only the smallest trace of urea is found in muscle, and that the amount is not increased by prolonged muscle work. Further, it can be shown that there is no increase in the amount of urea in the blood circulating through muscle. We must therefore look for the source of urea elsewhere, and all the evidence points to the liver. Thus, Cyon found that 100 c.cm. of blood transfused eight times through the fresh liver kept at the temperature of the body became richer in urea, from ·08 before transfusion to ·176 grm. after transfusion. Allowing for the obvious source of error that the repeated transfusions washed out urea previously existing in the liver, Noël-Paton shows that even in Cyon's experiment ·0766 grm. of urea was actually formed. Schroeder proved that in the liver of a fasting dog there was no increase in the urea after the blood had passed through the liver several times, while in a dog during full digestion there was an increase of 27·5 per cent., and the addition of carbonate of ammonia caused the enormous increase of 222·9 per cent. The view that the liver is the seat of origin of urea is strongly supported by the clinical observation that in acute yellow atrophy of the liver urea disappears from the urine while leucin and tyrosin exist in large quantities. Urea also diminishes considerably in the peculiar changes induced in the liver by phosphorus poisoning. Finally, Noël-Paton[1] has clearly demonstrated that the destruction of blood corpuscles, and the consequent setting free of hæmoglobin in the blood, cause not only a great increase in the secretion of bile, but also an increase in the amount of urea eliminated by the kidneys. This is well shown in Fig. 224, in which the dotted line indicates the number of red corpuscles per c.mm., and the continuous line the amount of urea, as determined in a dog which had passed, previous to the experiment, on an average, 7·679 grms. of urea *per diem.* On the 8th day 2 grms. of pyrogallic acid were injected, and 1·5 grm. on the 9th day. The average number of red blood corpuscles in this dog was 7,860,000 per c.mm. After the injection of the pyrogallic acid, the number fell on the 10th day to 5,190,000 per c.mm., showing a destruction of 2,670,000 per c.mm. This indicates a liberation of 48·9 grms. of hæmoglobin. The urea at the same time rises 11·855 grms. above the normal. It will be observed that when the destruction of corpuscles is greatest the amount of urea

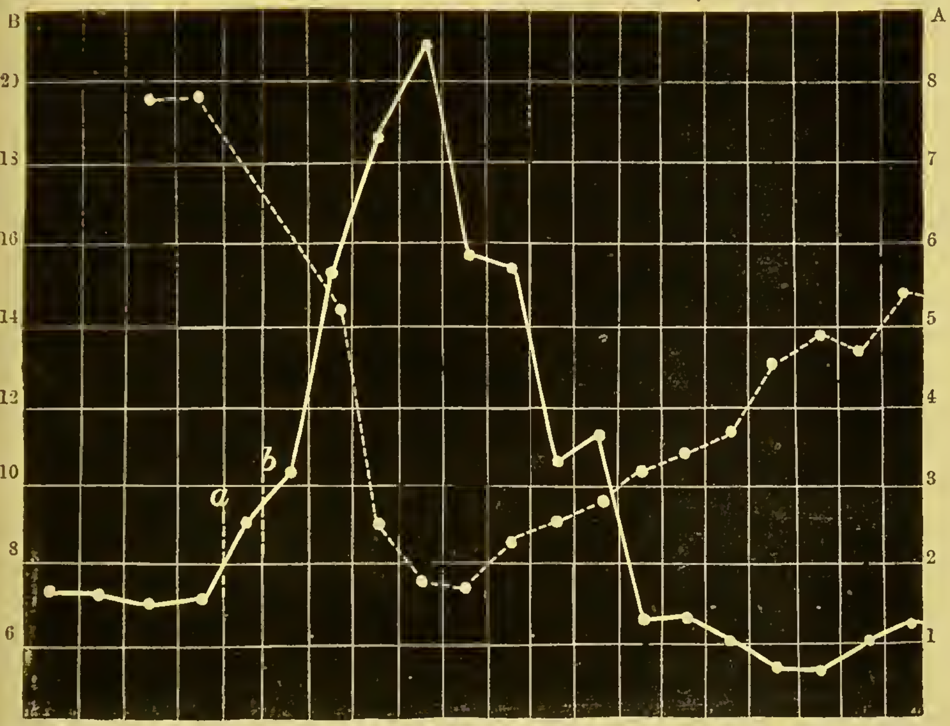

FIG. 224.—Influence of pyrogallic acid on urea excretion and on number of red blood corpuscles, according to Noël-Paton. 2 grms. given at *a* and 1·5 grm. at *b*. A, red blood corpuscles in millions per c.mm.; B, urea in grms.

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[1] D. Noël-Paton, "The Relationship of Urea Formation to Bile Secretion." *Jl. of Anatomy and Physiology*, 1886. See also *Brit. Med. Jl.* 1886.

is greatest. From similar experiments with toluylendiamin, Noël-Paton shows that urea production is increased by the destruction of blood corpuscles, and that the biliary secretion and urea formation bear a direct relationship to each other. One, and probably the chief, source of urea is the destruction of red corpuscles in the liver.

The excretion of urea shows a daily variation, sinking from 9 A.M. till noon or 1 P.M., then it rises and reaches a maximum about 4 P.M., then falls till 8 or 9 P.M., then rises towards 11 P.M., and then sinks during the night. These variations probably largely depend on the hours of taking food, and the maxima and minima will vary according to the custom of the person in this respect.

The next constituent of urine of special importance is *uric acid*. As already shown, it exists in human urine; it is often abundant in that of carnivora, but it may be absent from, or only in traces in, the urine of herbivora, except during suckling. It exists in large quantity in the urine of birds and in the excrements of snakes, in reptiles and birds taking the place of urea. Closely related to uric acid, we have xanthin and hypoxanthin, and it has been suggested that by oxidation these bodies are transformed into uric acid. Thus, xanthin is $C_5H_4N_4O_2$; less O is hypoxanthin, $C_5H_4H_4O$; plus O_2 is uric acid, $C_5H_4N_4O_3$. (Vol. I. pp. 97 and 103.)

It is highly probable that one of the nitrogenous waste products formed in muscle and nervous tissues is *kreatin*, $C_4H_9N_3O_2$. The body closely related to it, *kreatinin*, $C_4H_7N_3O$, is always found in the urine, and the transformation occurs in relation with the functions of the kidney. This is proved by the observation that there is no kreatinin in the blood. On the other hand, as ligature of the ureters does not cause the appearance of kreatinin in the structure of the kidney, it is probable that kreatinin is formed in the urine itself. The evidence is conflicting as to the transformation of kreatin into urea, and on the whole it is an unlikely supposition. (See Vol. I. p. 95.)

As already indicated, *hippuric acid* takes the place of uric acid in the urine of herbivora, and like uric acid, it is a product of the metabolism of albuminous food. It is also formed by a synthetic combination of glycocin and benzoic acid; but, as shown in Vol. I. p. 105, this cannot be regarded as the chief source of its formation in herbivora. If we could suppose albuminous matter splitting up so as to form, with other substances, glycocin and benzoic acid, then the formation of hippuric acid would be evident, but upon this point no satisfactory evidence exists.

It is well known that quinic acid, nearly related to benzoic acid, exists in hay, grass, etc., and if glycocholic acid were decomposed in the intestine into cholalic acid and glycocin, the glycocin, carried to the liver, might there combine with the acid belonging to the benzol series, to form hippuric acid. Salkowski has also suggested that the putrefaction of albumin in the intestine may form phenol-propionic acid, and that this may be oxidized into benzoic acid.

The *aromatic bodies* in urine, phenolsulphates, etc., are absorbed from the small intestine and then eliminated by the kidneys. They are well recognized products of the splitting up of the complex albuminous molecule by pancreatic digestion. In severe constipation, the amount of these substances is increased, and they make their appearance in the urine.

We have already discussed the origin of *urobilin*. It is derived from bilirubin which, in turn, is one of the products of the decomposition of hæmoglobin in the liver (p. 120). The source of *indican* is more doubtful, but considering its relation to indol (Vol. I. p. 110) it is probably derived from this substance, also one of the products of putrefactive processes in the intestine.

As we have seen, considerable quantities of *saline matters* are eliminated, and the amount depends chiefly on the supply of these salts by the food. Thus, if a large amount of common salt is taken in the food, the quantity is increased in the urine ; on the other hand, there is a continual separation of chloride of sodium, because if it is entirely withheld from the food, the amount excreted falls on the second day, and a minimum quantity continues to be excreted till death. After starvation from salt, if it be given, the quantity in the urine does not rise to the normal, but the blood and tissues are supplied in the first instance, and then the excess appears in the urine. The phosphates in the urine come from the food, and also from the metabolism of tissue. The sulphates are derived primarily from the sulphur compounds resulting from the decomposition of albumin. Food, as a rule, only contains traces of sulphates, and these do not nearly account for the amount of sulphates in the urine. On the other hand, their origin is betrayed by the fact that the excretion of urea and of sulphates always bears a fixed ratio, said to be 1 : 16–18. The bases also are derived from food, and from tissue metabolism.

The following conditions also affect the urine :—

1. **Age.**—Considering the weight of the body, an infant excretes more urine, and more urea and salts, than an adult. In the aged the quantity and the solids are much diminished.

2. **Sex.**—The female excretes less urine, and the proportion of solids is also less, than the male.

3. **Sleep.**—The urine passed in the morning is usually dense, highly coloured, and more strongly acid than at any other period of the day. The water is diminished, owing to the increased activity of the skin during the night. The amounts of urea, chloride of sodium, and sulphates are diminished, and phosphates alone are increased.

4. **Pregnancy.**—During this state, the urine is often high coloured and dense, and shows on the surface a pellicle, called *kyestin*, of an iridescent appearance and a peculiar odour. When examined microscopically, it is found to consist of numerous crystals of the triple phosphate, molecular matter, bright refractive particles like those of fat, and possibly minute *torulæ* or other microscopic organisms.

The following account of the urines of different animals is chiefly derived from Munk :—[1]

1. **Monkey.**—Sp. gr., 1007-1015 ; urea, 1-2 per cent. ; small amount of uric acid ; ·3 per cent. NaCl. ; rich in carbonates. Similar, on the whole, to human urine, when a man lives on a diet rich in vegetable matter.

2. **Pig.**—Sp. gr., 1010-1015; clear, acid, or alkaline, according to food; when alkaline, rich in carbonates ; rich in urea ; contains uric acid, xanthin, and guanin.

3. **Dog.**—Sp. gr., 1025-1055 ; dark coloured ; 4, 6, 8, or 10 per cent. of urea ; not much uric acid, but its place occupied by kynuric acid, $C_{10}H_7NO_3+H_2O$; contains kreatinin and indican ; rich in sulphates ; poor in chlorides.

4. **Cat.**—Similar to that of dog ; has a smell like that of onions, from the presence of a volatile sulphur-containing substance. On heating it, a sulphurous acid smell given off.

5. **Horse.**—Quickly becomes turbid ; alkaline ; becomes darker coloured after exposure to the air ; sp. gr., 1030-1055 ; contains much mucin ; rich in hippuric acid, $C_9H_9NO_3$, to the extent of 2 per cent., chiefly as hippurate of lime. Straw, grass, and hay in the food increase the amount of hippuric acid, while with unhusked grains, carrots, beet-roots, and potatoes—the amount is diminished. With meadow-hay alone a horse will excrete *per diem* about 50 grms., and with oats and a moderate amount of hay, 15-20 grms. of hippuric acid ; the aromatic substances are present in large amount, so that a horse fed with oats and hay yields *per diem* 3 grms. of phenol, and ·3 to ·5 grm. of indican ; carbonates present in large amount, so that when the urine cools carbonate of lime exists in a finely divided state ; sulphates also present to the extent of 15 grms. *per diem* ; chlorides, 25 grms. *per diem*. Salkowski states that the urine of the horse contains 3 to 4 times as much lime as human urine. It is important to note that in herbivora nearly the whole of the phosphates of the food are excreted with the fæces. Thus in carnivora 90 per cent. of the phosphoric acid of the food appear in the urine, but in the horse only ·1 per cent. Even in man, vegetable food diminishes the amount of phosphates eliminated by the kidneys. If there is an abundance of lime salts in the food, as is the case with vegetable food, then phosphoric acid is not eliminated to a great extent by the

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[1] Munk, *op. cit.* p. 210.

kidneys. On the other hand, if phosphate of potash is added to the food, the amount of phosphoric acid eliminated by the kidneys increases, while both the lime and magnesia are diminished. If lime and magnesia are present in the intestine, they unite with the phosphoric acid, and the salts, phosphates of lime and magnesia, escape in the fæces; but if these bases are not present, or present in small quantity, the phosphoric acid united to soda and potash passes into the blood, and phosphates appear in the urine.

A horse in the stable excretes 3 to 4 litres of water in twenty-four hours, if he is supplied with water to the extent of 10 to 15 litres, so that only about $\frac{1}{3}$rd of the water leaves by the urine, the remaining $\frac{2}{3}$rds being eliminated by the lungs and skin.

6. **Ox.**—Generally like that of horse, but in young animals, not milking, it is less in quantity than that of horse; sp. gr., 1020-1030; milk cows with rich food and plenty of water pass 20 to 25 litres *per diem*, having a sp. gr. of 1007-1015; with rich food, urea abounds, but if the food is deficient in albuminous matter, hippuric acid increases; phenol not so abundant as in horse. Suckling calves pass a clear, acid urine, rich in phosphates, uric acid, kreatinin, and allantoin; poor in urea and uric acid.

7. **Goat.**—Like that of cows; sp. gr., 1006-1015; average quantity, ·3 to ·5 litre.

8. **Rabbit.**—Turbid; alkaline; concentrated; viscid; rich in carbonates, so that it effervesces with an acid.

When we consider the very small percentages of urea, uric acid, etc., in the blood, it seems remarkable that they should be found in considerable quantities in the urine. This is less to be wondered at if we remember that the quantity of blood flowing through the kidneys in a given time is very great. This matter is clearly stated by Munk. In a dog weighing 30 kilogs. we have $\frac{30}{13} = 2{\cdot}31$ kilogs. of blood. The rapidity of the circulation is 15 seconds; in a minute, therefore, $4 \times 2{\cdot}31 = 9{\cdot}24$ kilogs. of blood will pass through the body, and in twenty-four hours, $9{\cdot}24 \times 60 \times 24 = 13{,}305{\cdot}6$ kilogs. The weight of both kidneys is $\frac{1}{200}$th of that of the body, so if we suppose the blood to be uniformly distributed, $\frac{13{,}305{\cdot}6}{200} = 66{\cdot}53$ kilogs. of blood will pass through the kidneys in twenty-four hours. Next, supposing the blood to contain ·5 grm. of urea per 1,000, in twenty-four hours 66·53 kilogs. of blood would supply about 33·3 grms. of urea to the kidneys. As the kidneys are very vascular in proportion to their weight, it is likely that even more blood flows through them than through any other glandular organ, so that 40 to 50 grms. of urea will probably be supplied to the kidneys. As a dog on a flesh diet excretes from 30 to 35 grms. of urea in twenty-four hours, we see that a very large proportion of the urea in the blood is caught by the secreting cells of the kidney. The matters secreted are removed as quickly as formed, so that only traces of urea are to be found in the kidneys.

CHAP. IV.—MECHANISM OF THE SECRETION OF URINE.

The kidneys are supplied with blood, through the renal arteries, directly from the arterial system; the blood is conveyed from them by renal veins, which empty themselves into the inferior cava, and they are also richly supplied with lymphatics. During its passage through the organs, the blood loses certain materials which constitute urine, and this is conveyed from the kidney to the bladder by the ureters. This loss might result from a process of transudation from the blood, or from activity of epithelial cells, or from both together. Numerous experiments and observations, first made by Ludwig, have shown that the secretion is always increased with an increase of blood pressure. It has been observed that the secretion ceases when the pressure is such that the renal venous circulation becomes very slow. Pressure on the aorta, or severe hæmorrhage, diminishes the secretion, while increased aortic pressure produced by ligaturing the larger arteries causes it to increase. The pressure in the renal artery is about the same as that of the carotid, thus, in a dog, amounting to 120 to 140 mm. of mercury, and it has been ascertained that if it sinks to 30 or 40 mm., there is no secretion of urine. Ligature of the ureter at once stops the secretion, and any influence which tends to increase the pressure in the ureter has the same effect. The rapidity of secretion depends on the difference of the pressure in the renal artery and the pressure in the urinary channels, and consequently when the pressure of the latter amounts to about two-thirds of the aortic pressure, the secretion stops. It would thus appear that the secretion depends partly upon difference of pressure in the vessels of the kidneys and in the ureter. If the pressure in the kidney be much increased, more urine will be secreted; and the reverse holds good. The state of the blood has also a certain influence. Thus an increased quantity of water, introduced as drink, by simply increasing the blood pressure, is followed by a larger excretion of water. From the anatomical arrangements of a Malpighian body, and especially from the fact of the efferent being smaller in calibre than the afferent vessels, it is evident that the pressure in the vessels forming the glomerulus must be great, and the rate of flow must also be slow. If so, water and saline matters amply, and albumin to a small extent, will be separated from the blood in the Malpighian body by a simple process of filtration under pressure, and will fall into the dilated end of the uriniferous tubule Bowman's capsule).

Various objections may be urged to the pressure theory, when it is stated without qualification. Thus, the urine in carnivora and in starving herbivora is acid, while the blood plasma is alkaline. Again, the quantity of the urea, salts, etc., in the urine is much greater than in the blood. It is also known that certain substances, such as kreatinin and hippuric acid, are not found in the blood. If urine were simply a transudate under pressure, one would expect its composition to be similar to that of the plasma, from which it came. Again, it is known that pressure or ligature of the renal vein, which would increase the pressure in the glomeruli, is followed by stoppage of the secretion, or at least by a diminution. Ludwig modified the pressure theory to a considerable extent by showing that the tubuli are surrounded by lymphatic channels, and he holds that diffusion takes place between the lymph and the fluid separated from the glomeruli into Bowman's capsule by pressure (and which we may suppose to be rich in water) and the blood-vessels containing concentrated blood (in consequence of the removal of water in the glomeruli), and also between the transudate in the uriniferous tubules and the lymphatic channels surrounding them. According to his theory, blood pressure plays the principal part; under its influence, the plasma of the blood, less the fats and albuminates, filters through the walls of the capillaries of the glomerulus. Then it is brought into contact with the epithelium of the tubes and the lymph in the channels surrounding the tubes; and some matters (chiefly water) are re-absorbed from the fluid in the tubules by the lymph, and possibly by the blood in the capillaries of the efferent vessel. It appears to the author that Ludwig's theory does not attach sufficient importance to the activity of the epithelium lining the tubes. In the positions where elimination would probably take place, as in the tube at its origin, and in the descending limb of Henle's loop, the epithelium is distinctly glandular; whereas, in the other portions, it has more of the appearance of protective epithelium, such as is found in the ducts of all glands. If we assume the activity of the cells, we can understand how the quantitative proportion of the substances in the urine is altogether different from that in which those substances exist in the blood, and we can account for the presence of substances in the urine which do not exist in the blood. Direct observations have also been made in the direction of demonstrating the activity of these cells. Thus Von Wittich has found uric acid crystals in the epithelial cells of the convoluted tubules of the kidneys of birds, while some were found in Bowman's capsule. Heidenhain has also shown that if sulpho-indigotate of soda (which gives a blue colour to the urine) be injected, the blue colour is always found in the convoluted tubes, and never in the glomeruli, nor in Bowman's capsule. Lastly, the synthesis of hippuric acid, already referred to (p. 422), undoubtedly occurs in the kidney, in the case of carnivora (Schmiedeberg and Bunge), as proved by the fact that if blood containing glycocin and benzoic acid is passed through the isolated kidney, at the temperature of the body, hippuric acid is formed. It has also been shown that even if the filtration of water stop from a great fall of blood pressure, the pigment above mentioned will still make its appearance in the convoluted tubules. It does not seem then to be so much a matter of pressure as of rapidity of flow that determines the elimination of the water, because a high blood pressure *per se* (as is caused by tying the renal vein) will not cause increased secretion, but the reverse. J. Munk has shown that in addition to rapidity of flow, the presence of oxygen and also of some of those substances which we find in the urine, such as urea and salts, favours secretion by stimulating the cells of the tubules. This explains also why celerity of flow favours secretion, because the faster these stimulating substances are brought near the cells, the quicker the cells will work, and the greater will be the secretion in amount.

There can be no doubt that the epithelial cells excrete, or rather, first secrete such matters as urea, uric acid, and possibly even a portion of the salts, and that these are flooded out of the convoluted tubes by the water separated mechanically in the glomeruli. The cells, however, are stimulated only when the amount of these substances in the blood reaches a certain height, and this will be largely determined by the quickness or slowness of the stream in the renal capillaries and by the amount of water in the blood. Thus, if we increase the water, or increase the quickness of the blood stream, we increase also the secretion of the urine. There is no proof that albumin escapes from the glomeruli, and it is highly probable that the layer of epithelium covering the glomerulus may explain why it does not escape.

It would appear that even in the bladder there may be slight changes in the quality of the urine. Thus Ashdown found that aqueous solutions of strychnin, eserin, and curara, and emulsions of chloroform and ether, were absorbed when injected into the bladder. Water, urea, and iodide of potassium may also be absorbed.

Chap. V.—THE INNERVATION OF THE KIDNEY.

The nerves of the kidneys are derived from the renal plexus and the small splanchnic nerves. Filaments have been traced as far as the apices of the papillæ. Little is known as to the exact influences of the central nervous system on the secretion of urine. After division of the renal plexus, the urine becomes abundant, and of low specific gravity, and albumin may appear in it. Section of the splanchnic slightly increases the secretion. This nerve contains the vaso-motor fibres (passing chiefly from the first dorsal into the sympathetic) and also the vaso-motor fibres of the intestine. There is thus paralysis not only of the renal vessels, but also of those of the intestinal tract, and the pressure in the renal vessels is consequently only moderately high. Stimulation of the distal end of the splanchnic augments it, an effect likely to be produced if we suppose that this nerve contains the vaso-motor filaments supplying the vessels of the kidney. A general vaso-motor paralysis causes a great fall of pressure in the renal vessels, and therefore a diminished secretion of urine. This is seen after section of the spinal cord in the cervical region. If, however, the lower end of the divided cord is stimulated, the blood pressure rises both in the vessels of the body and of the kidney, and the secretion is then more copious. Whilst there can be no doubt that the cerebral centres may affect the secretion of urine, as evidenced by the well known results of emotional conditions, the channels by which the influences pass are unknown. The centre of origin of the renal nerves is in the floor of the fourth ventricle, near the roots of the vagus, so that puncture of this spot may cause an increased flow of urine containing blood and albumin.

Roy and Cohnheim have shown by the use of the oncometer (p. 174) that the volume of the kidneys varies rhythmically, like that of the spleen. (See Plate *A*, Fig. 3.) If the contractile coats of the renal arteries contract, the organ diminishes in volume, and the reverse is the case when the calibre of the vessels is increased. The curves of the volume of the kidney do not run parallel with those of the blood pressure, but they show both the large respiratory waves and the individual heart beats. Any circumstance affecting the vaso-motor centres probably affects the volume of the kidney. Thus stimulation of the centres by venous blood, as in asphyxia, causes a diminution, and strong stimulation of a sensory nerve has the same effect. No vaso-dilator fibres exist, shown by the fact that stimulation of the splanchnics always diminishes the volume. Cohnheim has also shown that if water and urea are injected into the blood, the kidney first shrinks and then dilates, whilst a solution of acetate of soda always caused dilation. This points to the existence of an intra-renal nervous mechanism, especially as the results occur even after division of the renal plexus.

Chap. VI.—EXPULSION OF URINE FROM THE BLADDER.

The discharging apparatus of the kidney consists of the *pelvis* and the *ureter*. The wall is formed of three layers: innermost (1), a mucous membrane; within this (2), a muscular coat; and, most external (3), a fibrous coat (Fig. 225). The *tunica propria* of the mucous membrane is composed of connective tissue fibres, intermingled with cellular elements, and it passes into a *sub-mucosa* (*s*). The epithelium, *e*, covering the *tunica propria*, is stratified pavement epithelium, the uppermost layer of the cells being cubical, and hence termed transitional epithelium. A few racemose glands occur in the pelvis of the kidney, and in the upper part of the ureter. The muscular layer consists of an internal longitudinal (l) and an external circular (r) layer of plain fibres, and, in the lower half of the ureter, there is, outside of this, another longitudinal layer (l_2). The mucous membrane of the calyces is continued over the papillæ, and there is a circular ring of plain muscle round each papilla. The pelvis and ureter receive nerve filaments, passing to the muscular fibres.

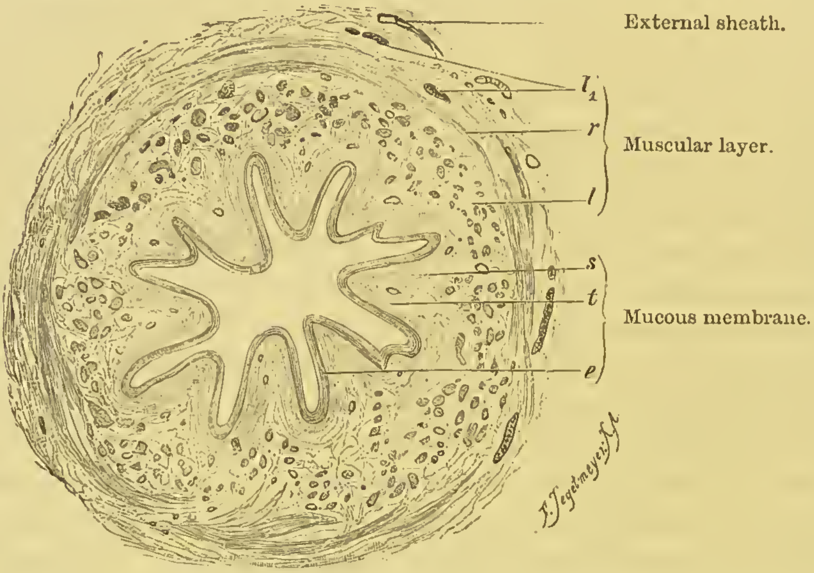

FIG. 225.—Transverse section through the lower end of the ureter. × 15 d. *e*, epithelium; *t*, tunica propria; *s*, submucosa; *l*, internal muscular layer; *r*, circular muscular layer; l_1, accessory external longitudinal muscular layer. (Method No. 82, Appendix.)

The *urinary bladder* has the same layers. The epithelium is like that of the pelvis and ureter, so that the one cannot be distinguished from the other (Fig. 226). In the *tunica propria* of the *fundus*, small racemose glands occur, and a few solitary masses of adenoid tissue exist. The muscular coat consists of an internal and external longitudinal layer, enclosing between them a circular layer, the different layers freely intermingling. Near the *fundus* the inner longitudinal layer is thicker than elsewhere, and near the *cervix* the circular layer is strengthened so as to form a sphincter (*sphincter vesicæ internus*). Vessels, lymphatics, and nerves abound, and on the course of the latter we find groups of ganglion cells.

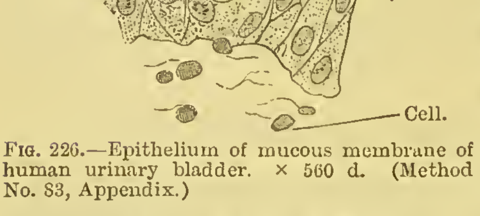

FIG. 226.—Epithelium of mucous membrane of human urinary bladder. × 560 d. (Method No. 83, Appendix.)

The *urethra* of woman has a mucous membrane, the *tunica propria* of which is formed of very fine connective tissue, richly intermingled with cells, and it is raised on its upper surface into numerous papillæ, more especially at its outer orifice. The epithelium is of the stratified pavement variety. A few racemose glands are found. The wall is strengthened by an internal longitudinal and an external circular layer of smooth muscle, having connective and elastic tissue between the layers. It is highly vascular.

The *urethra* in man has the same general structure as that of the woman, but it shows peculiarities in certain situations. In the prostatic part (*pars prostatica*), the epithelium is like that of the urinary bladder, but it gradually merges into stratified cylindrical epithelium in the membranous portion (*pars membranacea*), and in the cavernous part (*pars cavernosa*) of the urethra it is of the simple cylindrical variety. In the *fossa navicularis*, and onwards, it is flat stratified epithelium. There are well-developed papillæ in the *fossa navicularis*. Racemose glands (the *glands of Littre*) occur in the urethra. In the prostatic portion, the muscular layer consists of a longitudinal stratum, surrounded by a circular layer. The former layer is still seen in the membranous part, but it disappears in the cavernous part, and the circular layer also disappears in the anterior part of the cavernous portion. It is highly vascular.

The urine is secreted constantly by the kidneys, is forced along the ureters by the pressure of secretion, and is discharged into the bladder drop by drop. This phenomenon has been seen in cases of congenital malformation, in which the anterior wall of the bladder and of the abdomen are deficient, so as to expose the openings of the ureters. It is probable that the urine is propelled along the ureters by rhythmical muscular contractions (peristalsis) occurring in their walls. The urine is quickly driven from the pelvis of the kidney into the bladder. The bladder slowly fills, in consequence of the urethral orifice being firmly closed. Up to a certain limit, the closure of the neck of the bladder is involuntary and unconscious, and is due to contraction of involuntary muscular fibres forming a sphincter (*sphincter vesicæ internus*). The pressure in the bladder cannot force the urine up the ureters, as the orifices of the ureters are oblique, so that strong pressure occludes them. When the bladder reaches a certain degree of tension, the sensory nerves in its walls are affected, so as to give rise to a sensation of fulness. A slightly greater distension apparently causes reflex contraction of the muscular fibres near the neck of the bladder, which forces a few drops of urine into the prostatic portion. When this occurs, the desire may become so strong as scarcely to be resisted; and, after a short time, reflex contractions occur in the wall of the bladder (acting chiefly on the bands of fibres running from the fundus to the cervix, termed *detrusor urinæ*), which, assisted by voluntary contractions of the abdominal muscles, expel the urine. The last portions are emptied out of the urethra in jets, caused by rhythmic contractions of the muscles of the *bulbus cavernosus*.

The bladder of an adult man contains, when fully distended, from 1 to 1·5 litre. The pressure in the bladder has been stated at 130 to 150 mm. of mercury, and James found only a pressure of 4 to 5 inches of mercury, when both the walls of the bladder and the abdominal muscles were brought into action. In paraplegia, when only the walls of the bladder acted, the pressure was equal to only 20 to 30 inches of water (1 inch = 25·4 mm.)

The centre or centres of micturition are situated in the lumbar region of the spinal cord. The sensory fibres from the urethra and bladder find their way to the cord by the posterior roots of the 3rd, 4th, and 5th sacral nerves, and the motor fibres governing the circular muscular fibres of the urethra, and more especially those muscular fibres termed the *sphincter urethræ*, pass from the cord by the anterior roots of the 3rd and 4th sacral nerves. The centre in the cord is also related to the cerebrum by fibres passing from the cerebrum through the peduncles and the posterior part of the lateral columns, and these may be regarded as inhibitory fibres. Fibres probably also pass directly from the brain through the cord to the *sphincter urethræ*, which is, to a certain extent, a voluntary muscle. Finally, sensory and vaso-constrictor fibres pass to the urinary apparatus, but their exact course is unknown. When the cord is injured, so as to cause irritation, above the position of the centres, the bladder becomes distended with retention of urine, and the urine may trickle or pass drop by drop from the urethra. In voluntary micturition, a voluntary impulse, as already stated, causes a little urine to escape into the beginning of the urethra, probably influencing the circular fibres in that region. This excites sensory fibres which carry an impression to the centre in the cord. This centre is in a condition of constant action (not necessarily reflex), maintaining closure of the circular muscular layers at the neck of the bladder and thus preventing the escape of any fluid in it. The sensory impulses, however, inhibit the centre, so that the neck of the bladder opens, and at the same time impulses radiate to centres in the cord connected by motor fibres with the bladder itself and with the abdominal and other muscles that come into action. This view of the nervous mechanism explains how it is that painful impressions coming from any part of the body to the centre in the cord, as in children during teething, may act in a similar way, and cause involuntary micturition. Similarly, impressions from the brain may act from above, as it is well known not only that micturition is to a certain extent under the control of the will, but also that various psychical conditions may affect the process. The objection to this view is that tonus of the centre and of the *sphincter urethræ* has been denied, but no other theory yet offered explains the phenomena of micturition.

SECTION IX.

THE INCOME AND EXPENDITURE OF THE BODY.

Having considered the various processes concerned in nutrition, by which all the tissues are supplied with materials for their nourishment and growth, and for the performance of their functions, and by which the waste matters resulting from activity of tissue are removed, we have now to attempt to ascertain what relation exists in a healthy adult between the ingesta and the excreta. By *ingesta* are meant all the materials introduced into the body, either by the lungs, skin, or alimentary canal; whilst the term *excreta* signifies the matter thrown out by the various excretory channels. If we suppose the weight of the body to remain the same, it is evident that the ingesta would be exactly equal to the excreta; if at the end of the experiment, the body showed an increase of weight, the ingesta would be in excess of the excreta, and *vice versâ*.

The body is continually giving out by the lungs, carbonic acid and water; by the kidneys, urea, uric acid, etc., water and salts; by the skin, carbonic acid, fatty matter, and water. It is also daily losing matter in the form of epidermic structures—epidermis, hairs, nails, etc.—and it also loses by saliva and other digestive secretions, and by other secretions, such as lachrymal fluid, semen, milk, etc. On the other hand, it is daily receiving oxygen, water, albuminous matters, fats, carbohydrates, and salts. As already said, if the daily income were equal to the daily expenditure, a condition of physiological equilibrium would be attained. The chief constituents of the body are water, albuminous matter, fat, and salts. Carbohydrates form only about 1 per cent. of the total body weight, and they may be left out of any calculation in which we try to balance income and output. Volkmann and Bischoff state that 100 parts of the human body contain 64 of water, 16 of albumin and gelatin, 14 of fat, and 5 of salts, and as muscle consists of 21 per cent. of albumin and 75 per cent. of water, and forms about 42 parts of the total body weight, it follows that half of the albumin in the body and just about half of the water exist in the muscles of the body. We must now form an estimate of the exchanges of water, albumin, fats, and saline matters, by the following methods :—

1. **Water.**—This is determined by subtracting from the amount of water ingested as food or drink the quantity lost by the bowels, kidneys, lungs, and skin.

2. **Albumin.**—In this case, we must determine the amount of nitrogen eliminated as urea, uric acid, etc., and from this, estimate the amount of albumin that has undergone metabolism, as all the nitrogen of decomposed albumin appears as urea, uric acid, kreatinin, etc., in the urine. We find the amount of albumin taken up in the digestive process by the difference between the amount of nitrogen of the food and of the fæces. As albumin contains 16 per cent. of nitrogen, 1 part of N will be equivalent to 6·25 of albumin. Voit's method is to take the amount of N as the equivalent of the flesh substance that has undergone metabolism. Thus 1 grm. of N = 30 grms. of flesh.

3. **Fat.**—Subtract from the carbon eliminated by the bowels, kidneys, lungs, and skin, the amount of C in the metabolized albumin already determined (albumin contains 53·6 per cent. of C), and the remainder will be the amount of C representing fat that has undergone metabolism. Fat contains 76·5 per cent. of C; hence, to obtain the amount of fat, multiply the remaining C by 1·3 ($75 \times 1·3 = 100$).

4. **Salts.**—Estimate the amount in the food, and from it subtract the amount eliminated by the fæces, urine, and skin.

To simplify the problem, suppose we took an animal in which the income was represented by only one, or at most two, substances, we might determine how much was the output. Such a condition is that of starvation, in which an animal receives only oxygen, with small quantities of water. Pettenkofer and Voit made observations on a man weighing 71 kilogs., who fasted for periods of twenty-four hours, The daily loss was found to be 890 grms. of water, 78 grms. of albumin, and 215 grms. of fat, or about 1 grm. of albumin and 3 grms. of fat per kilog. The more fat is present, the less the consumption of albumin, and *vice versa*. A fat man, weighing 71 kilogs., showed on the second day of fasting a loss of only 50 grms. of albumin and 205 grms. of fat (Ranke), and a lean man, weighing 57 kilogs., on the first day of fasting lost 88 grms. of albumin and 160 grms. of fat, and on the fifth day 69 grms. of albumin and 125 grms. of fat (Zuntz). As in animals (observed by other physiologists) it was found that when starving begins, the amount of N eliminated falls, and soon reaches a daily amount of 3 to 4·5 grms. = 17 to 27 grms. of albumin, showing, by the constancy in the amount of N lost, that when the body is nourished by its own albumin, it uses the more of it the more it possesses. After a few days, the amount of N diminishes, and it always keeps a constant ratio to the loss of body weight. At first the loss of CO_2 decreases more than the diminution in the O absorbed, but by the third day they reach a minimal amount, and remain about equal till death. The loss of weight in starvation consists of $\frac{2}{3}$rds of water, $\frac{1}{12}$th of albumin, and $\frac{1}{4}$th of fat. If the animal receives water equal to that lost daily, the loss of other substances is reduced even to the extent of $\frac{2}{3}$rds, and hence starvation is borne better with water than without it. Children, in whom metabolism is more active than in adults, die sooner of starvation. During starvation, herbivora lose less albumin in proportion to the body weight than carnivora, but they do not bear starvation so well. Small animals, such as rabbits, use up the albumin very quickly.

Such being the conditions of metabolism in starvation, we have next to consider the effect of giving food. As during starvation an animal uses up a certain quantity daily of albumin, one would suppose that by giving the animal a quantity of albumin equal to that lost, the daily loss of weight would be arrested, or rather that the loss would be lessened by the albumin thus given. Such, however, is not the result of experiment. If an amount of albumin is given equal to that lost during starvation, the amount of N in the urine increases, and the body still loses in weight, that is to say, the processes concerned in the metabolism of albumin are stimulated to greater activity by the presence of the extra albumin in the food.

In the dog, it is found that to maintain the balance, about $2\frac{1}{2}$ times as much nitrogen must be given in the food as is given off by the excretions. Voit states that from 40 to 50 grms. of flesh per kilog. of body weight, or about $\frac{1}{20}$th that of the body weight, must be given before the condition of equilibrium is reached. During nitrogenous equilibrium, about 70 per cent. of the water drunk escapes by the urine, and 30 per cent. by the lungs and skin ; nearly all the N is eliminated by the kidneys, and $\frac{4}{5}$ths of the C escapes by the lungs, and $\frac{1}{5}$th by the kidneys. If the dog receives more than $\frac{1}{20}$th of its body weight in flesh, it eliminates less N than exists in the food, and it increases in weight. But the curious condition is thus induced that to maintain the nitrogenous balance, on a purely flesh diet, more and more flesh must be given, until a point is reached when the dog cannot eat it all, and its appetite fails. Then the plane of equilibrium becomes lower, and the animal requires less flesh. It appears also from the researches of Voit that a supply of albumin also lessens the loss of fat, so that, in a dog, 8 grms. of albumin per kilog. of body weight maintained the amount both of the fat and of the albumin. This occurs in an animal in good condition at the beginning of the experiment, but if it be lean, then the poorer it is in fat, the greater is the metabolism of albumin. It would appear, therefore, that part of the albumin taken into the blood—the circulating albumin—is decomposed in the tissues into urea, etc., and that a part of it, the tissue-albumin, passes directly into the tissues and becomes more stable. A small portion of the latter, however (1 per cent., Voit), is also converted into urea, etc. If fresh albumin is supplied in the food, urea, etc., are obtained both from the metabolism of circulating and of tissue albumin; but if it is not supplied, then only from tissue albumin, and if a little is supplied, then the metabolism of the tissue albumin is increased.

As regards the metabolism of fat, Voit has shown that if no albumin is given, the giving of even large amounts of fat (300 grms.) does not lessen the metabolism of albumin. It only lessens the loss of fat. Nor does the consumption of large quantities of carbohydrates lessen the changes in albumin, but the quantity of water eliminated is much increased. If both fats and albumin are given, then the metabolism of albumin is much diminished. Thus the fats save the waste of albumin, and by combining fat with albumin, a condition of nitrogenous equilibrium is much more readily attained than by giving albumin alone, and less albumin is also required. Fat added to albumin may save albuminous metabolism to the extent of even 7 per cent. The fat in the body also diminishes albuminous metabolism, so that a lean animal will require more albumin than a fat one to maintain equilibrium. Carbohydrates behave like fats, saving albumin, and also, to a smaller extent, fat. Thus, in feeding cattle, by giving carbohydrates one obtains all the advantages of fats at a less cost. (See also p. 31.)

To show how a balance may be struck between income and expenditure, we take the case of a healthy man, not performing active work, and weighing 70 kilogs., as observed by Pettenkofer and Voit.

Income.	N in grms.	C in grms.
137 grms. albumin.	19·5	315·5
117 ,, fat.		
352 ,, carbohydrate.		
2016 ,, water.		

Expenditure.	N in grms.	C in grms.	H_2O in grms.
Urine,	17·4	12·7	1279
Fæces,	2·1	14·5	83
Lungs,	...	248·6	828
	19·5	275·8	2190

Here the body was in nitrogenous equilibrium, and it eliminated more water by 174 grms., whilst it stored up 39·7 grms. of carbon, equal to 52 grms. of fat. The bearing of this on dietetics is obvious. These observations should be contrasted with another series of observations recorded by Pettenkofer and Voit upon the same man, in which the effects of active work on metabolism are shown.

Income.	N in grms.	C in grms.
137 grms. albumin.	19·5	315·5
117 ,, fat.		
352 ,, carbohydrate.		
2266 ,, water.		

Expenditure.	N in grms.	C in grms.	H_2O in grms.
Urine,	17·4	12·6	1194
Fæces,	2·1	14·5	94
Lungs,	...	309·2	1412
	19·5	336·3	2700

Again, there was a state of nitrogenous equilibrium. The body eliminated 434 grms. of water in excess and also 20·8 grms. of carbon, equal to 28 grms. of fat. Thus when the man had been engaged in hard muscular work 137 grms. of albumin, 145 grms. of fat (117 + 28) and 352 grms. of carbohydrate were taken, that is to say, he used up 60·5 grms. of carbon (= 80 grms. of fat) more than while at rest, and the amount of water eliminated was increased by about 24·3 per cent. It is important to notice that the amount of nitrogen excreted was not increased. At the same time, although, as already shown (p. 419), there is no direct relation between the metabolism of albumin and muscular work, it is necessary to give to a man doing hard work more albumin than to one who does not work. To make up for the loss of carbon in performing hard work, more fat and carbohydrate should also be given.

Temperature has also an influence on metabolism. Thus a cold external air increases the excretion of carbonic acid and more fat is necessary, and with a warm air the excretion of carbonic acid is diminished and less fat may be taken, but the metabolism of albumin is unaffected in both cases. One explanation of the increased consumption of carbonaceous food in cold climates is that of Zuntz, who asserts that irritation of the sensory nerves of the skin by cold acts reflexly through the spinal cord on the muscles, increasing chemical changes in these tissues. This condition has been termed *chemical reflex tonus.*

SECTION X.

ANIMAL HEAT.

All living organisms may be divided as regards temperature into two classes: (1) *Warm-blooded (homoiothermal)*, or those having an almost constant temperature; and (2) *Cold-blooded (poikilothermal)*, or those whose temperature varies through wide limits with that of surrounding media, being always, however, a few tenths of a degree above that of the medium. The former includes mammals and birds, the latter reptiles, amphibians, and fishes. As regards invertebrate animals, our knowledge of the temperature of individuals is limited and untrustworthy.

The temperature of man taken in the axilla with a thermometer (Fig. 227) is between 36·6° and 37·4° C.; the oscillations, in a state of health, being included in the compass of ·5 of a degree.

The temperature of the horse, donkey, and ox is 37·5° to 38° C.; of the dog and cat, 38·5° to 39° C.; of the sheep and rabbit, 38 to 39·5° C., and of the mouse, 40° C. (Munk). Birds have a high temperature, that of the common fowl and pigeon being 42° C. The temperature of fishes is usually about ·05 to ·1° C. above the temperature of the water; amphibians, like the frog, about 1° C. above that of the surrounding medium, and reptiles from 1° to 4° C. above the temperature of the air.

The temperature of organs is higher than that of the surface of the body; thus, Bernard found 40·6° C. registered in the brain, liver, glands, lungs, and muscles. The blood passing through the right side of the heart is a little warmer than that returned from the lungs, a fact which has been explained by supposing (1) that the blood coming from the liver is warmer than that of ordinary systemic venous blood, and (2) that the blood is cooled during its passage through the lungs. As the blood passes through the lungs it loses heat. The temperature of venous blood is high or low according to the organ from which it has returned. Thus, while the temperature of the blood in superficial veins is lower than that of corresponding arteries, on the other hand, venous blood returned from muscles and glands is warmer than the arterial blood entering these. The temperature of the body shows a diurnal variation. Thus, in man, it is lowest in the morning

(36·8° C.), rises towards 10 A.M. (37·1° C.), sinks till noon (37·03° C.), rises towards 3 P.M. (37·5° C.), sinks till 8 P.M. (37·3° C.), sinks still towards 11 P.M. (36·9° C), and during the night it falls to 36·8° C.), reaching its minimum about 3 A.M. As these variations are not observed during starvation, it is probable they are due to the influence of supplies of food. Want of nourishment causes a fall of temperature, so that towards the close of a period of starvation it may be as low as 30° C. or even 26° C. Newly born children have a temperature, for a few days, of 37·9° C., it then falls to 37·8° C, and they have not the same degree of power of maintaining a constant temperature as adults possess. The temperature, up to the age of 40 or 50 years, is about 37·4° C. for the average; it falls to about 37·1° C. on to 70 years, and after that time it rises again to about 37·4° or 37·5° C. Active muscular exercise raises the temperature ·5 to 1° C. Munk states that prolonged trotting may raise the temperature of a horse 1·5° C. During various diseases it may rise to 44° C., and in the horse to 45° C.

Heat is produced in the living body by chemical and mechanical actions.

1. **Chemical Actions.**—As has been frequently pointed out, most of the operations occurring in the tissues involve chemical changes, principally those of oxidation. Such changes cause the liberation of heat, and it is important to observe that any given oxidation will produce the same amount of heat. Thus, if we oxidize 1 grm. of hydrogen, a given amount of heat will be produced. Even supposing the element exist in a chemical compound, the amount of heat produced by its oxidation will be the same as if it were free. Consequently, the quantity of heat evolved by the oxidation of a complex substance may be ascertained experimentally. The following figures show the approximate number of (small) calories (see p. 441) produced by the combustion of 1 grm. of the following substances:—

Hydrogen,	34·5	Urea,	2	Fat,	9·4
Carbon,	8·1	Albumin,	5·8	Sugar,	3·9

It will be observed that a given weight of complex organic substances yields less heat than an equal weight of the simple elements, a fact explained by remembering

FIG. 227.—Thermometer suitable for clinical or physiological observations.

that in the combustion of compounds *complete* oxidation may not take place. Every chemical change therefore which occurs in the body, whether it be oxidation, hydration, or decomposition, results in the production of heat. The oxidation of carbon, producing CO_2, is the chief source of heat. This is strongly indicated by the fact that the daily variation of temperature already referred to (p. 439) runs almost parallel with the daily variation in the excretion of carbonic acid.

2. **Mechanical Actions.**—All frictional movements, such as that of the blood in the vessels, the movements of the muscles, the contact of articular surfaces and of tendons, produce heat; but it is impossible to estimate the amount generated by these different causes.

3. **The Localities where Heat is Produced.**—The organs in which the largest amount of heat is liberated are the muscles. This is indicated by the activity of chemical changes occurring in these, by the fact that an increase of temperature may be detected directly, and by the blood returning from a muscle being warmer than that going to it. The muscles, however, are not the only producers of heat, inasmuch as chemical activity manifested in nervous centres, and in the liver and other glands, must produce a certain amount. The heat produced in the lungs by the oxidation of hæmoglobin is more than compensated by the loss due to the passage of carbonic acid in venous blood into the gaseous state.

The blood in the aorta of a dog has a temperature of 38·4° C.; in the portal vein, 39·4° C.; in the hepatic vein, 39·8° C.; in the inferior vena cava, 39·5° C., and in the right auricle, 38·8° C. An active condition of the liver raises the temperature of the blood flowing from it. Thus, Bernard found the temperature of the hepatic vein to be 2° C. warmer during active secretion, after a full meal, than during starvation. The blood of the right ventricle is about ·3° C. warmer than that of the left. The blood in the veins of the head and neck shows about 36·5° C., and that in the crural vein, 37·2° C.; the lower temperature being due to the ready loss of heat from the exposed position. The blood flowing from the salivary glands during active secretion is ·1° to 1·5° C. hotter than the blood flowing to them. The temperature of the rectum, vagina, and bladder is ·8° to 1° C. higher than that of the axilla. The exposed parts of the body have a much lower temperature, that of the tip of the nose or lobe of the ear being as low as 26° C.

4. **Amount of Heat Produced by the Living Body.**—This is measured by a process termed *calorimetry*, first practised by Lavoisier. His apparatus, a *water calorimeter*, as modified by Dulong, is seen in Fig. 228. In this experiment, the animal is placed in a metallic box, the air of which is supplied by a gasometer, whilst the vitiated air is drawn away. The box is plunged into a space filled with water or ice, and the whole apparatus is so surrounded by bad conductors of heat as to render the influence of external media as small as possible. The temperatures of the animal and of the water in the calorimeter are taken at the beginning of the experiment. After the animal has remained in the chamber for some hours, the temperatures

are again taken, when either of the two following cases may be the result: (1) there is no change in the temperature of the animal at the end of the experiment; or (2) the temperature of the animal is different from what it was at the beginning. In the first case, it is evident that the quantity of heat produced by the animal must have been equal to the quantity of heat given up to the calorimeter, and in the second, supposing the final temperature to be less, the amount of heat lost may be found by subtracting from the number of units of heat gained by the calorimeter the number of heat units lost by the body of the animal during the experiment, which will be found by multiplying the weight of the animal by its specific heat, and by the number of degrees lost during the experiment. If, on the other hand, the final temperature is greater, the two quantities must be added to each other instead of subtracted. The amount of heat is calculated in *units of heat*, of which the *calorie* is the most convenient, a calorie being the amount of heat required to raise the temperature of 1 kilog. of water 1° C., or strictly from 15° to 16° C. The calorie may be expressed by the symbol Ca. The term *small calorie* is $\frac{1}{1000}$th part of Ca, or the heat required to raise 1 grm. of the substance 1° C.

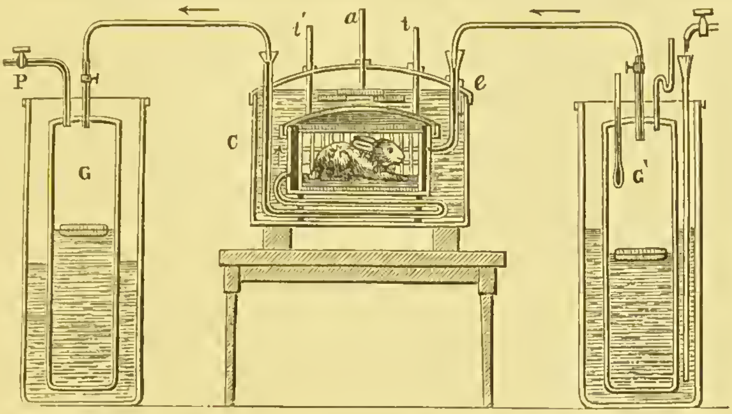

FIG. 228.—Dulong's apparatus. C, calorimeter, consisting of a vessel of cold water, in which the chamber holding the animal is placed; G^1, gasometer from which air is expelled by a stream of water. The air enters the respiratory chamber. G, gasometer receiving the gases of expiration and the excess of air; t, t'. thermometers; *a*, a wheel for agitating the water. Observe the delivery tube on the left is much twisted in the water chamber, so as to give off its heat to the surrounding water.

Hirn has calculated the number of Ca produced during repose and during work. The average number during twenty-four hours in a state of repose, is 2,700 Ca, which gives about 112 Ca per hour. During active work, the amount is considerably increased, as may be shown by the following table:—

	Day of rest.		Day of work.		
	Rest. 16 hrs.	Sleep. 8 hrs.	Rest. 8 hrs.	Work. 8 hrs.	Sleep. 8 hrs.
Ca produced, - - -	2470·4	320	1235·2	2169·6	320
Total, - -	2790·4		3724·8		

Von Helmholtz has calculated that during eight hours of sleep, about 40 heat units or calories per hour are produced by a man of average size. The above table shows very clearly the increased production of heat by work.

To obtain a fair method of comparison in estimating the amount of heat produced by the bodies of different animals in a unit of time, say one hour, it is useful to divide the number of Ca by the weight of the body, and thus obtain the amount per kilog. We may term this HCaK, or hour-calorie-kilog. The following are the HCaK for various animals: Horse, 2·1; man, 2·3; ram, 2·6; large dog, 2·5; duck, 6; pigeon, 10·1; rat, 11·3; sparrow, 32; greenfinch, 38. It will be observed that the heat production is much greater in smaller animals than in larger ones, and especially great in birds. The smaller the animal the greater will be the proportion between its area of surface and its volume, and as heat is lost by conduction and radiation, the greater will be its loss of heat in proportion to its volume. Thus the surface of a cube increases with the square while its volume increases with the cube. Thus a cube, each side of which measures 10 mm., has a superficial area of 600 sq. mm., and it has a cubic content of 1,000 c.mm. If doubled, its superficial area will be 2,400 sq. mm., but it will contain 8,000 c.mm.; so that the smaller the animal and the greater the ratio between its surface and cubic content, the more rapidly it must lose heat, and consequently the more heat must be produced in a given time. For the same reason young animals, before they are fully grown, lose more heat than adults.

4. **The Distribution and Loss of Heat.**—The heat produced in various organs and tissues is *distributed* partly by conduction and partly by the agency of the circulating blood. As regards *conduction*, the law regulating it is that the amount of heat passing from one part of the body, *a*, to another part of the body, *b*, is greater in proportion to the cross-section of the intervening tissue, the density of the medium through which it has to pass, and the initial difference of temperature in the two parts, *a* and *b*. This law holds good for all temperatures up to 40° C. Heat is also lost by *radiation*, in which the heat does not pass from particle to particle but through spaces, and it obeys the same laws as regulate the motions of the ether we call light. Heat may also disappear by becoming *latent*, and thus much heat disappears during the evaporation of water from the skin. The vessels containing warm blood may be regarded as a system for the equable distribution of heat, so as to produce a more or less uniform temperature. The temperature of any particular part will depend on (1) the absolute amount of heat produced in the organ or tissue; (2) the temperatures of neighbouring organs or tissues and the conductivity, as regards heat, of the tissues between them; (3) the heat given up to the blood as it passes through the vessels; and (4) the heat given up in the case of a superficial organ, such as the skin, to the surrounding medium.

Heat is lost from the body either (1) by radiation from the cutaneous surface; (2) by heating the air of inspiration; (3) by heating cold foods or drinks introduced into the alimentary canal; and (4) by becoming *latent*, in the evaporation of water from the surface of the skin. It has been estimated that of 100 calories of heat produced, 2·6 are lost in heating food and drink, 2·6 in heating air inspired, 14·7 in evaporation, and 80·1 by radiation, conduction, etc. It will be observed how large a part of the percentage (94 per cent.) is accounted for by the skin, showing the importance of this organ as a regulator of heat. Its activity depends largely on the temperature and on the hygrometric state of the atmosphere, behaving precisely like any evaporating surface. The *movement* of the air is of great importance. When layers of the air in contact with the surface of the body are renewed at frequent intervals, the skin loses heat at each instant both by radiation and evaporation, so that by keeping a layer of air next the body by means of clothing, the cooling of the body is more slowly accomplished. This result is still further effected by wearing articles of clothing which are bad conductors of heat.

5. **Equilibrium between Loss and Gain of Heat.**—The maintenance of a uniform temperature is essential to the life of a warm-blooded animal. To maintain it, it is evident that there must be arrangements by which the production and the loss are balanced. Thus :—

1. The temperature may *increase*—(*a*) by an increased production, the loss not changing ; (*b*) by a diminution in the loss, the production not changing ; (*c*) by an increased production and diminished loss ; (*d*) by an increased production and insufficient increase in loss, and (*e*) by a diminished amount of loss along with a diminished production, if the first be in excess of the second.
2. The temperature may *diminish* in the contrary cases.

These phenomena are chiefly regulated by the relative activities of the skin and of the circulation.

Cold causes the *arrectores pilorum* to contract, the small vessels also contract, and less blood flows through a unit area of skin in a unit of time. Cold also diminishes the amount of sweat secreted and evaporated, and thus less heat becomes latent. Thus the effect of cold is to lessen the loss of heat. The saving of heat is increased by covering the body with non-conductors, either as clothing, or by the hairy coverings of animals (thicker in winter). These non-conductors also keep a layer of hot air near the skin. If the protecting coverings become wet, they conduct heat better and they take up heat from the body ; but in mammals living in water there is a thick cushion of fat below the skin which, acting as a bad conductor of heat, prevents to a large extent an escape of heat from the deeper organs.

If the skin of a warm-blooded animal be coated over its whole extent with an impermeable varnish, it will soon die, showing difficulty in breathing, diminished and frequent pulse, *a fall of temperature* from 40° C. to 19° or 20° C., and albuminous urine. This is caused by the cutaneous vessels becoming dilated, and by the large quantities of blood thus passing through the skin rapidly losing heat through the layer of varnish which is a better conductor. If the loss of heat be prevented by covering the varnished layer with bad conductors, the animals will survive.

Von Helmholtz has endeavoured to strike a balance between the amount of heat produced and the amount of heat lost in twenty-four hours thus :—

(1) *Heat income.*—(*a*) a healthy adult weighing 82 kilogs. expires in twenty-four hours say 878·4 grms. of CO_2. The combustion of the C. therein produces 1730·76 calories (kilogramme-degrees) ; (*b*) but the man takes in more O than reappears in the CO_2, and the excess may be assumed to oxidise H to form H_2O, and thus 13·615 grms. of H will yield 318·6 calories, or a total of 2049·360 calories ; (*c*) about 25 per cent. of the heat obtained by the body may be assumed to come from other sources than combustion, say from warm fires, etc., so the total heat is 2732 calories. This amount of heat is sufficient to raise the temperature of a quantity of water equal to the weight of the body of an adult weighing 80 to 90 kilogs. from 0° C. to 33·8° C., or to heat 27 litres of water to 100° C.

(2) *Heat expenditure.*—(*a*) Heating food and drink to a temperature of 12° C., 70·157 calories, or 2·6 per cent.; (*b*) heating the air respired,—16,000 grms., with an initial temperature of 20° C., to that of the blood,—70·032 calories, or 2·6 per cent.; (*c*) heat rendered latent by the evaporation of 656 grms. of water by the lungs, 397·536 calories, or 14·7 per cent.; (*d*) the remainder lost by radiation, conduction, and evaporation of sweat, 2194·275 calories, or 80·1 per cent.

The regulation of heat goes on only within narrow limits, ranging from 37° to 40° C. If the temperature rises to 43° or 44° C., there is greatly increased frequency of the pulse and of breathing, and death soon occurs. In air saturated with aqueous vapour at 80° C. rabbits have died in half-an-hour. If the temperature of a rabbit is lowered to 20° C. it soon dies. The body survives exposure in cold air much longer than in cold water, as the latter is a much better conductor of heat.

The influence of the nervous system on heat is still obscure. As explained, in treating of the sympathetic nerve, section of the nerve causes increased temperature on the affected side. This effect has been explained chiefly by the increased afflux of warm blood from the dilated state of the vessels. Section of the cord causes a fall of temperature which may be accounted for by dilatation of vessels throughout the body, causing an increased loss of heat by radiation and conduction, because it has been ascertained that if the animal is kept in a warm chamber, the temperature increases instead of diminishing. After death from tetanus or from fevers, a *post mortem* rise of temperature has been observed up to 44·7° C., indicating that heat-producing processes were at work even after death. The coagulation of the blood and the development of cadaveric rigidity produce heat, and, in consequence of the stoppage of respiration and of the circulation, a dead body will lose, in a given time, less heat than a living one.

The temperature of hybernating animals, such as the marmot, brown-bear, and hedgehog, falls during the profound sleep of winter. For example, with an external temperature of 5° C. down to − 8° C., the respirations of a marmot were 7 to 8 per minute, the pulse 24 to 36 per minute, and the temperature of the body was only from 3° to 5° C., so that it was cold to the touch. The amount of oxygen consumed in these circumstances is $\frac{1}{30}$th of the normal, and only ⅖th to ½ of this reappears in carbonic acid, the respiratory quotient falling to ·4-·015. They thus store up ·5 to ·6 of the received oxygen. The fat of the body is gradually consumed so that they wake up in the spring time lean and weak.

The Relation between Heat and Mechanical Work.—In contrasting the energy of heat and work, it is important to remember that the heat-unit may be transmuted into the work-unit by multiplying by 425, and that the reverse is accomplished by dividing by the same number, that is, a weight of a kilogramme falling one metre in height in one second will produce the same amount of heat as will raise one kilo. of water from 15° to 16° Cent. in one second.

During sleep, the principal mechanical activities in operation are the contractions of the heart and of the inspiratory muscles. The total cardiac work in twenty-four hours may be valued in round numbers at 88,000 kilog.-met. (205 Ca).[1] The work of the respiratory muscles is about 14,000 kilog.-met. in the same time. Together these amount to 102,000 kilog.-met. The whole of this work is resolved into heat in overcoming the resistance to the passage of the blood in the vessels. During eight hours of sleep, we may estimate ⅓rd of 70,000, or about 23,000 kilog.-met., as representing the internal work of the body. This figure divided by 425 gives nearly 52 Ca in the same time. But it has been seen that during sleep about 320 Ca are produced, so that then, in the operations of the living body, from ⅕th to ⅙th of the total energy appears as mechanical work. Again, in a day of work, to the 102,000 kilog.-met. representing the work of the heart and respiratory muscles, we add 213,344 kilog.-met. produced by eight hours' work (26,668—the energy in kilog.-met. appearing as mechanical work in one hour—×8=213,344), the figures given by Hirn; we have then 315,334. This divided by 425 gives about 743 Ca, as representing in heat units the amount of energy expended in the internal work of the body, plus the external work done in eight hours. As seen in the table (p. 441), however, during a day of work 3,724 Ca are produced as heat; to obtain the total amount of energy expended in twenty-four hours, we must add to this sum 743 Ca, representing in heat units the mechanical work done by the body during eight hours of work. Together they amount to 4,467 Ca, the total energy of the body during twenty-four hours, eight of which were occupied in mechanical work. It will be observed that about ⅙th part of the total energy appears as mechanical work. The superiority of the human body as an apparatus for the utilization of energy, becomes more apparent when we compare the amount of heat formed *during eight hours of work*, and the amount of mechanical work expressed as heat. In these circumstances, it will be found that about ¼th, or 25 per cent., of the total energy appears as mechanical work, about twice that of the best constructed steam or gas engine, which yields only from 12 to 15 per cent. as work, the remaining 88 or 85 per cent. of heat being lost.

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[1] The calculation given on p. 219 gives the approximate numbers as 85,233. The difference is immaterial.

SECTION XI.—THE NERVOUS SYSTEM.

A.—General Introduction.

Chap. I.—THE ORIGIN OF THE NERVOUS SYSTEM.

Before discussing the physiology of the nervous system, we may point out the methods by which physiologists have acquired the information they now possess. In elucidating any problem in innervation, say the functions of a nerve, or the mode of action of a particular nerve centre, four lines of evidence are brought to bear upon the question, namely: (1) the inferences derived from *anatomical* examination of the origin, course, distribution, and general relations of the part, and the gradual development of the organ in the animal kingdom; (2) the facts derived from a careful examination of the *histological* structure of the part, as found in the adult and at various periods of embryonic life; (3) the *clinical* and *post mortem* results observed by physicians, surgeons, and pathologists of the changes produced by diseases affecting nerves and nerve centres; and (4) the *experimental* facts observed by the physiologist when he cuts a nerve or nerve centre and stimulates the parts exposed. For many years knowledge chiefly depended on the first and third of these modes. Certain nerves were traced to muscles and they were assumed to be motor; others were found in connection with organs of sense and they were therefore supposed to convey sensory impressions; or to take another instance, the cerebrum was found to increase in size and in complexity from the lower to the higher forms of vertebrates—being small in animals of low intelligence, whilst it was large and complex in those of high intelligence—and the inference was drawn that this part of the brain was related to mental activity. Again, these inferences were corroborated by the observations of the physician and surgeon on man. Thus, when a certain nerve was cut in a surgical operation, the parts supplied were found to have been removed from the influence of the will or to have lost sensibility; tumours pressing on certain nerve centres produced paralytic symptoms; hemiplegia or paralysis, say of the left side, was found, on post-mortem examination, to be frequently caused by a clot of blood in the right brain, and *vice versâ*. Still, such observations left much that was uncertain. Then the experimental method in the hands of Sir Charles Bell, John Reid, the Webers, Claude Bernard, and Brown-Séquard, threw new light on many obscure questions. They exposed a nerve, cut it, and observed the results. They then stimulated each end, say by a weak electric current, and noted the effect. If muscular movements followed, the nerve was held to contain motor fibres; or if pain was the result, it had sensory fibres in its course. By such methods also, our knowledge of the functions of the cranial nerves, of the roots of the spinal nerves, of the influence of the nervous system on the heart, the lungs, and the stomach has been rendered more or less precise and accurate. Again, the experimental method has more recently given much information regarding nerve centres by the method of electrical stimulation in the hands of Ferrier, Hitzig, Fritsch, Schäfer, and others. It is true that here, from the importance to the economy of the parts involved, from the influence of shock caused by the operation, and from our comparative ignorance of the structure of the parts, the results of the experimental method are less satisfactory, but by comparing the results of stimulation with those following the removal of the portion of the centre under investigation, and finally by tracing the path of degenerated nerve fibres according to the method of Waller, to be afterwards described, much valuable information has been obtained. Lastly, the histological method has added much to our knowledge. It is the youngest of all the methods and has still much to do. There is still much to be learned regarding the terminal organs, and more as to the topographical histology of the brain. It may be stated generally that when any theory regarding the physiology of a nervous organ is supported by concurrent evidence derived from these lines of inquiry, it may be accepted as true; but if it be contradicted by one or more, there is a fallacy to be discovered. Thus, the anatomist, histologist, physician, surgeon, pathologist, and physiologist are all engaged in the work of unravelling the intricacies of nervous mechanism, a work which cannot fail to have important influences in the future, as it has had in the past, on the diagnosis and treatment of nervous diseases.

We have already seen (Vol. I. p. 251) that the central nervous system originates in the epiblast, the layer which corresponds to the external layer, or epiderm, of the lowest invertebrates. This layer also supplies the essential elements of the organs of special sense, that is to say, the sensory expansions which, in each organ of sense, are adapted to a particular kind of stimulus. The sense organs, therefore, were in the first instance certain cells on the surface of the body, which became the recipients of specific stimuli, and, by the long-continued action of such stimuli, the cells became more and more attuned to stimuli of a special kind. For example, if by the accumulation of pigment in certain cells, the ether vibrations of light were absorbed by these cells, more than by others on the surface of the body, such cells would become more and more susceptible to light, and a rudimentary organ of vision would result. The stimulation of light would cause movement of the whole or of a part of the body of the primitive animal, by certain cells in the vicinity of the pigment spots transmitting the stimulus to cells that were further distant, and deeper in the substance of the body. Such transmitting cells, more and more differentiated, would become nerve cells, and, sinking below the surface, they would form the rudiments of a central nervous system. Processes passing from the primitive sense organ to the deeper-lying nerve cells, and processes passing from one cell to the other (uniting by anastomosis), would, according to this view, constitute nerves, and, finally, similar processes would blend with the processes of contractile cells, and thus establish a communication by which the results of a stimulus, acting on the sense organ, in the first instance, would be transmitted to the contractile tissues of the body as a whole. Nor is this merely a fanciful sketch of the process of evolution, because some of its stages may be observed in certain humble invetebrate forms. Thus, in sea anemones, there are no organs of special sense, and no central nervous system, but in the epiderm and in the lining of the digestive sac there are peculiar cells, each furnished with a long hair at one end, while processes pass from the other end into the deeper parts of the body (Fig. 229). These processes also anastomose to form a network under the epithelial layer, and this network of fibres is regarded by F. M. Balfour as essentially nervous.[1] Such cells are called *neuro-epithelial*, and here and there in the network formed by their processes there are other cells, also having processes which may be regarded as modified sense cells. According to this view, the modified sense cells are primitive nerve cells; they are sense cells which have travelled inwards and lost their epithelial character (Balfour). In certain medusæ, the transition between a neuro-epithelial cell and a ganglionic or nerve cell may be traced. Thus, in the same animal, two kinds of

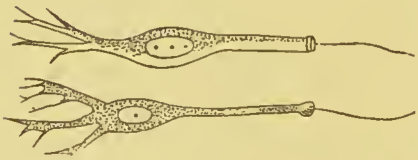
FIG. 229.—Neuro-epithelial sense cells of *Aurelia aurita*.

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[1] F. M. Balfour, *Comparative Embryology*, vol. ii. p. 332.

cells are found: (1) a cell having a hair-like process, or sense-hair, passing to the surface, and processes, on the other hand, which join a ring of nerve fibres containing ganglion cells; and, (2) a cell which has no sense-hair, or only one which is too short to reach the surface (Fig. 230). The central nervous organs thus took their rise from modified sense cells, and the network formed by the processes of the latter constitute primitive nerves. The connection of these with muscular elements has not been traced. In the lower forms no one has yet seen the ending of a nerve filament in a muscular element, and it is only in the higher forms that we meet with the differentiated end-plates, already described (Vol. I. p. 358). Processes from neuro-epithelial cells, probably in rudimentary forms, simply anastomose with the processes of myo-epithelial cells (Vol. I. p. 356), and in this way an organic continuity is established between neural and muscular tissues.

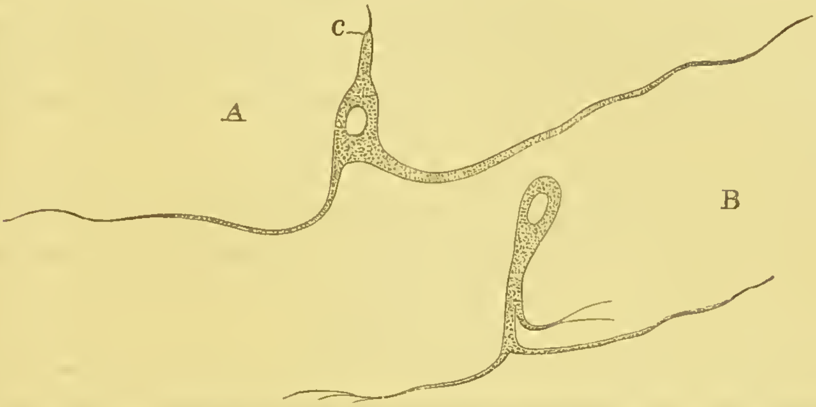

FIG. 230.—Isolated cells belonging to the upper nerve-ring of *Carmina hastata*. *A*, neuro-epithelial cell; *c*, sense-hair; *B*, transitional cell between a neuro-epithelial cell and a ganglion cell. (Hertwig.)

The nervous system in man and in the higher animals consists of (1) *central* masses of nervous matter, or *ganglia*, constituting the brain and spinal cord, containing nerve cells; (2) *peripheral* or *terminal* organs existing in the organs of sense, in muscle, and in electric organs; and (3) *nerves*, or internuncial cords connecting the central with the terminal organs. The nerves are conductors of a mode of energy termed nerve-force, originating either in the nerves themselves on the application of a stimulus, or in the terminal organs, or in the central organs. Thus, if a nerve is irritated at any point, a change is set up in the nerve fibres at the point of irritation, and this change is propagated along the nerve fibres to a central or terminal organ, producing phenomena of various kinds, such as a sensation of pain or of pleasure, an involuntary movement, the contraction of a muscle, or a discharge of electricity. Again, the stimulus may act on a terminal organ, such as the retina, setting up a change which is then conveyed to the brain by the optic nerve, there causing a sensation of light or colour. Finally, the nervous action may originate in a central organ, as when a voluntary movement is made. The voluntary impulse, in this instance, originates in the brain, a change passes along nerve fibres from the brain to the muscles, and the muscles contract. We have therefore to discuss the general properties and modes of action of nerves, terminal organs, and central organs.

CHAP. II.—THE GENERAL STRUCTURE AND FUNCTIONS OF PERIPHERAL NERVES, GANGLIA, AND TERMINAL ORGANS.

1.—Nerves.

The cerebro-spinal nerves consist chiefly of medullated nerve fibres, the structure of which has already been described (Vol. I. pp. 315-316), varying in diameter, and intermingled with a small number of non-medullated fibres. The fibres are enclosed in an external sheath, the *perineurium externum*, or *epineurium*, formed of loose connective tissue (Fig. 231). The epineurium sends partitions into the nerve, dividing it into secondary bundles, each of which is thus surrounded by a sheath of connective tissue, the *perineurium internum*. Still more minute septa exist, penetrating into the secondary bundles. These constitute the

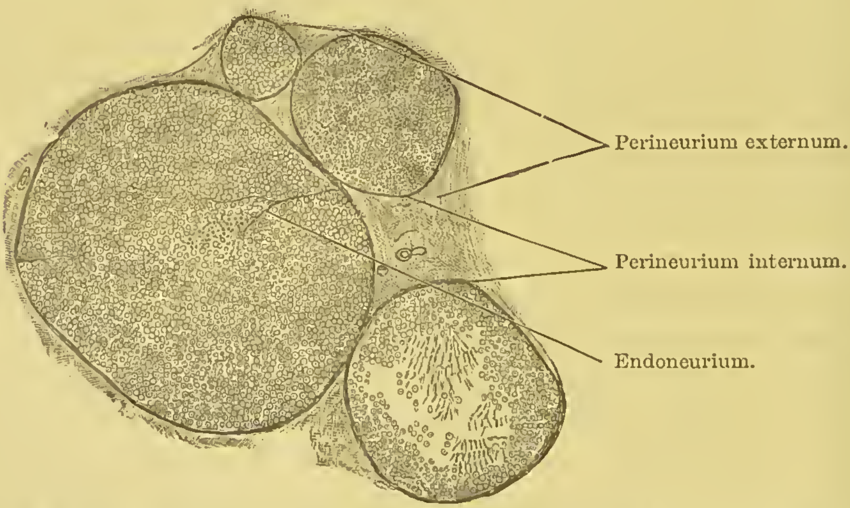

FIG. 231.—Portion of a transverse section of a peripheral spinal nerve of a rabbit. × 50 d. In the lower nerve bundle on the right, the transverse sections of the individual fibres have to some extent fallen out of their section, while others are seen from the side, having been pushed aside by pressure. (Method No. 84, Appendix.)

endoneurium, and from the endoneurium delicate folds or lamellæ pass round each nerve fibre, corresponding to the perimysium of individual muscle fibres. These coverings of a nerve are anatomically continuous with the connective tissue coverings of the brain and spinal cord. The perineurium consists both of ordinary connective tissue and also of elastic tissue, and it is lined by two, and in small nerves by one, layer of endothelial cells, forming the *sheath of Henle.* The margins of the cells forming this sheath are shown by the use of nitrate of silver (Vol. I. p. 272).

Nerve fibres never divide during their course, but only near their termination. The fibres of individual nerve trunks often join and become inextricably mixed with those of adjacent nerve trunks, and thus a reticulum or meshwork may be formed.

The nerve fibres in the sympathetic system of nerves are chiefly non-medullated (Vol. I. p. 316), and from the preponderance of this kind of nerve fibre, sympathetic nerves are whiter than those of cerebro-spinal nerves, or have a pale grey hue. Nerves vary much in this respect. Thus the splanchnic nerves contain many medullated fibres, while the sympathetic in the neck and in the pelvis consist almost wholly of the non-medullated variety. A perineurium holds the fibres together. Large sympathetic trunks in the liver, kidneys, and spleen often contain tubular, probably lymphatic, spaces, round which the nerve fibres are arranged.

Capillary blood-vessels are distributed to large nerve trunks, branching on the perineurium and epineurium. Lymph spaces exist between layers or lamellæ of the perineurium, and it would also appear that each individual nerve fibre is surrounded by a lymphatic space, which is continuous with the sub-dural and sub-arachnoid lymph spaces of the spinal cord and brain, while it has no communication with the lymphatics in the vicinity of the nerve. It follows that any increase of pressure in the lymphatic spaces of the central organs will affect the nerve ramifications throughout the body.

Physiological Classification of Nerves.—Functionally, nerves may be divided into motor, sensory, vascular, secretory, and inhibitory. The original meaning attached to the term *motor* nerve was a nerve entirely composed of fibres by the excitation of which influences were conveyed to a muscle which caused the muscle to contract. As these influences passed outwards from a nerve centre towards the periphery of the body, they were also termed *efferent.* On the other hand, nerves were found which, when stimulated, gave rise to sensations of pleasure or of pain, and these were called *sensory* nerves. Finally, it was shown that a third class of nerves was composed both of sensory and of motor fibres, and they were called *senso-motor* nerves. Sensory nerves were also subdivided into those of *general* and those of *special* sensibility. This was an artificial classification based on the fact that when a nerve of so-called special sensibility, such as the optic, was stimulated in any way the same kind of sensation followed. Thus stimulation of the optic nerve, by cutting, pricking, pressure, or electricity, is always followed by a luminous sensation. But the progress of research showed that when certain nerve fibres were stimulated the result was not necessarily a contraction of voluntary muscule: it might be contraction of a blood-vessel, secretion of a gland, or a diminution or arrest of some kind of nervous action. These facts demand another classification of nerves such as the following:—

- CENTRIFUGAL, or EFFERENT, or MOTOR, conveying influences outwards from a nerve centre.
    1. *Motor*, sometimes termed *efferent*, to muscles, exciting contraction.
    2. *Secretory*, to the cells of glands, causing secretion, possibly a particular kind of secretion.
    3. *Vascular*, or *vaso-motor*, to the walls of blood-vessels, so as to cause contraction (*vaso-motors*) or dilatation (*vaso-dilators*, or *vaso-inhibitors*).
    4. *Inhibitory*, so affecting other centres of nervous activity as to moderate or neutralize their action.
    5. *Electrical*, so affecting a special organ as to call forth electrical discharges, as in electric fishes, *Torpedo*, *Gymnotus*, *Malapterurus*, etc.
- CENTRIPETAL, or AFFERENT, or SENSORY, conveying influences inwards towards a nerve centre.
    1. *Sensory*, causing more or less acute sensations.
        - a. *General*, conveying to nerve centres in brain influences which cause sensations of a vague character, scarcely perceptible to consciousness, and not permanent, as from lungs, heart, stomach, etc.
        - b. *Special*, conveying to nerve centres in brain influences which cause visual, auditory, gustatory, olfactory, or tactile sensations.
    2. *Afferent*, or *reflex*, conveying to nerve centres influences which usually cause no sensation, and which may or may not be followed by movements, secretions, changes in calibre of vessels, etc.

In addition there are nerve fibres connecting nerve cells in the great centres, to which no special functions can be attributed.

2. Ganglia.

These are small groups of ganglion cells placed in the course of peripheral nerves. They contain nerve fibres in small bundles, embracing groups of ganglion cells which form either elongated or round masses. A continuation of the perineurium of the nerve forms a connective tissue sheath round the ganglion, and partitions of connective tissue sometimes penetrate into the body of the latter. Ganglia are rich in capillaries, and each ganglion cell is surrounded by a vascular ring, indicating the necessity for active nutritive processes occurring in the cells.

The ganglia, connected with the cerebro-spinal system, contain large, round ganglion cells (Vol. I. Fig. 174, p. 314). Each cell is surrounded by a layer of flat endothelial cells, continuous with the sheath of Henle of medullated nerve fibres. Ganglion cells are unipolar, one process issuing from the cell which, after running a short distance, divides in the form of a T into two branches. Nerve fibres connected with ganglia are medullated and possess the sheath of Schwann, but the exact arrangement of the fibres in the interior of the ganglion is still unknown. No one has yet shown that motor nerve fibres end in or are connected with the ganglionic cells. Probably one of the fibres from the T-shaped division above alluded to, proceeds to the nerve centre, while the other travels to the periphery, and these fibres and the cell connected with them have sensory not motor functions. Dr. W. H. Gaskell[1] has shown that when medullated nerve fibres enter a ganglion, they lose their medullary sheaths, and issue from it as non-medullated fibres.

The following ganglia present the general characters above described:—Gasserian ganglion on the fifth cranial nerve, the jugular ganglion of the pneumogastric nerve, the petrosal ganglion on the glosso-pharyngeal nerve, the ganglion on the auditory nerve, the geniculate ganglion on the facial nerve, and the ganglia on the posterior roots of the spinal nerves.

A remarkable form of ganglion cell was discovered by Lionel Beale in the ganglia of the tree frog. It is pear-shaped. A straight nerve fibre passes out from the pointed end, and this is surrounded by one or more spiral fibres, also containing nuclei. These spiral fibres arise from the outer part of the cell, increase in thickness as they pass spirally round the central straight fibre, and then run off as spinal fibres.

The *sympathetic* ganglia contain smaller ganglionic cells. They are multipolar, except in fishes, where they are bipolar. The fibres connected with such ganglia are both medullated and non-medullated, but

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[1] W. H. Gaskell, F.R.S., "Structure and Function of Visceral Nerves." *Journal of Physiology*, vol. vii. No. 1.

nothing is known as regards their connection with the ganglionic cells. In this connection, Dr. Gaskell's observation above noticed is of great importance.

3. Terminal Organs.

The mode of termination of nerve fibres in muscle has already been described (Vol. I. p. 358), and Pflüger's views as to the termination of nerves in gland cells have also been mentioned (Vol. I. p. 484). Nerve fibres terminate in other peripheral structures. The structure of the other terminal organs will be considered in describing the physiology of the senses.

Although a nerve may be stimulated in any part of its course, the stimulus is usually applied to a special structure adapted to receive a particular kind of stimulus. Such a special structure is called a "terminal organ." For example, in the arrangements for vision there are the retina or terminal organ, the optic nerve or conductor, and the brain or portion of it, the recipient of the impression. The fibres of the optic nerve are not affected by light, but when they are mechanically or electrically irritated the result is a luminous sensation, because the impulse sent along the fibres of the optic nerve initiates in the brain the molecular changes connected with luminous sensations. But light has a specific action on the retina, and the active retina in turn stimulates the fibres of the optic nerve. The retina is therefore the terminal organ adapted for the reception of rays of light. In like manner each sense has its appropriate terminal organ. It is necessary to understand clearly the functions of the terminal organs. They are liberating mechanisms. They do not transform physical energy into physiological (nervous) energy; but they call the latter into action. Thus light acting on the retina is not directly transformed into nervous energy, but it excites changes in the retina, which in turn produce activity of the optic nerve. The different modes of nerve termination may be here briefly classified.

Anatomical Organ.	*Terminal Organ.*
Skin. etc., touch, pressure, temperature,	Tactile cells of Merkel, in the epidermis of the skin.
	Tactile corpuscles of Wagner and Meissner, in papillæ of the skin.
	End-bulbs of Krause, in conjunctiva, penis, and clitoris.
	Pacinian bodies, attached to nerves of hand or foot, or in the mesentery.
	Corpuscles of Grandry, found in bills of birds.
	Network of fibres as in the cornea of the eye.

Anatomical Organ.	*Terminal Organ.*
Ear, hearing, - - -	Hair cells, supported by arches of Corti, connected with the basilar membrane, etc.
Eye, vision, - - -	Rods and cones of retina.
Nose, smell, - - -	Rods and olfactory cells.
Tongue, taste, - -	Taste-buds and gustatory cells.
Muscles, motion, - -	Motorial end-plates of Doyère, Kühne, etc.
Glands, secretion, - -	Nerve-endings in secreting cells—Pflüger, Küpffer, and Maccallum.
Electric-organs, electricity,	Laminæ with cilia-like processes in electric fishes.

CHAP. III.—THE CHEMISTRY OF NERVOUS TISSUE.

Both grey and white matter contain a considerable amount of connective tissue and it might have been expected that they would have yielded gelatin, but the non-nervous matter of the centres is more nearly related to albuminous than to gelatinous substances, and while it yields gelatin, it gives a larger proportion of albuminous matter than is obtained from ordinary connective tissue. The specific gravity of grey matter varies between 1029 and 1038, and that of white matter between 1039 and 1043, showing that the latter contains less water. The amount of water varies in different parts of the brain. Thus Bernhardt found in the *cortex cerebri*, 86 per cent.; in the white matter of the cerebrum, 70 per cent.; in the *medulla oblongata*, 74 per cent.; in the cervical spinal cord, 73 per cent.; in the lumbar spinal cord, 76 per cent., and in the sympathetic, 64 per cent.

Both nerve cells and axis cylinders contain albuminous matter, the axis cylinders especially becoming red when heated with Millon's re-agent (Vol. I. p. 64). This albuminous matter is not myosin, inasmuch as it is insoluble in a 10 per cent. solution of common salt. Further, the axis cylinder is dissolved in weak solutions of ammonia and caustic potash, it is hardened, by the separation of water, in solutions of chromic acid, bichromate of potash, and corrosive sublimate, and it reduces chloride of gold. The white substance of Schwann is blackened by perosmic acid, showing its fatty nature, and this is also indicated by its solubility in alcohol, ether, and oil of turpentine. Artificial digestion of nerve fibres by tripsin (a ferment of the pancreas) shows that they contain a matter allied to or identical with keratin. This substance, *neuro-keratin*, is said to exist in a layer immediately round the axis cylinder, but chiefly in the sheath of Schwann, outside the white substance. The white substance therefore lies between two layers containing keratin, and it is important to notice that medullated fibres in the central organs, which have no sheath of Schwann, have still the thin layer of keratinous matter round the axis cylinder. The axis cylinder also contains lecithin and probably cholesterin.

The nuclei of ganglion cells contain a substance apparently identical with the *nuclein* of Miescher (Vol. I. p. 78), and it has been found to the extent of ·14 per cent. of the cerebral mass. The presence of albumin and of nuclein in nerve cells and nerve fibres indicates also the presence of phosphorus. Even supposing that nuclein is not a definite chemical substance, but a mixture of other bodies, the fact remains that tissues rich in nuclein are also rich in *phosphorus* and makes it highly probable that the phosphorus exists in this substance. In this connection it is also striking that nuclein is the substance in the nuclei of cells closely related to their reproductive powers. Fresh grey matter of the brain yields ·49 per cent. and the white matter ·89 per cent. of phosphorus. Contrast with this the amounts in the muscles of a calf, ·48 per cent.; human blood, ·1 per cent.; woman's milk, ·38 per cent., and yolk of egg 1·15 per cent. No conclusions as to the amount of phosphorus in the brain can be drawn from analysis of the excretions, as the total amount in the brain is small compared with what exists in other organs. For example, Voit has estimated that the entire nervous system of man contains only 12 grms. of phosphoric acid, while 130 grms. exist in the muscles and no less than 1800 grms. in the bones. (Meynert.)

Hoppe-Seyler found that at a high temperature caustic potash liberated from nuclein, prussic acid and ammonia ; and it has been suggested that in epileptic convulsions, due to the withdrawal of arterial blood, metabolic products may be formed having a physiological action similar to that of the cyanides.

The reaction of the grey matter of the brain and spinal cord is faintly acid. After death these organs become more acid during the slow loss of vitality of the tissue elements, and this has been supposed to be due to the development of lactic acid. White substance, on the other hand, is neutral, and becomes alkaline during dying.

Petrowski gives the following result of an analysis of white and of grey matter :—

	Grey Matter.	White Matter.
Water, - - - - - - -	81·60	68·35
Solid Matter, - - - - -	18·40	31·65
Albumin and Gelatin, - - - -	55·37	24·73
Lecithin, - - - - - - -	17·24	9·90
Cholesterin and Fats, - - - -	18·68	51·91
Cerebrin, - - - - - - -	0·53	9·55
Substances soluble in anhydrous ether,	6·71	3·34
Salts, - - - - - - - -	1·45	0·57
	99·98	100·00

The substances thus found are numerous and complicated in chemical characters, and such an analysis can by no means be regarded as final.

Improved methods will no doubt yield more accurate results, but in the meantime we may classify the chemical substances, in addition to water, albuminous and gelatinous matters already referred to, under the five following heads :—

(1) *Lecithin* ($C_{44}H_{90}NPO_9$), a substance containing phosphorus and soluble in alcohol and ether (vol. I. p. 82); (2) *cholesterin*, obtained from the ethereal extract after removing the lecithin; (3) *cerebrin*, probably consisting of a group of substances crystallizing out of hot alcohol, because they are insoluble in cold alcohol; (4) *saline* matters; and (5) matters obtained from an *aqueous extract* of nervous substance. The substances soluble in water consist of *inosite*, ·08 per cent.; *lactic acid*, ·04 per cent.; *kreatin*, ·04 per cent., and smaller quantities of *uric acid*, *xanthin*, *hypoxanthin*, *leucin*, and *urea*. The substance in brain tissue richest in phosphorus is *protagon* (vol. I. p. 82), having the formula $C_{160}H_{308}N_5PO_{35}$. *Cerebrin* differs from it in containing no phosphorus. Gamgee has extracted from brain matter by alcohol at 45° C. a substance provisionally named *pseudo-cerebrin*, and having the formula $C_{44}H_{92}NO_8$, and Parcus gives a provisional formula for the substance—$C_{69\cdot08}H_{11\cdot47}N_{2\cdot13}O_8$. Lastly, *lecithin*, $C_{44}H_{90}NPO_9$, can be obtained not only from actively growing cells, yolk of egg, etc., but it also exists in brain matter. The theory mostly in favour is that protagon is the parent of cerebrin and lecithin, and also of the phosphorised bodies (*kephalins*, *myelins*, and *lecithins*) obtained by Thudichum, and referred to in Vol. I. p. 83. From these, in turn, we may derive *phospho-glyceric acid*, *neurin* (a basic substance containing no phosphorus), and *fatty acids*.

B.—NERVES.

CHAP. I.—THE PHYSICAL PROPERTIES OF NERVES.

1. **General Properties.**—Grey matter is soft and diffluent. The white matter, even in nerves, presents little consistence or cohesion, and what it has is probably due to the connective tissue it contains. The elasticity of nerves is very imperfect. White matter, consisting entirely of nerve fibres, absorbs fluids containing different saline substances at very different rates. Thus, chloride of sodium is not absorbed, sulphate of soda is absorbed only in small amount, while the acid phosphate of soda and the salts of potash are absorbed with avidity.

2. **Electrical Properties.**—When a portion of living nerve is placed on the cushions of the galvanometer so that the transverse section touches one cushion, whilst the longitudinal surface touches the other, a current passes through the circuit of the galvanometer from the longitudinal surface to the transverse section, and when a nerve is excited to action there is a negative variation of this current. It will be observed that the phenomena are the same in kind as in the case of muscle. (See Vol. I. p. 448.)

3. **Production of Heat by Nerves.**—It is extremely doubtful whether the production of heat by a nerve in action has been detected,

although theoretically one would expect heat to be so produced. Schiff observed an increase of temperature on tetanization in the nerves of warm-blooded animals that had been artificially cooled; on the other hand, Von Helmholtz and Heidenhain's experiments yielded negative results.

Chap. II.—THE VITAL PROPERTIES OF NERVES.

1. Nutrition of Nerves.

Probably nerves are nourished by the plasma reaching the axis cylinder at the nodes of Ranvier; but it would appear from the researches of Waller that the nutrition of the nerve fibre is influenced by the nerve cell with which it is connected. The so-called *law of Waller* is well illustrated in the case of division of the roots of the spinal nerves. Each of these nerves has two roots—a posterior, sensory, on which there is a ganglion; and an anterior, motor (Fig. 232). If the anterior root is divided, in the course of a few days the end of the nerve cut off from the spinal cord is found to be undergoing degeneration, whilst the end attached to the cord is still normal. Again, if the posterior root is divided between the ganglion and the cord, the end remaining in connection with the ganglion remains unaffected, whilst the other end undergoes degeneration. This degeneration, in the case of a motor nerve, affects the nerve to its very terminations. The axis cylinder disintegrates into drops of fatty matter, and the medullated structure entirely disappears (Fig. 233). It is well known that when a nerve is cut the ends may reunite so completely as to ensure a return of the normal function in from two to five weeks. According to Ranvier, the axis cylinders in connection with the central portion play an important part in this regeneration. They become larger, striated, and by and bye form new axis cylinders, which pass into the cicatricial tissue and come into contact with the other end of the divided nerve. This is a remarkable confirmation of the view of Waller that the nutritional activity of a nerve fibre is in the direction of its physiological activity.

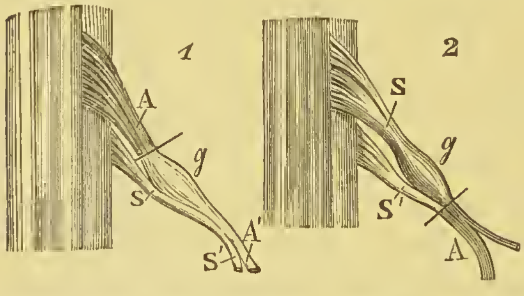

Fig. 232.—Diagrams showing the effects of dividing the roots of the spinal nerves, and illustrating Waller's Law. *A*, portion of nerve root undergoing degeneration; *S*, posterior, and *S'*, anterior root; *g*, ganglion. 1, division of posterior above ganglion; 2, division of both roots beyond ganglion.

2. Excitability.

The special property of a nerve fibre is termed *excitability*. Every kind of living protoplasmic matter is irritable—that is, it responds in some way to a stimulus. Thus, if a morsel of protoplasm, such as an amœba or a cartilage cell or a white blood corpuscle, be stimulated mechanically or by shocks of electricity, it will contract or change its form. Again, if living muscular fibre be thus stimulated it also will contract. This property of responding to a stimulus is termed *irritability*, and in the structures mentioned the property is manifested by movement as the obvious phenomenon, but it is known that more obscure phenomena follow the application of the stimulus. In the case of living nerve there is irritability also—that is, the nerve responds to a stimulus; but in a portion of isolated nerve no change is visible. If, however, the nerve be connected at one end with its appropriate central or terminal organ, we may have evidence of something having been transmitted along the nerve. Thus there may be sensation or movement, or both. Nerves are more irritable than contractile matter, and the term *excitability* is applied to the special irritability of nerve. The same strength of stimulus will act more powerfully on a nerve than on a muscle.

1. The excitability of nerves is affected by certain conditions. Injury to the nerve, the application of caustics, and drying quickly destroy it. When a nerve is divided the excitability is increased for a short time, then rapidly diminishes, and finally disappears near the point of section (*Valli-Ritter's law*). The end of the nerve still connected with central organs undergoes these changes in excitability more quickly than the portion cut off. As shown by Waller, when a nerve is separated from its central organ, namely, the grey matter of the spinal cord for the motor roots, and the ganglia on the posterior roots for the sensory roots, the end of the nerve separated from the centre undergoes fatty degeneration (Fig. 232). If, however, the cut ends of the nerve are brought into accurate contact, union soon takes place. Surgeons have frequently observed a return of sensibility to a part within a few days after the sensory nerve had been divided and the cut ends again brought into

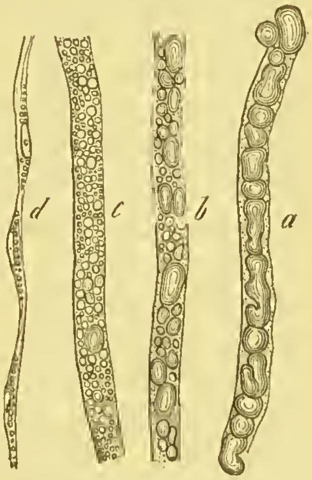

Fig. 233.—Peripheral ends of divided cerebro-spinal nerves. *a*, after three days; *b*, after two weeks; *c*, after four weeks; and *d*, after two months. × 300 d. (Rindfleisch.)

contact. Continued or excessive activity of a nerve soon lowers and may abolish excitability, thus producing exhaustion. On the other hand, a lengthened period of absolute repose lowers excitability, and if the nerve be inactive beyond a certain time it wastes, becomes thinner, and fatty degeneration occurs in its substance (Fig. 233). Heat increases, whilst cold diminishes, excitability. In the case of frogs' nerves, temperatures above 45° C. destroy excitability the more rapidly as they approach 70°, at which point it is almost instantaneously destroyed. Below 45° a rise of temperature first increases and then diminishes excitability, and it has been observed that whilst increasing its intensity it diminishes its duration. Finally, a diminished supply of blood quickly causes a fall of excitability.

2. Nerves may be excited by various kinds of stimuli: (*a*) mechanically, as by intermittent pressure, beating, section, pricking, etc.; (*b*) thermally, by variation of temperature; (*c*) chemically, by the application of such substances as acids, alkalies, or metallic salts; (*d*) electrically, by continuous or induced currents; and (*e*) normally, by changes in the central or terminal organs. Mechanical irritation is applied during life when the trunk of a nerve is pressed upon. Radiant heat acts on the nerves of the skin, or heat may be applied by conduction from a hot body in contact with the surface. Little is known as to the specific effects of heat on the nerves of the human being. In the frog, it has been found that a temperature of from 34° to 45° C. stimulates the motor nerves; about 40° C., sudden alterations of temperature may cause twitching of the connected muscles. Many chemical substances, in sufficient concentration, will quickly destroy a nerve; but, if they are in weak solutions, the result may be stimulation. Thus, concentrated solutions of the mineral acids, alkalies, alkaline salts, concentrated lactic acid, and concentrated glycerine may act as strong stimulants.

3. The influence of *electrical stimulation* of nerves demands more elaborate description. The effects, as already indicated, can be observed only when the nerve is connected with a muscle or with a central organ. In the first case, electrical stimulation is followed by contraction of the muscle; in the second, by a sensation, if the central organ is the brain. Consequently we have to consider the phenomena following electrical stimulation (*a*) of a motor nerve, and (*b*) of a sensory nerve.

(*a*) Electrical Stimulation of a Motor Nerve.

A perfectly constant current of electricity, of moderate quantity and intensity, flowing through a portion of nerve, produces no evident effect on the muscle, but any variation in the intensity or density of the current causes irritation, and the muscle gives a twitch. The effect is most apparent when the current is allowed to flow into the nerve, and when it is suddenly cut off, or, in other words, at the moment of opening and of closing the circuit. The rapidity with which the variation in the density of the current is effected also has an important influence. Thus the shocks of frictional electricity stimulate strongly, because, although the amount of electricity is small, the currents are extremely rapid in appearing and disappearing. In like manner, the quick shocks from induction coils, produced by rapidly opening and closing the primary circuit, are strongly stimulating. Again, a very powerful current may pass through a nerve without exciting it, if it pass gradually. Occasionally a very weak current sent through a portion of nerve will cause a contraction, whilst a very strong current may fail to do so. In fact, the phenomenon of contraction of a muscle is influenced (*a*) by the direction, and (*b*) by the strength of the current sent through the nerve. When the current is transmitted from the muscle in the direction of the spinal cord it is called an "upward" or "centripetal" current; when from the cord in the direction of the muscle, it is called a "downward" or "centrifugal" current.

Its strength is graduated by employing small Grove's cells: one cell giving a weak current, two or three giving a medium current, and four to six or seven a strong current. To graduate its amount more precisely, resistance coils may be introduced into the circuit, or we may employ a rheochord, by which a portion of the current is shunted back to the battery, whilst the remainder is allowed to pass to the nerve. In the circuit, a key or interrupter is interposed, and so arranged that, when the key is opened, the current is broken or interrupted, and, when the key is closed, the circuit is completed and the current passes to the nerve.

With these arrangements, and employing the sciatic nerve of a frog attached to the limb, the following results are readily obtained:—

Current Strength.	Key.	Upward Current.	Downward Current.
Weak.	Close.	Contraction.	Contraction.
Weak.	Open.	Rest.	Rest.
Medium.	Close.	Strong contraction.	Strong contraction.
Medium.	Open.	Strong contraction.	Strong contraction.
Strong.	Close.	Rest.	Rest.
Strong.	Open.	Very strong contraction.	Contraction.

That is to say, on beginning with a very feeble current, neither opening nor closing causes a contraction; but, on strengthening it up to a certain point, contraction appears first on closing, whilst opening produces no effect. By increasing the strength of the current, a contraction is obtained both on opening and on closing the key, and by and bye, when a certain strength of current is reached, the closing contraction becomes weaker, and finally disappears, leaving only a contraction on opening the key. Thus the effects of a strong current are usually the reverse of those caused by a weak current. These facts are usually included under the term the *Law of Contraction*, and the following is the explanation offered by Pflüger, and generally accepted by physiologists.

Suppose that the sciatic nerve of a frog connected with the isolated limb is stretched over two wires, passing from the positive and negative poles of a combination of Grove's elements, with the distance of an inch and a half between the wires. If a key be interposed in the circuit, a current will thus pass along one and a half inches of nerve when the key is closed, and be cut off when the key is opened. By having also a commutator or reverser in the circuit, we can send the current up or down the nerve at pleasure. Arrangements can also be made for irritating the nerve by another couple of wires coming from an induction machine, either near the negative or near the positive pole of the current coming from the Grove's elements.

It will be found that near the negative pole the excitability of the nerve is increased, whilst near the positive pole it is diminished; that is to say, a stimulus from the induction coil, not sufficient to excite the nerve so much as to cause a muscular contraction if applied near the positive pole, will at once do so if applied near the negative pole; or, a stimulus so strong as to cause tetanus in the muscle when applied near the negative pole may produce no effect when applied near the positive pole. In other words, the nerve near the negative pole is more excitable than in the normal state, whilst near the positive pole it is less so, indicating that at least one of the physiological properties of the nerve has been changed by the action of the continuous current. But a nerve fibre has also the property of conducting the effects of an impression, or the nerve force travels with a certain velocity along a nerve, as will be shown hereafter. It has been ascertained that near the negative pole the rate of conductivity is increased, whilst near the positive pole it is diminished. Finally, a piece of living nerve, when connected with the terminals of a galvanometer, so that the one terminal touches the surface whilst the other touches the transverse section of the nerve, shows the existence of a current of electricity travelling from the surface of the nerve through the galvanometer to the transverse section; that is, the surface is positive to the transverse section. This condition is also modified by the transmission through the nerve of a continuous current, so that the difference of potential is increased near the positive pole and diminished near the negative. These results are thus summed up:—

State of Nerve.	Functions of Nerve.		
	Electromotive Force.	*Conductivity.*	*Excitability.*
Near positive pole.	Increased.	Diminished.	Diminished.
Near negative pole.	Diminished.	Increased.	Increased.

The properties of the nerve, therefore, are altered by the passage through it of a continuous current, and the altered condition is termed the "electrotonic state," the condition in the neighbourhood of the positive pole, or anode, being termed "anelectrotonic," whilst that near the negative pole or kathode is called "katelectrotonic." A certain portion of nerve near each pole is thrown during the passage of a continuous current into these conditions of anelectrotonus and of katelectrotonus, whilst the amount of nerve thrown into the one condition or the other depends on the strength of the current. Further, there is always between the two poles a point of indifference, in which the properties of the nerve seem to be unaltered, and the position of this point depends on the strength of the current. Thus, with a current of medium strength the point is midway between the poles; with a weak current the point is near the positive pole—that is, a large portion of the nerve near the negative pole is in the katelectrotonic state, in which the excitability is increased; and with a strong current the point is near the negative pole—that is, a large portion of the nerve near the positive pole is in the anelectrotonic state, in which the excitability is diminished. Now, according to Pflüger, the stimulating effect of closing the current occurs at the kathode only, whilst the stimulating effect of opening the current occurs at the anode only, or a nerve is stimulated by a current on the appearance or increase of katelectrotonus, on closing the circuit, or by the disappearance or diminution of anelectrotonus on opening the circuit. If we suppose that this depends on the modification of excitability near the negative pole, by the molecules of the nerve becoming more mobile, the matter is intelligible. Thus the passage of the molecules from the normal stable condition to the katelectrotonic less stable condition acts as a stimulus, whilst tho passage backwards has no effect. On the other hand, tho passage from the more stable condition in anelectrotonus to the normal stable condition acts as a stimulus, whilst, again, the reverso action has no effect.

This explains why it is that a weak current gives contraction on closing, because, on closing, a large portion of the nerve near the negative pole passes from the normal into the katelectrotonic state, and this acts as a stimulus. On the other hand, a strong current causes contraction on opening, because, on opening, a large portion of nerve near the positive pole passes back from the anelectrotonic state into the normal state, and this acts as a stimulus. Again, with currents of medium strength, as both states are equally produced, there is contraction both on opening and on closing. Thus Pflüger's theory accounts for most of the facts; but its weak point is that no reason can be given why a nerve is stimulated only by the appearance of katelectrotonus and by the disappearance of anelectrotonus. It remains only to add that currents passing transversely through nerves produce no stimulating effect. In ascending currents, the shorter the piece of nerve between the electrodes the greater the stimulating effect, whereas in descending currents the reverse holds good.[1]

Electricity in Medicine.—The resistance of the human body ranges from 1000 to 2000 ohms. To pass 1 ampère through the body would require a current of from 1000 to 2000 volts, equal to that given by from 600 to 1200 Bunsen clements of large size, and having an internal resistance of ·25 ohm. The e. m. f. of each B. = 1·9 volt. As a current of 1 ampère is too strong, in the use of electricity in medicine, a current of only 20 milliampères is usually employed. Faradic or galvanic currents are employed (see Vol. I. p. 363). We should note, with regard to galvanic currents: (1) that the negative pole excites more strongly than the positive, and (2) that the shock on closing is stronger than that on opening the current. Such currents are employed for testing the excitability of nerves and muscles. Apply the negative pole (kathode) over the position of the muscle or nerve to be tested (the positive pole—anode—being held in one hand), and note if a contraction occurs on closing the current. If so, weaken the current as much as possible, until a feeble contraction is obtained on closing. If no contraction occurs in the first instance, strengthen the current until a contraction is seen. Note the number of milliampères employed. The contraction (C) obtaining by shutting (S) the key (closing), on applying the negative pole (K), is written thus: KSC. Normally, by increasing the current, the following contractions are obtained: (1) *weak current*—contraction on closing (S) at kathode=KSC; (2) *medium current*—contraction on closing at anode=ASC, or contraction on opening anode=AOC; (3) *strong current*—tetanus (T), on closing at kathode=KST. In practice, increase the intensity of the current until on closing there is a contraction at kathode=KSC. This current gives no contraction on opening. Or, increase the strength of the current till there is a contraction on closing at the anode=ACS. This current also gives a contraction on opening=

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[1] An excellent method of demonstrating the influence of electrotonus on the excitability of a nerve is that described by M'Gregor-Robertson in *Physiological Physics*, p. 82.

AOC. In the latter case, substitute the anode for the kathode, and we may obtain a contraction on closing=KSC. Finally, still increase the current until a contraction on opening occurs at the kathode=KOC; with this current, tetanus occurs on closing=KCT, and contraction occurs both on opening and closing at the anode=AOC, ASC. In a healthy condition, the *contraction on closing* at the kathode (KSC) occurs with 1 to 3 milliampères. This is the standard. In paralysis of cerebral origin, the electric irritability of the muscles is normal. The response is reflex, and it shows that the centre in the cord is intact. In paralysis due to lesions, the irritability of the paralysed muscles is normal, if the lesion is below the segment of the cord corresponding to the muscles. Lastly, in paralysis of peripheral origin, the irritability disappears in several days. Irritability is increased in tetanus, at the beginning of cerebral paralysis, and in some spinal paralyses, but it is diminished in infantile paralysis, in peripheral paralysis, and in old paralysis, accompanied by muscular atrophy. When a motor nerve is separated from its centre, there is a paralysis, and there is degeneration of the nerve, and, later, of the muscles supplied by it. At first the nerve is irritable both to Faradic and galvanic currents, but at the end of fifteen days the excitability disappears. The muscle also gradually loses its excitability to Faradic currents, but at the end of three weeks there is an increase in its irritability to galvanic currents, so that extremely feeble currents are sufficient to cause a contraction. These contractions are slow and prolonged, not quick, as in the normal state, and, with a current of the same intensity, ASC appears as well as KSC, and KOC as well as AOC. This peculiar state may last for nine weeks; it then slowly disappears. This reaction is termed the *reaction of degeneration*, and it shows destructive lesion in the grey matter of the cord and in the peripheral nerves.

(*b*) Electrical Stimulation of Sensory Nerves.

The effect of stimulating sensory nerves as distinguished from the direct stimulation of sensory or terminal organs has not been sufficiently studied, but, so far as is known, the laws seem to be the same as those relating to motor nerves. When a sensory nerve is stimulated the test must be the resulting sensation. As stimulation of the motor nerve in the condition of anelectrotonus or of katelectrotonus may or may not be followed by a contraction, so stimulation of the sensory nerve may or may not be followed by a sensation, or the character of the sensation may vary, just as the muscular contraction may be weak or strong. Further, electrical stimulation of the vagi is attended by analogous phenomena, so far as the movements of the heart are concerned.

(*c*) Unipolar Excitation.

Chauveau has studied the comparative influence of the two poles in any arrangement supplying a continuous current—that is, he has tried the stimulating effect, supposing either the positive or the negative pole be applied to the nerve whilst the other is in contact with another part of the body. He has found, amongst other more abstruse and less practical results, that there is in each case a certain intensity of current corresponding to the physiological condition of the nerve, by which the influence of one pole is the same as that of the other. If the intensity of the current is below this medium strength the effect of the negative pole on motor nerves is greater than that of the positive; but, if the intensity is above, the reverse is the case—that is, the positive pole is the stronger excitant. In the case of sensory nerves, Chauveau found that application of the negative pole with a moderately strong current was more painful than application of the positive pole. Thus the influence of unipolar excitation with a strong current on motor nerves is the reverse of that on sensory nerves—that is, the positive pole is the more powerful on motor nerves the negative pole on sensory nerves.

(*d*) Production of Tetanus.

(See Vol. I. p. 414.) A continuous current usually causes contraction only at the moment of opening and closing the circuit, but occasionally tetanus may be seen *during* the passage of the current. Tetanus during

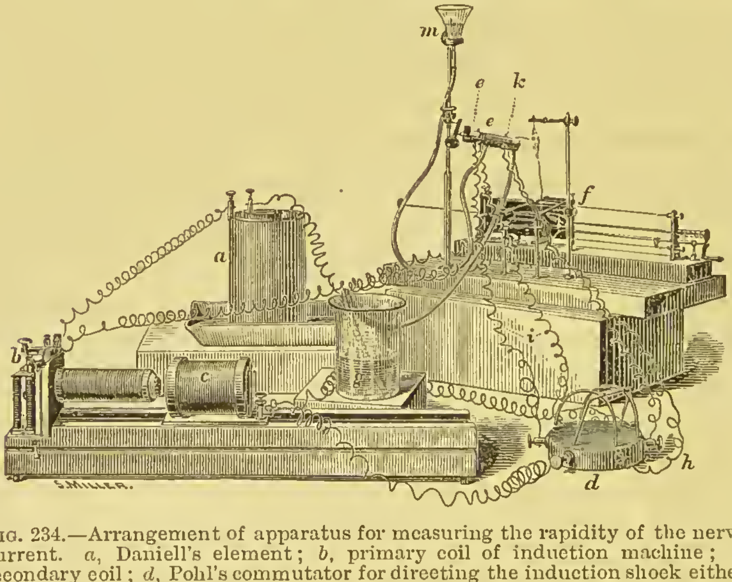

FIG. 234.—Arrangement of apparatus for measuring the rapidity of the nerve current. *a*, Daniell's element; *b*, primary coil of induction machine; *c*, secondary coil; *d*, Pohl's commutator for directing the induction shock either along the wires *h* or the wires *i* to the electrodes in the vulcanite box *e* at *e* or *k*. *f*, spring myograph, consisting of smoked-glass plate, which is driven in front of the stylet by the recoil of the spring seen to the right of the apparatus. Above the lever of the myograph the muscle is secured by fixing the lower end of the femur in the brass forceps, and the nerve is stretched across the electrodes, *e*. These electrodes consist of an elongated vulcanite box into which platinum wires are fixed at *e* and *k*. The roof of the box is formed of a copper plate, and through it, from the funnel *m*, either hot or cold water may be allowed to flow through an india-rubber tube to the beaker, *g*. The latter arrangement is for the purpose of subjecting the nerve to different temperatures.

the passage of a constant current has been attributed to electrolytic changes in the nerve. Pflüger holds that this is a normal production of tetanus and may be seen even with feeble currents; but certainly it is very difficult to demonstrate. Long ago, Ritter showed that, if a constant current of sufficient intensity be sent up a nerve for a considerable time, say half an hour, and then be suddenly interrupted, tetanus lasting for eight or ten seconds may be seen, which disappears on again closing the current. Ritter's tetanus, according to Pflüger, is really due to the stimulation caused by the disappearance of anelectrotonus, which occurs, as we have seen, when the current is opened, and the proof he offers is that the tetanus disappears when the muscle is cut off from the anelectrotonic portion. Tetanus may also be caused by the mechanical irritation of the nerve, or by heat, or by chemical substances.

3. Nervous Conductivity.

When a nerve is irritated at any point in its course a change is produced which is propagated along the nerve—that is, the nerve conducts, and the phenomenon is called the "nerve current." The velocity of transmission can be measured only by the use of delicate apparatus, as the time occupied is too short to directly affect consciousness. For example, when the tip of the finger is touched, the mind apparently perceives the contact without any loss of time. But it can be shown that an appreciable interval of time elapses between the instant the finger is touched and the instant the mind perceives the impression. During this time, a change passes along the nerve from the point touched to the brain. The method usually employed for determining the velocity of the nerve current consists in preparing the gastrocnemius muscle of a frog with the sciatic nerve attached, and connecting it with a recording apparatus, so that if the muscle be caused to contract by irritating the nerve the record of the contraction may be made on a rapidly-moving surface. If, then, the nerve be irritated in two consecutive experiments, first close to the muscle, and secondly at a distance from it, and the muscle be caused to contract in each case, it will be found that it does not contract so soon when the nerve is irritated at a distance from the muscle as when it is irritated close to it; in other words, if the nerve be irritated at a distance from the muscle, the transmission of the nervous impression from the point irritated to the muscle occupies an appreciable time. If, then, we know the length of nerve between the two points irritated, we can determine the length of time the nerve current took in passing along that distance of nerve.

1. **Measurement of Velocity of Nervous Impulse in Motor Nerves.**—Many methods have been devised for this purpose, but the simplest is the use of the *spring myographion* of Du Bois-Reymond (see Figs. 248 and 249, p. 391, Vol. I., and Figs. 234 and 235). The apparatus consists of a smoked-glass plate, which is driven in front of the recording stylet of the myograph by the recoil of a steel spring, C. Underneath the frame carrying the glass plate are two binding screws, 1 and 2, to one of which is attached a rectangular arm of brass, 1, which can so move horizontally as to establish metallic connection between the two binding screws (marked B, F). By means of these binding screws, the myograph is interposed in the circuit of a galvanic element and the primary coil, I, of an induction machine, and the brass arm is so placed as to connect both binding screws, thus completing the circuit. From underneath the frame carrying the smoked-glass plate there descends a small flange, which (when the glass plate, by releasing a catch not seen in the figure, but close to C, is driven across by the spiral spring from left to right) pushes the brass arm aside and thus interrupts the circuit of the primary coil. When this occurs, an opening shock is transmitted from the secondary coil, II, to a commutator, E, an instrument by which electric currents may be transmitted to the nerve either at a point close to the muscle at A, or at a distance from it at B. Suppose the apparatus all arranged so as to send the shock to the nerve at a point close to the muscle, A, the muscle stimulated contracts, and draws by means of the stylet, on the smoked surface of the glass, the curve seen in the lower part of it at A. This leaves the horizontal line (which would be drawn by the stylet were the muscle at rest) at A. Arrangements are then made for another experiment, in which the nerve will be stimulated at a distance from the muscle, at the point B in the upper part of the diagram. This is done by again placing the smoked-glass plate in proper position, closing the primary circuit by the brass arm at the binding screws, as already described, and reversing the commutator so as to send the shock along the wires to B. The muscle again contracts when the primary circuit is opened, and this time it describes on the smoked surface the curve B, seen to the left of the curve A. It will be perceived that this curve leaves the horizontal line at B—that is, a little *later* than when the nerve was stimulated close to the muscle. It follows, therefore, that the distance on the horizontal line from A to B represents the time occupied by the transmission of the nervous impulse from B to A of the nerve. With suitable arrangements, the rate of movement of the glass plate can be measured by bringing into contact with it a marker on one of the prongs of a vibrating tuning fork. The waves thus recorded enable the experimenter to measure with accuracy the rate of movement of the glass plate, and consequently the minute interval of time between A and B. In the diagram it will be observed that there are 2½ waves between A and B—each

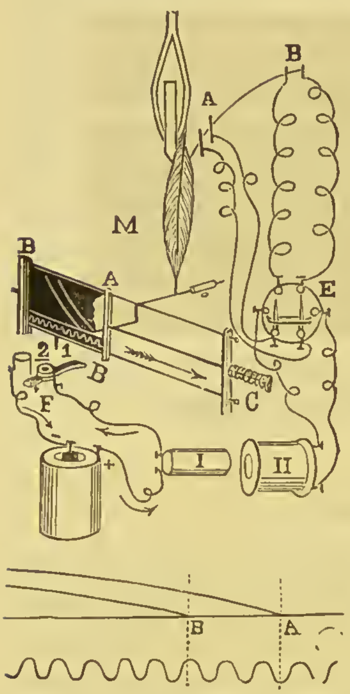

Fig. 235.—Diagram showing arrangement of apparatus in measuring rapidity of nerve current.

represents $\frac{1}{200}$th of a second; therefore the $\frac{1}{80}$th of a second is the time represented by the distance A, B; or, in other words, the $\frac{1}{80}$th of a second was occupied by the nerve current in passing along the portion of nerve from B to A. The experiment may also be conveniently made by the *pendulum myograph* (Vol. I. Fig. 264, p. 408). Two tracings are shown in Fig. 236.

FIG. 236.—Chronograph = 250 vibs. per sec. *e*, nerve excited far from muscle; *r*, near muscle; *a* and *b*, two separate experiments. The rapidity of the nerve current in the motor nerves of man has been measured by irritating the ulnar nerve at the wrist and near the elbow, the thumb being in connection with the recording apparatus.

2. **Measurement of Velocity in Sensory Nerves.**—Suppose a sensory nerve to be excited in the hand, the theory of nervous conduction is that a change is propagated along the nerve to the brain, and that in the brain the molecular changes occur which result in a sensation. The individual having the sensation may feel it and make no sign by which any one else might be made aware that he has felt it, or the subject of the sensation might, by a muscular movement, such as the motion of an arm, let any one else see that he has felt the sensation. We have no means of knowing whether or not an individual has felt a sensation except by the individual making some kind of gesture or muscular movement. Now it is clear that, if we regard the brain as the seat of the changes resulting in sensation, the nearer any stimulated portion of skin is to the brain the sooner will the brain feel and respond to the stimulus. Thus, if the skin on the big toe of the right foot be stimulated, the effect of the stimulus will pass to the brain and there call forth a sensation; but if the stimulus be applied to the skin at the top of the thigh it is evident the effect will have to pass along a shorter length of nerve, and that the sensation in the brain will be aroused sooner. If we suppose that in each case the individual who is the subject of the experiment indicates the moment he feels the sensation, and that the instant the stimulus is applied successively to the skin on the toe and on the thigh is also accurately recorded, it is clear that he will signal the sensation of stimulation of the toe a little later than when he signals stimulation of the skin on the thigh, and that the difference will indicate the time required by the change in the nerve to pass along the length of nerve from the toe to the thigh. In the observation, it is assumed that the time required for the changes in the brain resulting in sensation and volition, for the transmission along the motor nerve, and for the muscular contraction required to signal, is the same in each experiment. Thus, supposing the total time between the moment of stimulating to the moment when the signal that the sensation has been felt and responded to is x, it is clear that this time is composed of a, the time required for the passage of the nerve current in the first experiment from the toe to the brain;

of b, the time required for the changes in the brain involved in sensation and volition, and of c, the time required for the transmission along the motor nerves and for the muscular contraction to move the signal,—that is, $x=a+b+c$. But, if the time between the moment of stimulating the thigh to the moment of signalling be shorter, and supposing that b and c are constant, then a will vary according to the length of the nerve. Suppose the difference of time between the registration of stimulating at the toe and at the thigh to be y, then in the second experiment $x=a-y+b+c$,—that is, $y=$ the time occupied by the passage of the nerve current from the toe to the thigh. This method has also been used to measure the time required for signalling a nervous impression in various circumstances, or what is usually called the "reaction period." The most convenient apparatus for the purpose is a chronograph made by König of Paris.

The general result of measurements made by these methods is that the nerve current travels slowly compared with the velocity of electricity or of light. In the motor nerves of the frog the velocity is about 87 feet (26 to 27 metres) per second, and in man and warm-blooded animals somewhat faster, 115 to 130 feet (35 to 40 metres) per second. The results as to velocity in sensory nerves vary from 50 to 100 metres per second. Cold retards, heat accelerates, the velocity. As already stated, the velocity is also retarded in a nerve in an anelectrotonic, and accelerated in a katelectrotonic state. The remarkable point is that the transmission of the nerve current is slow, and that events appearing to our consciousness instantaneous require a considerable time for their occurrence. It may be laid down as a general truth that all kinds of nervous actions, even those considered as purely psychical, require time.

Nature of Nerve Currents.—The intrinsic nature of the change in a nerve fibre effected by a stimulus is unknown; but it is evident that a nerve is both a receiver and a conductor of impressions. It can be stimulated in any part of its course, and from the stimulated point some kind of change is propagated along the nerve. This change is analogous to the passage of electricity along a conductor, or to the rapid passage onwards of a series of chemical decompositions, as when a long thin band of gun-cotton, properly prepared, is seen to burn slowly from end to end, or to the quick transmission of isomeric changes; but the analogy is not complete in any case. Whatever the change may be, however, it does not appear to pass from one nerve fibre to another running alongside of it. Each fibre conducts only its own impression, and there is nothing analogous to the inductive effect of one electrical conductor upon an adjacent one. Another question much debated is whether sensory and motor nerves act in the same way; or, in other words, is there any essential difference between them? There appears to be no difference in mode of action; the difference in the effect produced depends on the apparatus in which the nerve ends. Thus there may be contraction of a muscle if the nerve terminates in a muscle, change of the calibre of a blood-vessel if the nerve ends in that structure, secretion from a gland if the nerve is in connection either with the vessels or the cells of a gland, an electrical discharge if the nerve ends in the electrical organ of an electric fish (*e.g.*, *Torpedo* or *Gymnotus*), and a feeling or sensation if the nerve fibres go to a sentient brain. In all these instances, the nature of the change in the nerve and the mode of its transmission are the same, and the results are different because the nerves terminate in different kinds of structure. It would appear from experimental evidence that, when a nerve fibre is irritated, say about the middle of its length, a change is simultaneously propagated towards each end; but, as only one end is in connection with an apparatus capable of responding, the effect at this end is the only one observed. Thus, if a motor nerve is irritated, there is muscular contraction, in consequence of the stimulus rousing the muscular substance into activity, probably through the agency of the end-plates; but there will be at the same time a backward wave along the nerve to the motor centres in the cord or brain. It is doubtful whether the nerve energy becomes weaker or gathers intensity as it passes along a nerve; but the balance of evidence is in favour of the view that the so-called "avalanche theory" of Pflüger, according to which the nerve energy gathers intensity as it passes along, is incorrect.

C.—General Physiology of the Central Nervous Organs.

Chap. I.—ACTION OF GREY MATTER.

As grey matter contains both nerve fibres and nerve cells, and as these cannot be separated in any experiment, it is clear that no precise results can be obtained from any effort to distinguish the *excitability* of grey matter from that of white. The excitability of the grey matter depends on blood supply and on the rapid removal of waste products. If the first be deficient either in quantity or quality, or if the second be not carried on so rapidly as to get rid of the waste products as they are formed, the activity of the nerve cells must suffer. The sudden deprivation of blood, as when the heart ceases to beat for even half a second, will cause unconsciousness; the mixture with the blood of a small quantity of bromide of potassium, or of alcohol, or of chloroform or other anæsthetic, or of morphia, will affect the activity of the brain. And it is well known that, when disease of the kidney, or such a disease as an acute fever, affects the body, matters may accumulate in the blood which so contaminate it as to make it unfit to carry on the vital changes on which activity of brain depends, and the result is delirium or unconsciousness. There is reason to believe that the activity of nerve cells is delicately attuned to surrounding conditions. A small excess per cent. of carbonic acid, or a small amount of a poison, is sufficient to modify or arrest their action. The rhythmic action of various centres is in favour of the view that the activity of such centres depends on delicate equipoises. If, during expiration, there be for the moment a deficiency of oxygen in the blood, or an accumulation of carbonic acid, the result will be an attempt at inspiration. This gets rid of the carbonic acid and introduces oxygen, and an expiration ensues. If this is the case, there is little doubt that a similar effect is produced on other centres by the nature of the blood supplied, and that the quality and quantity of the supply are important factors in the production of all conscious conditions.

Chap. II.—REFLEX ACTIONS.

Impressions made on sensory nerves are conveyed to nerve centres, where they may or may not awaken consciousness. A *sensation* may be defined as the consciousness of an impression which may or may not be followed by motion. Motion may be either voluntary, or it may be caused by direct stimulation of the motor nerve distributed to the muscles. The latter kind of action in the living body is not common. Usually motor nerves are acted on by the will or by emotional states; but it not unfrequently happens that physical stimuli occasion motion in an indirect manner, the impressions being carried along sensory nerves to a central organ, where changes are excited which result in a discharge of nervous energy along motor nerves to various muscles. Thus a frog in which the brain and *medulla oblongata* have been destroyed will draw up its limbs if the foot be pinched. Such motions, unassociated with consciousness, were known to Whytt in 1754, but were attributed by him to a kind of sensation remaining in connection with the spinal cord, an opinion which has been revived in later years and has been accepted by some, but which is contradicted in the only manner possible, namely, by the facts of the clinical experience of diseases and injuries of the spinal cord of man. In 1784, the nature of actions of this kind was clearly stated by Prochaska, who also indicated in not a few instances the sensory and motor nerves which appeared to him to be the channels through which the influence causing them was conveyed, and, in 1832, Marshall Hall gave them the name of *reflex actions*, and stated the conditions of this class of nervous actions in precise terms. Actions taking place without consciousness are called *reflex actions*, and the mechanism required for their performance may be thus described: (1) excitation of a sensory or afferent nerve, (2) excitation of an intermediate nervous or reflex centre, and (3) excitation of a motor or efferent nerve, which causes a muscular contraction. The diagram in Fig. 237 shows the simplest mechanism; but it is rare to find the arrangements so simple, and the mechanism may become more complex (see Fig. 238) either by the existence of a number of cells or groups of cells in the nerve centre, or by the existence of numerous afferent or efferent nerves. In a reflex action, there is the transmutation by means of the protoplasm of a nerve cell of afferent into efferent impulses. The following is a summary of the facts relating to reflex action :—

Fig. 237.—Simple reflex action. 1, sensory surface; 2, muscle; *a*, sensory nerve; *b*, nerve cell; *c*, motor nerve. The arrows indicate the direction in which the influence travels.

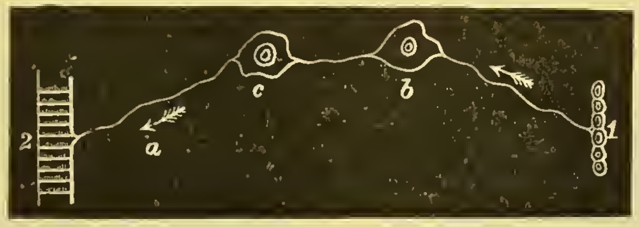

Fig. 238.—Double reflex action, or action in which two or more nerve cells are involved. 1, 2, as in Fig. 237; motor nerve passes from 1 to *b* on the right; *b*, *c*, nerve cells.

(*a*) The initial excitation may occur both in nerves of general sensibility and in those of the special senses; but certain nerves more easily excite reflex actions than others. Thus when light falls on the retina there is contraction of the pupil, the afferent nerve in this case being the optic.

(*b*) A reflex movement may occur whether we excite a sensory nerve at its commencement or at some point in its course, but in the latter case the action is less intense than in the former.

(*c*) Grey matter containing nerve cells constitutes the chief portion of reflex centres, and groups of such reflex centres are frequently associated by internuncial fibres. The excitability is increased when these centres are severed from communication with psychical centres which preside over voluntary movements. Thus, after decapitation, reflex movements occur with greater intensity than in the uninjured animal; they are also more active during sleep. It is evident, therefore, that reflex actions may be restrained or hindered in their development by the action of higher centres. This is termed the *inhibition of reflex action.*

(*d*) Reflex movements may occur in one muscle, or in many muscles or groups of muscles. One or more groups of muscles may be involved according to the strength of the stimulus applied to the sensory surface and the degree of excitability of the reflex centre at the time (see Fig. 239). The facts are thus summarised by Pflüger. *Unilateral action*: if, in a decapitated frog, we excite the skin of the hind foot, *p*, the excitation is transmitted from the centre, *a*, to the muscles, 1, of the foot on the same side. *Symmetrical* action: if the excitation is more intense, it is transmitted to a centre on the opposite side, *b*, and contractions may occur in the muscles of the hind limbs on both sides, 1, 2. *Irradiation*: if the excitation is still increased in intensity, it affects higher centres, *c*, *d*, and there may be contraction of the fore limbs, 3, 4. *General action*: if the excitation be still further increased, it may pass to a still higher reflex centre, *e*, and the result will be general convulsions.

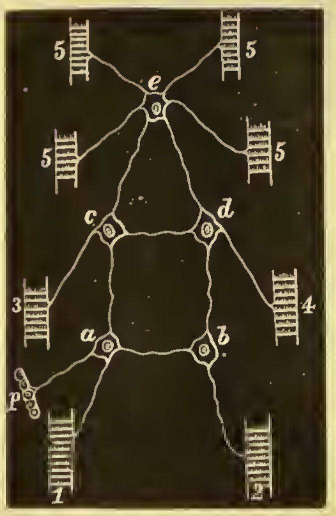

FIG. 239.—*p*, sensory surface; *a*, *b*, *c*, *d*, *e*, nerve cells; 1, 2, 3, 4, 5, 5, 5, 5, muscles.

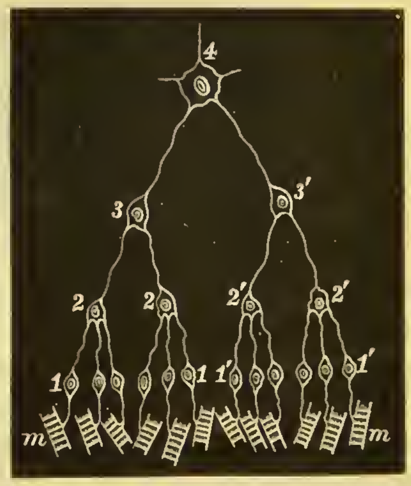

FIG. 240.—Diagram illustrating the superposition of reflexes. *m*, *m*, muscles; 1, 1, series of reflex centres on one side, under the control of 2, 2, which are again governed by 3. There is a corresponding series, 1', 1'; 2', 2'; 3' on the other side. Both sides are presided over by 4. Thus a stimulus reaching 4 might excite the activity of all the muscles, *m*, *m*; if it reached 3, only one half of the muscles; if it reached 2, to the left, only three of the muscles; and, finally, if it affected 1, to the left, only one muscle, *m*.

(*e*) Reflex centres may be so arranged in the body as to constitute a series in which those of the cerebrum govern or control others in the deeper ganglia of the brain, while these, in turn, have an influence over still lower centres in the spinal cord. This arrangement is termed the *superposition of reflexes* (see Fig. 240).

(*f*) Stimulation of a sensory surface may simultaneously produce, by a reflex mechanism, movement, secretion, and consciousness. Thus a condiment in the mouth may cause involuntary twitchings of the muscles, secretion of saliva, and a sensation (see Fig. 241).

Fig. 241.—Diagram illustrating a complex reflex mechanism. The arrows indicate direction of currents. 1, sensory surface; 2, muscle; 3, gland; *a*, sensory nerve; *b*, reflex centre, connected with another reflex centre, *d*, by internuncial fibre, *e*; *c*, motor or efferent nerve; *f*, secretory nerve passing to gland 3. From the other side of *d* is seen a fibre passing to the brain, and there exciting changes which result in a sensation.

(*g*) Certain substances, in particular strychnin, increase reflex excitability, so that the slightest external stimulation of the sensory nerves of the skin is sufficient to cause severe convulsions. On the other hand, bromide of potassium, hydrate of chloral, and atropin diminish reflex excitability.

(*h*) Individual stimuli only excite a reflex act when they are very powerful, but stimuli applied at frequent intervals act the more quickly and powerfully the more rapidly they succeed each other. To produce the reflex change in the centre, therefore, a *summation* or addition of centripetal excitations is required. When these reach a certain number, the centre responds.

(*i*) Reflex actions involve time. Thus the time between the stimulation and the movement can be measured, and if we take into consideration the time occupied by the passage of the nerve current along the nerves involved, and the latent period of muscular contraction, and subtract this from the total time, the remainder will represent the time occupied by the changes in the centre, or the reflex time. This has been found to be from ·0555 to ·0471 of a second. It is lengthened by cold and shortened by increasing the strength of the stimulus and by strychnin.

(*k*) In compound reflex acts the initial excitation may occur in psychical centres, as when the recollection of an odour causes nausea, or when a feeling of ennui is followed by a yawn.

(*l*) Some reflex movements are the result of inherited peculiarities of structure, as those made by a new-born child when it seizes the breast. Other reflex movements are acquired during life. Such are at first voluntary, but they become automatic by repetition.

The following are the more common examples of reflex movements —*m*, motor; *s*, sensory; and *c*, reflex centre:—

1. Motions of the muscles in any part of the limbs or trunk, caused by tickling, shuddering, etc.: *s*, sensory nerves of skin; *m*, motor nerves; *c*, spinal cord.

2. Shuddering from grating noises: *s*, auditory; *m*, motor nerves; *c*, brain and cord.

3. Contraction of pupil by light: *s*, optic; *m*, third, to circular fibres of iris; *c*, *corpora quadrigemina*.

4. Winking: *s*, ophthalmic of fifth; *m*, facial; *c*, *medulla oblongata*.

5. Sneezing: *s*, ophthalmic branches of fifth to Schneiderian membrane of nose; *m*, muscles of expiration; *c*, medulla. Also by glaring light when *s* is the optic.

6. Spasm of glottis: *s*, superior laryngeal of vagus; *m*, inferior laryngeal of vagus; *c*, medulla.

7. Laughing, caused by tickling: *s*, sensory nerve of skin; *m*, facial and expiratory muscles; *c*, brain and cord.

8. First respiration after birth: *s*, sensory of skin; *m*, phrenics to diaphragm and nerves to elevators of ribs (inspiratory muscles); *c*, medulla.

9. Respiratory movements: *s*, sensory from skin, branches of vagus from lungs; *m*, phrenic nerves to diaphragm, and nerves to muscles of inspiration.

10. Sucking in infancy: *s*, fifth, to mouth; *m*, facial to mouth and hypoglossal to tongue; *c*, medulla.

11. Deglutition: *s*, lingual of fifth, glosso-pharyngeal, superior laryngeal of vagus; *m*, glosso-pharyngeal to muscles of pharynx, facial to palato-pharyngeus, fifth to palato-glossus, supra-hyoid muscles, muscles of mastication and branches of vagus to larynx and œsophagus; *c*, medulla.

12. Vomiting from irritation in stomach: *s*, vagus; *c*, medulla; *m*, vagus to stomach, phrenics to diaphragm, vagus to glottis, fifth and facial to muscles of mouth. If irritation in fauces, then *s* are branches of fifth and glosso-pharyngeal.

13. Forced contractions of sphincter ani, and sphincter of urinary bladder, of vagina, from local irritation, or from irritation of another sensory surface: *s*, sensory nerves of mucous membrane; *m*, motor nerves to sphincters; *c*, spinal cord.

14. Erection and Emission: *s*, sensory of penis; *m*, sacral plexus; *c*, spinal cord (lumbar).

15. Rhythmic movements of all kinds where there are sensory and motor filaments and ganglia, such as heart, lymphatic hearts in reptiles, etc.

16. Peristaltic movements of intestinal canal: *s*, splanchnics and vagus; *c*. spinal cord; *m*, splanchnics, and vagus (?).

17. Expulsion of urine from bladder: *s*, nerves in bladder and urethra; *m*, muscles of bladder and nerves to abdominal muscles; *c*, spinal cord.

18. Expulsive action of uterus: *s*, in uterus, or sensory of skin; *m*, to uterus and abdominal and other muscles; *c*, spinal cord.

19. Contractions and dilatations of vessels under influence of vaso-motor nerves: *s*, sensory from skin, or sensory from brain (blushing); *m*, vaso-motor filaments; *c*, medulla.

20. Convulsions of teething: *s*, fifth to gums; *m*, spinal nerves; *c*, medulla and cord.

21. Convulsions from worms in intestinal canal: *s*, splanchnics, or vagi; *m*, spinal nerves; *c*, spinal cord.

22. Dilatation of pupil from worms: *s*, splanchnics and vagi; *c*, spinal cord; *m*, sympathetic to radiating fibres of iris.

23. Grinding teeth from worms: *s*, splanchnics and vagi; *c*, spinal cord, or fifth to muscles of mastication.

24. All kinds of excito-secretory actions, such as flow of tears on irritation of conjunctiva: *s*, fifth; *c*, medulla, or local ganglion; *m*, filaments from ciliary ganglion to the lachrymal gland and to the blood-vessels.

D.—Special Physiology of the Central Nervous Organs.

Chap. I.—THE EVOLUTION OF THE CENTRAL NERVOUS ORGANS.

The central organs of the nervous system consist of ganglia, constituting a *cerebro-spinal axis.* As one of the best ways of obtaining a conception of the complicated nervous system of man is to trace its various forms in the scale of animal existence, and to observe the close correspondence between complexity of structure and complexity of function, a short introductory review of its comparative anatomy, from the physiological side, will be given. In the first place, we find that the different forms of nervous systems may be divided into (*a*) those consisting of ganglia, or chains of ganglia, as found throughout the invertebrates; and (*b*) those having an axis of nervous matter forming a brain and spinal cord, the *cerebro-spinal axis,* as seen in vertebrates.

In the simplest forms of animals the protoplasmic cell is the seat of sensation and of motion; but, as the contractile or muscular layers become differentiated, sensation is relegated to the cells of the outer layer. As portions of this sensory layer become of higher value to the organism, their protection is accomplished by some of the sensory cells sinking into the body of the organism, so as to be covered by less important structures. The portions, originally on the surface, thus differentiated and protected, become ganglia, and processes pass from them, on the one hand, to cells in the periphery, so that they may still be influenced by external energies, and, on the other, to the contractile parts of the organism by which movements are accomplished. Still

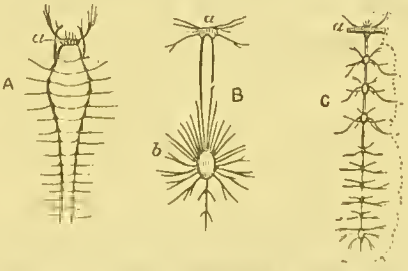

Fig. 242.—Typical forms of nervous system in invertebrates. A, in *Serpula*, a marine annelid; *a*, cephalic ganglion. B, in a crab; *a*, cephalic ganglion; *b*, ganglia fused under cephalo-thorax. C, in a white ant (*Termes*); *a*, cephalic ganglion. (Gegenbauer.)

higher in the scale of life, the ganglia are connected by internuncial fibres, and the plan of the primitive nervous system bears a relation to the type of structure of the animal. Thus, in radiate animals the gangliated cords show a radiated arrangement, and, when the animal form is bilateral and symmetrical, the nervous arrangements are on the same type. The ganglion connected with the rudimentary organs of sense attains a size and importance proportionate to the development of the sense organs. The nerves of the sense organs are chiefly connected with the supra-œsophageal ganglion. When the body of the animal becomes more complicated by the development of similar segments, we find that, by a reduplication, as it were, of the subœsophageal ganglion, a ventral chain of ganglia is formed, a pair of ganglia for each segment, the individual ganglia being connected by longitudinal and transverse commissures. Such an arrangement is seen in the ringed worms and in arthropods. The next step is a fusion of ganglia into masses, according to the size and importance of the part of the body to be innervated.

The cerebro-spinal axis of the vertebrate begins in the embryo as a tube of nervous matter produced by an infolding of the epiblast. The tube widens at its anterior end, and, by constrictions in its walls three primary cerebral vesicles are formed, which afterwards become the anterior, middle, and posterior parts of the brain (Figs. 243 and 245). In the

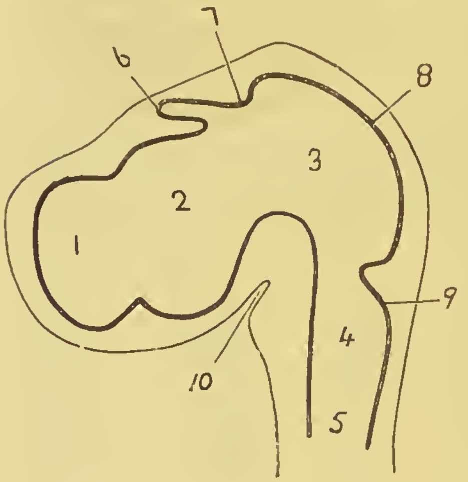

FIG. 243.—Longitudinal section of head of chick of $4\frac{1}{2}$ days. 1, Prosencephalon ; 2, thalamencephalon ; 3, mesencephalon ; 4, epencephalon ; 5, metencephalon ; 6, pineal body ; 7, posterior commissure ; 8, corpora quadrigemina ; 9, cerebellum ; 10, hypophysis cerebri or pituitary body, partly formed by invagination of epithelium of palate. (After Mihalkovics.)

FIG. 244.—Frontal section of head of human embryo of $2\frac{1}{4}$ months, showing invagination of anterior cerebral vesicle and the development of corpus striatum. 1, Primordial septum ; 2, lateral ventricle ; 3, 3rd ventricle ; 4, corpus striatum.

fully developed condition, the cavity of the tube remains as the central canal of the spinal cord and the ventricles of the brain, whilst the various parts of the brain and cord are formed by thickenings in its walls. The three cerebral vesicles are called the fore-brain, the mid-brain, and the hind-brain (Fig. 245). A protrusion from the anterior cerebral vesicle, at first single, but afterwards divided by a median cleft, becomes the rudiment of the cerebral hemispheres (*prosencephala*), the cavity remaining in the adult condition as the lateral ventricle on each side. From each cerebral vesicle another hollow process protrudes which constitutes the olfactory lobe (*rhinencephalon*). The remainder of the cavity of the first vesicle becomes the third ventricle (*thalamencephalon*). In the outer and under walls of the *prosencephala* thickenings are formed, which become the *corpora striata*, two large bodies in the floor of the lateral ventricles of the adult brain, whilst the roof is modified into the substance of the cerebral hemispheres (Fig. 244). Immediately behind the *corpora striata*, and in the floor of the thalamencephalon, two similar thickenings occur which become the *thalami optici*, a thin layer between the two constituting the *tænia semicircularis*, and the Y-shaped canal passing from the cavity between the thalami to the cavities in the cerebral hemispheres (lateral ventricles) is the *foramen of Monro.* The floor of the third ventricle is produced into a conical process, the *infundibulum*, at the blind end of which is the *pituitary body*, or *hypophysis cerebri.* The roof of this ventricle is thin, and in connection with it is developed the *pineal body* or *epiphysis cerebri.* Transverse fibres pass from the one *corpus striatum* to the other, constituting the *white commissure*, whilst the two *thalami optici* are connected by two *grey commissures.* In mammals, the two cerebral hemispheres are connected by commissural fibres, forming the *corpus callosum.* In addition, there

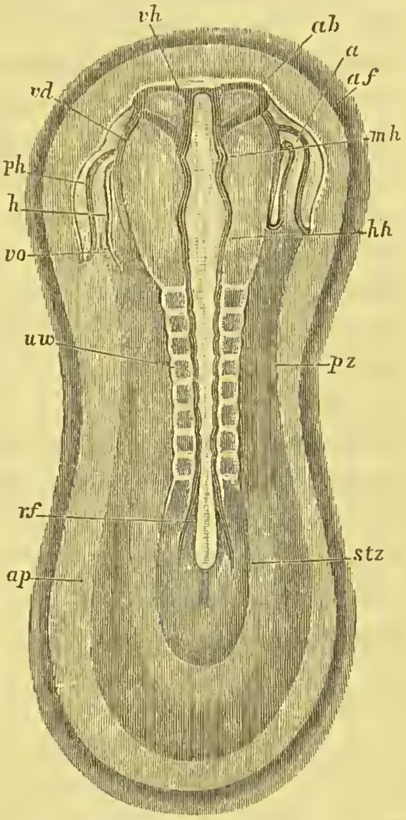

FIG. 245.—Embryo rabbit of 9th day, seen from the dorsal aspect. × 21 d. *ap*, area pellucida; *rf*, medullary groove; *h*, medullary plate in the region of the future fore-brain; *hh*, medullary plate in the region of the future mid-brain; *vh*, fore-brain; *ab*, optic vesicle; *mh*, mid-brain; *hh*, hind-brain; *uw*, mesoblastic somite; *stz*, vertebral zone; *pz*, lateral zone; *ph*, section of body cavity; *vo*, vitelline vein; *af*, fold of amnion. (Von Kölliker.)

are certain sets of longitudinal commissural fibres. As in highly-formed brains the *corpus callosum* passes across considerably above the level of the fornix, a portion of the inner wall of the hemisphere on each side and a space between are intercepted. The two inner walls constitute the *septum lucidum*, and the space the cavity of the fifth ventricle. By a thickening of the floor of the middle cerebral vesicle (*mesencephalon*), two large bundles of longitudinal fibres, the *crura cerebri*, are formed, whilst its roof is modified into the optic lobes, *corpora bigemina* or *corpora quadrigemina*. The cavity, reduced to a mere tube, is the *iter a tertio ad quartum ventriculum*, or the *aqueduct of Sylvius*. The third cerebral vesicle undergoes less modification than the others. The upper wall is exceedingly thin anterior to the cerebellum so as to form a lamina, the *valve of Vieussens*, whilst the part behind is covered only by membrane, and opens into the posterior sub-arachnoid space. The *cerebellum* makes its appearance as a thin medullary lamina, forming an arch behind the *corpora quadrigemina* across the wide primitive medullary tube. The portion forming cerebellum, *pons Varolii*, and the anterior part of the fourth ventricle is termed the *epencephalon*, whilst the remaining portion, forming the *medulla oblongata* and fourth ventricle, is the *metencephalon*.

The complex structure of the brain in the higher animals arises to a large extent from the great development of the cerebral hemispheres. At a very early period these grow forward and project more and more beyond the region of the first primary vesicle, which, as has been noticed, never advances farther forward than the pituitary fossa (*lamina terminalis*); in expanding upwards, they take the place previously occupied by the mid-brain, and fill the most prominent part of the head; and by a downward and lateral enlargement they form the temporal lobes. Thus frontal, parietal, and temporal lobes come to be distinguishable, and somewhat later, by a farther increase posteriorly, the hindmost lobes constitute the occipital lobes, and the cerebrum at last covers completely all the lower parts of the brain. The hemispheres therefore, which are small in the early embryo of all animals, and in adult fishes permanently, attain so large a size in man and in the higher animals as to conceal all the other parts. Whilst this general development is going on, the layer of grey matter on the surface of the hemispheres increases to such an extent as to throw the surface into folds or convolutions. The upper surface of the hemispheres is at first smooth. The first appearance of division into lobes is that of a blunt notch between the frontal and temporal parts below, in what afterwards becomes the *Sylvian fissure* (Figs. 246 and 247). In the fourth and fifth months there appear the vertical fissure, separating the parietal and occipital lobes, and the transverse fissure, called the *fissure of Rolando*, which divides the frontal and parietal lobes superiorly, and which is characteristic of the cerebral type of man and of the apes. Then the convolutions appear from the formation of secondary grooves or *sulci*, for even at birth they are not fully perfected; and by the deepening of the grooves and the formation of subordinate ones the process goes on during the first years of infancy.

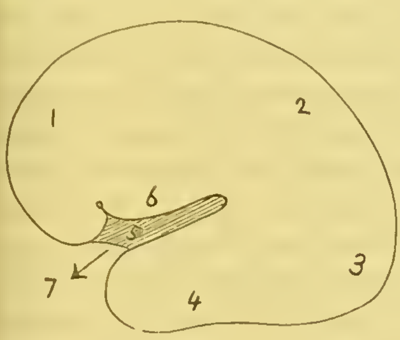

FIG. 246.—Brain of human embryo of 4½ months. 1, frontal lobe; 2, parietal lobe; 3, occipital lobe; 4, temporal lobe; 5, island of Reil; 6, Sylvian fissure. (Edinger.)

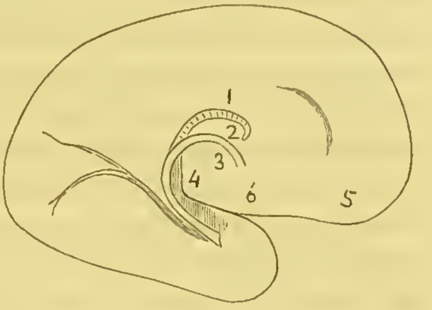

FIG. 247.—Internal face of same brain as shown in Fig. 246. 1, corpus callosum; 2, septum lucidum; 3, fornix; 4, thalamencephalon; 5, anterior lobe; 6, point where the anterior lobe joins the thalamencephalon.

The evolution of the brain throughout the animal kingdom shows a graduated series of increasing complication, proceeding out of the same fundamental type; so that the forms of brain found permanently in fishes, amphibians, reptiles, birds, and in the lower mammals are repetitions of those shown in the stages of the embryonic development of the brain of one of the higher animals.

In the whole class of fishes the brain retains throughout life the elementary form—that is, it consists of a series of enlargements, single or in pairs (see Fig. 248). The simplest of all forms is in the lancelet (*Branchiostoma*), in which there is no distinction between brain and cord. In the *Cyclostomata*, as the lampreys, the form is nearer that of the embryo when the five fundamental parts of the brain can be distinguished. At this stage the cerebrum and cerebellum

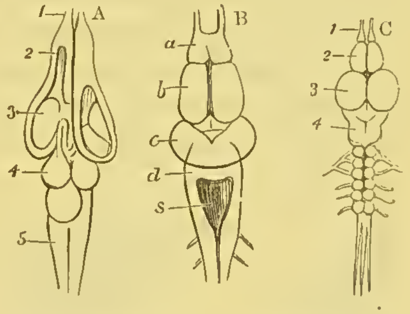

FIG. 248.—Typical forms of brains of lower vertebrates. A, Brain of tortoise (*Testudo*). 1, olfactory; 2. cerebral lobes; 3, corpora striata; 4, optic lobes; 5, medulla. Part of the surface of the cerebral lobes has been removed to show the cavities in the interior, termed "the ventricles." Immediately behind 4, the optic lobes, is the imperfectly developed cerebellum. B, Brain of common frog (*Rana*). *a*, olfactory; *b*, cerebral lobes covering corpora striata; *c*, corpora quadrigemina, or optic lobes; *d*, cerebellum (rudimentary); *s*, back of medulla, showing fossa. C, Brain of gurnard (*Trigla*). 1, olfactory: 2, cerebral lobes; 3, optic lobes; 4, cerebellum.

are small, whilst the ganglia developed are those connected with the organs of sense, especially those of vision. In the sharks and skates (*Selachii*), the cerebral portion is larger. In osseous fishes (*Teleostei*) the thalamencephalon is so fused with the mesencephalon as to make the homology of the parts difficult to trace, but both cerebellum and cerebrum are still small relatively to the rest of the brain. The most important part of the brain of a fish is the part behind the mesencephalon, as from it all the cerebral nerves originate. Thus, not only are the optic lobes relatively important as being the centres of vision, but the *medulla oblongata* is usually very large.

In the *Amphibia* the hemispheres are larger, and are divided into two parts (see Fig. 248, B). In the *Urodela* the mesencephalon remains small, and consists of one lobe, but in the *Anura* there is an advance in this part, it being divided into two. In reptiles there is an advance in the size of the thalamencephalon and mesencephalon, and the prosencephalon is so large as to pass backwards and overlap the thalamencephalon. The cerebellum (metencephalon) is small, especially so in *Ophidii* and *Saurii*, but in the *Chelonii* and in *Crocodilini* it is larger.

In birds (Fig. 249) the vesicles of the mid-brain are partially hidden by development of the cerebral hemispheres. These are connected by an anterior commissure, and they contain a large amount of ganglionic matter bulging into the primitive cavity or ventricles. The middle portion of the cerebellum shows a laminated structure and a differentiation into white and grey matter. But there is no *pons Varolii* nor *corpus callosum*, nor *fornix*. In the floor of the lateral ventricles may be seen a ganglionic mass corresponding to *corpus striatum* and *thalamus opticus*. The optic lobes are relatively large.

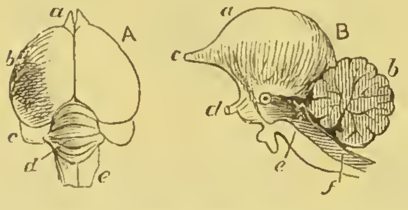

Fig. 249.—Typical brain of bird. A, view from above; B, lateral view of a bisected brain. A.—*a*, olfactory; *b*, cerebral lobes; *c*, optic or bigeminal lobes; *d*, cerebellum; *e*, medulla oblongata. B.—*a*, cerebrum; *b*, cerebellum; *c*, olfactory; *d*, optic nerves; *e*, medulla; *f*, spinal cord.

Mammals not only show a general enlargement of the cerebral hemispheres, but a commissure, the *corpus callosum*, uniting them. This commissure is of small size, and is confined to the fore part of the hemispheres in *Monotremata* and *Marsupialia* and in some of the *Edentata*, but it extends farther and farther back as we ascend to the higher orders. The chief changes thus occur in the prosencephalon. In the lower orders of mammals, the hemispheres are small and simple, and do not present any division into convolutions, and little distinction of lobes. The cerebral hemispheres grow backwards covering mid-brain, cerebellum, and *medulla oblongata*, as we find in the higher *Primates.* There is also a general enlargement of the brain. The development of a posterior lobe takes place in the higher orders, and in these also the enlargement of the frontal lobes brings the front of the cerebrum more over the nasal cavities, causing a development of forehead. But the internal arrangements of the brain also become more complicated. The fornix establishes, by its longitudinal and commissural fibres, a connection between the anterior and posterior lobes of the cerebrum. In the *Monotremata* and *Marsupialia* the mid-brain retains a bifid form, constituting the optic lobes, or *corpora bigemina*, but in all higher animals each is divided into two by a transverse groove, forming the *corpora quadrigemina*, of which the anterior pair is the larger. As we ascend, we find the surface of the brain becoming more convoluted (Figs. 250 and 251). This is the general fact; but whilst the convolutions are most numerous and deepest in the highest orders there is no regular gradation, as in each group there are very great variations in the degree of convolution. Thus in the *Monotremata* the *Echidna* has a more convoluted cerebrum than the *Ornithorhynchus*, whilst in the *Primates* the brains of the marmosets show a comparatively smooth non-convoluted surface, in contrast to the rich convolutions seen on the brains of the higher monkeys.

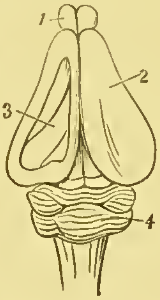

FIG. 250.

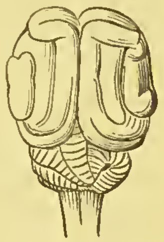

FIG. 251.

FIG. 250.—Rabbit's brain. 1, olfactory; 2, surface of cerebral hemisphere; 3, lateral ventricle, in the floor of which is seen the corpus striatum; 4, cerebellum.

FIG. 251.—Cat's brain, showing convoluted surface. Contrast the form of the cerebellum in the cat and the rabbit. In the cat the central lobe is small, whilst the lateral lobes are largely developed.

The cerebellum also becomes more and more complicated from the lower to the higher groups. At first merely a lamina or band, as seen in fishes and amphibia, it is a centrally differentiated body in crocodiles. In birds there is an indication of a division into three portions, a central and two lateral, whilst the central is the larger, the two lateral being feebly developed. In *Monotremata* the central portion is larger than the lateral, but, whilst it is larger in *Marsupialia*, *Edentata*, and *Cheiroptera*, it is clear that the lateral portions are increasing in size so as to make the disproportion less. But in *Carnivora* and in *Ungulata* the lateral lobes of the cerebellum develop to a much greater size; and in most of the *Primates* they are much larger than the median portion, which is now called the *vermiform process.*

The spinal cord does not show any marked peculiarities of structure in different animals. The grey matter is found in the centre of the cord, and it is most abundant in the regions associated with the development of limbs. The white matter is external, and, in the cords of the higher animals, can be differentiated by fissures into columns. The size of the cord is influenced by the masses of nerves given off from it, so that it attains its greatest thickness and development in the four higher divisions of the vertebrates possessing limbs. Thus, too, are formed cervical, dorsal, and lumbar enlargements, contrasting with the more uniform and ribbon-like shape of the cord in fishes, although even in these there are special enlargements corresponding to the points of exit of important spinal nerves.

Size and Weight of Brain.—The increase in the size of the brain, as compared with that of the body, which is observed as we rise in the animal scale, has a proportional relation to a corresponding increase of mental endowment. After considering the measurements of several thousand skulls made by different observers, Allen Thomson arrived at the conclusion that the cranial capacity is on the whole greater among the highly-civilized than among the savage races, and that there is even a manifest difference to be found between those of persons of higher mental cultivation and acknowledged ability and those of the uneducated class and of inferior intellectual powers; and he states further that the amount of this difference may be from 5 to 7½ per cent. in persons of the same race, and about double that range in those of different races. The average adult brain of men in Britain weighs 49½ oz. avoir. (women, about 44 to 44½ oz.).[1] The cranial capacity is about 90 cubic inches. The brain of the uneducated class falls 2·5 oz. below the average, whilst that of the more cultivated persons rises to the same amount above it, or to 52½ oz. The average brain-weight of an Australian aboriginal man is about 42 oz. There are, however, great variations in all races. Thus the brain of Cuvier, the great naturalist, weighed 65 oz. avoir. In Europeans, the brain-weight has fallen as low as 32 oz. The brains of the anthropoid apes are all inferior to man in their dimensions. In the gorilla the brain does not attain more than a third of the weight of the average human brain, and in the chimpanzee and orang it does not reach a fourth. The ratio of brain-weight to body-weight in these animals may be as 1 to 100, whilst in man it ranges from 1 to 40 to 1 to 50. Among the largest animals of any group the brain does not reach a size proportionate to the greater magnitude of the other organs or of the whole body, so that in the smaller members of the same order a considerably greater proportional size of the brain is observed. Thus in the small marmosets the proportion of the brain-weight to the body-weight may be 1 to 20, or more than double the proportion in man.

Although the proportion of brain-weight to the body-weight in a male child at birth is 1 to 10, yet so rapidly does the brain continue to grow during the early period of childhood that by the age of three years it has attained more than three-fourths of its full size, by the age of seven years it has reached the proportion of nine-tenths, and after this, only by slow and small gradations, it attains the full size between the ages of twenty and twenty-five years. The following figures express the ratio of the brain-weight to the body-weight in various animals:—Pike,

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[1] 1 oz. = 28·35 grammes. 1 cub. inch = 15,625 cub. mm.

1 : 1300 ; ox, 1 : 800 ; horse, 1 : 540 ; elephant, 1 : 500 ; sheep, 1 : 350 ; dog, 1 : 110 ; pigeon, 1 : 104 ; monkey, 1 : 40 ; man, 1 : 40-50.

From this survey of the comparative development of the brain the following general conclusions can be drawn :—

1. The first and essential portion of the cerebro-spinal axis is the portion forming the spinal cord and *medulla oblongata*, inasmuch as it is found throughout the vertebrates, and is connected with the reflex movements on which locomotion, respiration, and the circulation depend. This part is associated with the sense of touch.

2. When higher senses are added—taste, smell, hearing, vision—portions of the anterior part of the cerebro-spinal axis are differentiated to form centres. The earliest and most important of these senses is vision, hence the high degree of development of the optic lobes even in the lowest forms ; to these are added the *thalami optici*, which may be regarded as the centres of tactile sensations involving appreciation of differences of touch as to softness, smoothness, hardness, etc., requiring in the periphery special terminal organs. The special centres for hearing, taste, and smell are not differentiated, but are fused together to form a portion of the cerebral mass. The organs relating to the sense of smell are most anterior and most closely related with the prosencephalon, indicating that this sense is one of the earliest in appearance, and along with vision and touch, one of the most necessary to existence. It is striking that the origin of the auditory nerves should be placed so far back as in the *medulla oblongata* and cerebellum, indicating the primitive nature of auditory impressions and their relations to co-ordination of movement. The sense of taste originates in nerves springing from the *medulla*, and in close connection with those regulating the movements of the tongue and swallowing.

3. When sensations of a simple character are elaborated into ideas and give rise to psychical changes, correlated to mental states, involving memory, emotions, volitions, and intellectual acts, a part of the cerebro-spinal axis is differentiated for these functions in proportion to the extent to which such mental phenomena are manifested by the animal. Judging from the facts obtained by comparing animal intelligences, we infer that in proportion to the degree of development in size and complexity of structure of the brain so is the mental condition of the animal. Taking it broadly, there can be no question that the intelligence of a bird is higher than that of a reptile, amphibian, or fish, and that the intelligence of the higher mammals, such as one of the *Primates*, is superior to that of the lower, as one of the *Insectivora*, or of the *Marsupialia* ; and along

with the higher intelligence is the more complex brain. In proportion to the degree of development of the prosencephalon do we find the intelligence of the animal, and we regard this portion as superadded to the cerebro-spinal axis as the organic mechanism for mental operations.

4. There is a correspondence between the development of the cerebellum and the faculty of co-ordination of movement. Movements of the members of the body may be of a simple character, or they may be complex. They may be due to the action only of flexor and extensor muscles, causing the limb to move in the same plane, or they may be associated with the action of adductor and abductor muscles, by which there may be many kinds of circular or rotatory movements. There is a great difference between the movements of a fish's fin, of a bird's wing, of a horse's fore-leg, and of the arm of a monkey or a man. In the first three, they are almost to-and-fro movements, unlike the delicate movements of flexion, extension, pronation, supination, and prehension seen in the latter. Delicacy of movement of the anterior limb reaches its highest condition in man. Simplicity of movement is associated with a less complex cerebellum, whilst in animals having the power of complicated movements, involving the adjustment of movement in special circumstances, the cerebellum is highly developed. From this point of view, the degree of development of the cerebellum is as characteristic of man as the degree of development of the cerebrum.

CHAP. II.—THE MINUTE STRUCTURE OF THE CENTRAL ORGANS.

The elements of the nervous system, nerve fibres and nerve cells, having been described (Vol. I. pp. 313 to 317), we shall next direct our attention to the general arrangement of these elements to form the central nervous system. The special physiological anatomy of these organs will be described when we discuss the functions of the cerebro-spinal centres, considered as organs.

1. The Spinal Cord.

The spinal cord consists of two kinds of nervous matter, distinguishable by the naked eye, the *white* and the *grey* matter. Their relative position in the spinal cord is seen in a transverse section of the cord (Fig. 252). The white substance surrounds the grey substance. The cord is divided anteriorly into a right and left half by a deep anterior longitudinal fissure, and posteriorly by a septum, formerly called the posterior longitudinal fissure. Each half of the cord also is divided into columns by a groove along the line of exit of the anterior roots of the spinal nerves, and by another corresponding to the line of entrance of the posterior roots. Three columns are thus formed—anterior, middle, and posterior. In the lower cervical and upper dorsal region, each posterior column is divided into an inner, next the posterior median septum, called the column of Goll, and the outer, termed the column of Bùrdach.

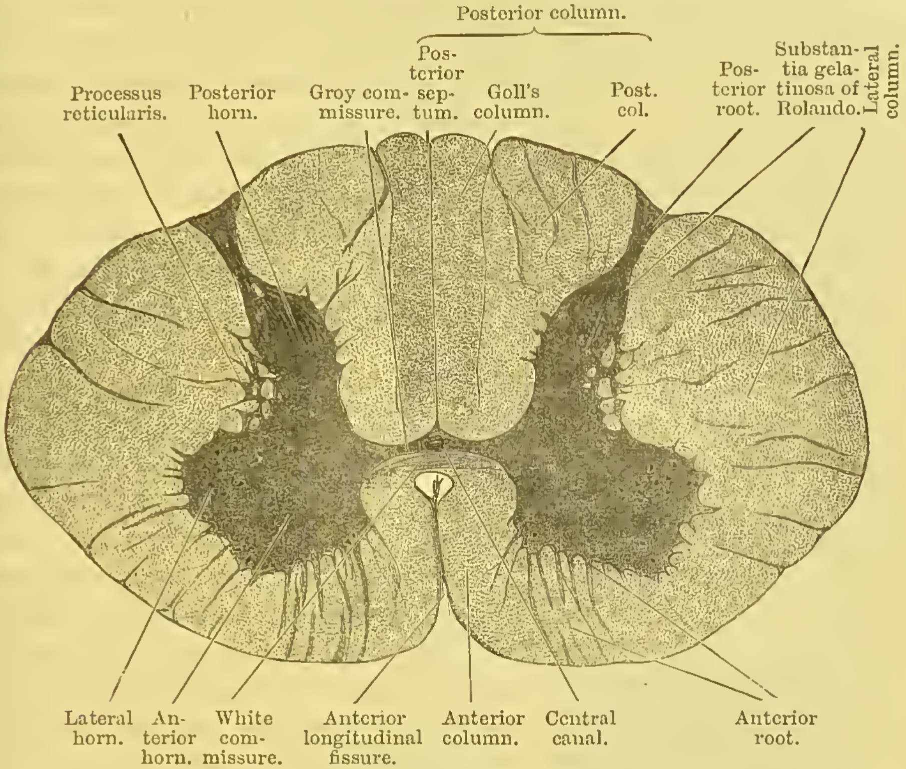

FIG. 252.—Transverse section of human spinal cord in cervical region. × 8 d. White matter light in colour, grey matter dark. The lines in the lateral and posterior columns running from the outer margin are laminæ of the pia mater. The large ganglion cells of the anterior and lateral horns may be seen even with this low power. (Method No. 85, Appendix.)

The *grey* matter in a transverse section has a bi-crescentic form, the backs of the crescents being joined by a broad band of grey matter, the *grey commissure*, in the centre of which we see the central canal of the cord, ·05 to 1 mm. in breadth, and lined, in the earlier years of life, by a layer of ciliated epithelium. The grey matter may thus be regarded as consisting of two lateral columns, united by the grey commissure. In each half we observe a thick and rounded anterior horn, and a more slender and pointed posterior horn. On the lateral aspect of the anterior horn there appears, more especially in the lower cervical region, another horn or bulging portion of grey matter, to which the name of the lateral horn has been given. From the anterior margin of the anterior horn spring the anterior roots of the spinal nerves, and from the posterior horn the posterior roots originate. Towards the base of the posterior horn we find a reticulated structure consisting of grey matter, the *processus reticularis*, and posterior to this we find a jelly-like substance, also consisting of grey matter, termed the *substantia gelatinosa Rolandi.* A small portion of grey matter of a similar kind surrounds the central canal, and is known as the *substantia gelatinosa centralis.* The portion of the grey commissure lying in front of the central canal is the *anterior commissure*, and the portion behind it is the *posterior commissure.* The grey matter is more abundant in the cervical and lumbar regions than in the dorsal region, but throughout it maintains the same general form. The lower termination, the *conus medullaris*, is formed only of white matter.

The *white* matter consists of medullated nerve fibres, which do not show the sheath of Schwann. The fibres vary in diameter, the thickest occurring in the anterior columns and in the lateral portions of the posterior columns, and in the lateral columns where the white matter touches the grey matter. In other parts thick fibres are mixed in all proportions with finer ones of varying degrees of thickness. Most of the fibres run parallel to the longitudinal axis of the cord, so that in transverse sections of the cord they are cut across (Fig. 253), but one may also see fibres running obliquely. These latter lie in front of the grey commissure, and, crossing at acute angles, form the *white commissure.*

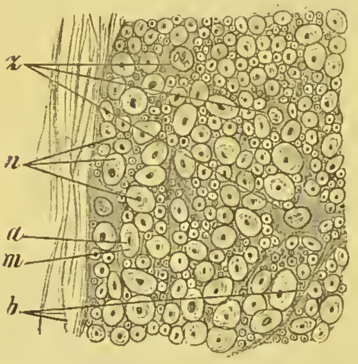

FIG. 253.—White matter in a transverse section of human spinal cord. × 560 d. *b*, connective tissue (*pia mater*); *z*, nuclei of cells of the neuroglia; *n*, small and large nerve fibres divided transversely, so that we observe *a*, the axis cylinder, and *m*, the white substance surrounding it. (Method No. 86, Appendix.)

The *grey* matter contains both nerve fibres and nerve cells. The *nerve fibres* are partly medullated and partly non-medullated. The medullated, after an irregular course, pass partly into the white substance, while another portion lose their white substance, becoming non-medullated fibres, and the latter are lost in a network of extremely delicate fibres. The poles of the nerve cells also pass into the same network of fine fibrils.

The *nerve cells* are multipolar ganglionic cells, varying in size, and their poles or processes terminate in, or give origin to, the axis cylinders of medullated nerve fibres. The cells are isolated, one here and another there, or they are found in well-defined groups. One conspicuous group is situated in the anterior horn. It contains numerous large multipolar cells. In the lower thoracic and upper lumbar region, and in the middle half of the posterior horn, near the grey commissure, there is another well marked group, known as *Lockhart Clarke's column.*

The structures that support and bind together the elements in the white and grey matter are (1) processes of connective tissue derived from the *pia mater* which enter the cord along with the blood-vessels, and envelop the nerve fibres in the white substance, ending in the white substance, and becoming thinner and thinner towards the grey matter, and (2) the neuroglia, a whitish homogeneous substance of epithelial origin. The neuroglia is a kind of cement formed of a substance allied to keratin substance, binding together individual nerve fibres and ganglion cells. It contains a smaller number of flattened or stellate nucleated cells, the *neuroglia cells* (Fig. 254). The neuroglia coagulates after death and then appears as a delicate network. On the posterior surface of the cord, and in the *substantia gelatinosa* there is another network of fine fibrils, which is also epithelial in its nature and consists of cuticular matter ; it is known as the granular matter, or spongy horn substance. It also contains nucleated cells.

Fig. 254.—From a thin transverse section of the human spinal cord. × 560 d. Neuroglia, with two neuroglia cells, *z*. The sections of the nerve fibres have fallen out. (Method No. 87, Appendix.)

The central canal of the cord is lined by a simple layer of columnar ciliated epithelial cells. The cilia are to be seen only in early life, and in advanced life there may be complete closure of the canal, the cells then becoming much altered in form, probably by pressure. Spongy horny matter immediately surrounds the central canal. The *substantia gelatinosa* of Rolando consists of horny matter, nerve fibres, and multipolar ganglion cells.

2. The Brain.

The comparatively simple arrangements of the white and grey matter in the cord become more complicated in the *medulla oblongata*, in consequence of the passage of strands of nerve fibres through the grey matter and also of the appearance of new masses of grey matter, constituting nuclei, such as the *nucleus dentatus* of the olivary body. In the cerebellum and cerebrum the white and grey matters are placed in a totally different manner from the arrangement in the cord, and their mutual connections are so complicated that they cannot be traced by histological methods. The evidence on which our knowledge of the functions of these organs rests will be placed before the reader in treating of the functions of the brain, and here we shall give only a general outline of their histological structure.

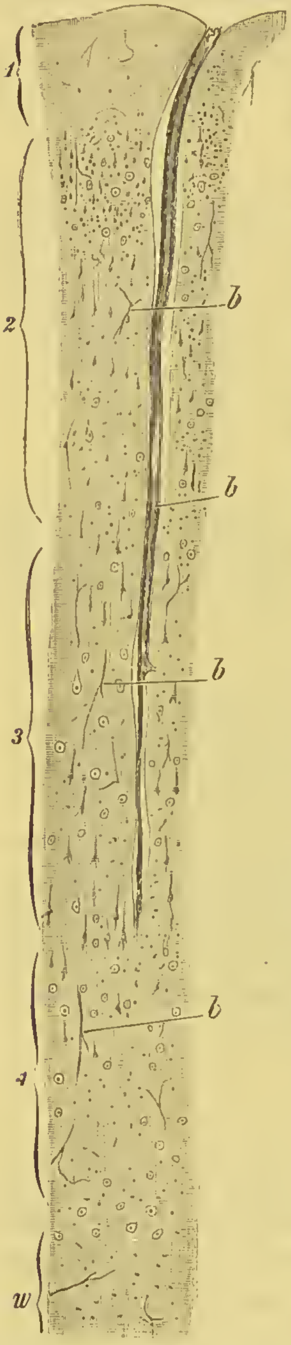

Fig. 255.—Portion of a vertical section of human cerebrum, × 50 d. 1, stratum containing very few cells; 2, stratum containing small pyramidal cells; 3, stratum containing large pyramidal cells; 4, stratum containing small nerve cells; *w*, striation of white matter; *b*, blood-vessels. (Method No. 88, Appendix.)

Fig. 256.—Portions of section shown in Fig. 255, × 240 d. *A*, from the stratum of the small pyramidal cells, *p*; *B*, from the stratum of the large pyramidal cells, *P*; *a*, prolongation of axis cylinder; the swollen cells, *z*, are probably altered by the mode of preparation. (Method No. 89, Appendix.)

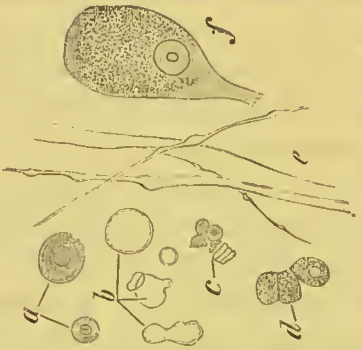

Fig. 257.—Teased out grey matter from human brain. × 240 d. *a*, *corpuscula amylacea*; *b*, drops of myelin; *c*, red blood corpuscles; *d*, cells of neuroglia; *e*, medullated nerve fibres; *f*, ganglionic cell. (Method No. 90, Appendix.)

The brain, like the cord, consists of white and grey matter, and these, although differing in details, show the same general structure as in the cord. In the brain, the grey matter is located in four chief masses: (*a*), an expansion or web covering the entire upper surface of the hemispheres of the cerebrum, the *cortex of the cerebrum*; (*b*), masses or nuclei in the interior of the ganglia of the cerebrum, the *corpora striata*, *thalami optici*, and *corpora quadrigemina*; (*c*), a grey layer lining the cavities or ventricles of the brain, the *central grey substance*, continuous with the grey matter of the spinal cord; and (*d*) an expansion or web covering the upper surface of the cerebellum, the *cortex of the cerebellum*. Nuclei of grey matter also exist in the cerebellum. All of these masses of grey matter are united by fibrous strands of white matter, the arrangements of which are of a very complex character.

(*a*) **Cortex of Cerebrum.**—This consists of two chief zones, each of which is composed of two strata, blending into each other and not sharply defined. The *chief external zone* is formed of: (1) A stratum containing very few cells, and having chiefly numerous fine medullated nerve fibres, crossing in all directions so as to produce a dense network, while the general direction of the most superficial fibres is parallel with the upper surface; (2) A stratum containing small pyramidal cells, the cells lying in a network of fine medullated nerve fibres. This layer also contains small irregularly-shaped ganglion cells, the so-called granules, and small pyramidal cells. The apex of the latter is turned towards the surface of the brain, and the base, from which one or more poles spring, is directed towards the central white matter of the brain. Between this layer and the next stratum there is a dense network or reticulation of medullated nerve fibres (Figs. 255 and 256).

The *internal or principal zone* consists of the following strata: (1) A stratum of large pyramidal cells. These cells show the same general form as those in the stratum last described, the small pyramidal cells, and they only differ in being larger, their length being from 11 to 120 μ. This stratum also contains large bundles, or strands, of nerve fibres, which apparently come from the stratum immediately below, and these fibres form a dense reticulum near the surface of the stratum containing the large pyramidal cells. (2) A stratum of small nerve cells. Here we find numerous very small nerve cells, in connection with which no axis cylinder has yet been traced. Running through the stratum are numerous strands of nerve fibres, on their way from the underlying white matter to the more external layers of grey matter.

The connective tissue matrix is formed of prolongations of the *pia mater* and of minute blood-vessels, and here also we find, as in the cord, neuroglia, or cement substance. Everywhere there is a dense feltwork of the most minute non-medullated nerve fibres, which have probably originated from the poles or processes of the ganglion cells. It is a mistake to describe the grey substance as consisting only of finely-granular or molecular matter, in which nerve cells lie embedded, and through which nerve fibres pass, as the granular or molecular appearance is due to the intricate interlacing of the minute fibres, which can be seen only after the employment of special methods of preparation.

(*b*) **Ganglia of the Cerebrum.**—The grey matter of the ganglia of the cerebrum consists of ganglion cells of various sizes, of medullated nerves, and of neuroglia.

(*c*) **Central Grey Matter.**—This stretches from the bottom of the rhomboidal space, through the aqueduct of Sylvius, into the 3rd ventricle, and onwards to the *tuber cinereum* and the *infundibulum.* This grey layer or tube is of special interest, as being that from which the cerebral nerves originally spring. It consists of neuroglia, nerve fibres, and ganglion cells, which are chiefly multipolar. In certain places, as in the nucleus of the hypoglossal (9th cranial) nerve, these are of very large size, and, in other places, they have a peculiar globular form, as in the *corpora quadrigemina.*

As the central canal of the cord is surrounded by neuroglia, and lined by columnar ciliated epithelium, and as the canal communicates with the ventricular cavities (with the exception of the 5th ventricle, between the layers of the *septum lucidum*), so we find the lining of the cavities, including the 4th, 3rd, and lateral ventricles, the aqueduct of Sylvius, and the foramen of Monro, is formed of a single layer of columnar ciliated cells. The cilia are only found in early life.

(*d*) **The Cortex of the Cerebellum.**—This is formed of three strata : (1) The *outermost* grey stratum, of a distinct greyish hue, is formed of neuroglia and of certain cells, which are probably not of a nervous character. There is also a dense reticulum of minute fibrils, produced by the ramifications of the processes or poles of ganglionic nerve cells. (2) The *middle* stratum is formed of a single layer of large, round, or oval-shaped multipolar cells, known as the *cells of Purkinje.* From the narrow end of the cell, which is directed towards the upper surface of the cerebellum, two processes or poles issue, and these branch out in the outer grey layer. Sometimes, if only one such process is visible, the cell has a tadpole-like form; but, if two are seen, then the ramifications more resemble the antlers of a stag. A process or pole arises from the opposite end of the cell, which passes through the inner layer and enters the white substance. Numerous medullated nerve fibres run horizontally along the boundary between the outer and the inner layers. (3) The inner layer, sometimes called the rust-coloured or granular stratum, is formed of many layers of small cells, with large nuclei, surrounded by only a small amount of protoplasm. Some of these cells are bipolar nerve cells, while others are probably connective tissue or neuroglia cells. In this stratum there is also a reticulation of small medullated nerve fibres (Fig. 258).

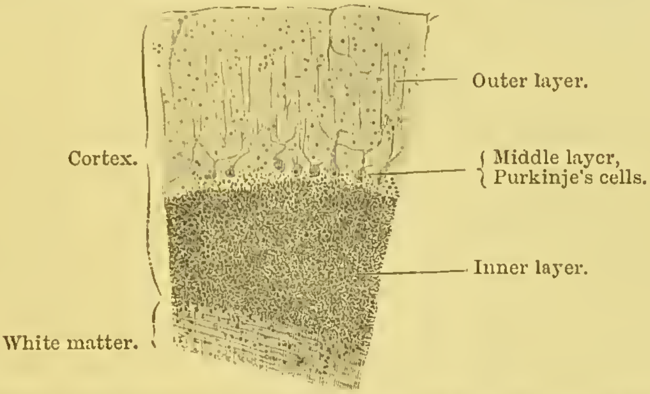

Fig. 258.—Portion of a vertical section through the cortex of the cerebellum. × 50 d. (Method No. 91, Appendix.)

The white substance of both cerebrum and cerebellum is formed of neuroglia, and of numerous medullated nerve fibres, varying in diameter between 2, 5, and 7 μ. The sheath of Schwann is absent.

We not unfrequently find in the grey matter, especially in the brains of old people, round or biscuit-shaped bodies (Fig. 257, *a*), showing concentric rings or laminæ. These bodies, *corpora amylacea*, are tinged violet with iodine and sulphuric acid, showing a chemical consitution allied to that of starch. They are often found in the walls of the ventricles, and they exist both in white and in grey matter.

Membranous Coverings of the Central Nervous System.

Two connective tissue membranes cover the brain and cord—one strong and hard, the *dura mater*, and the other delicate and soft, the *pia mater*, and *arachnoid* membrane.

1. The *dura mater spinalis* consists of a strong reticulum of connective tissue fibres, intermingled with a small number of elastic fibres, and having connective tissue corpuscles in the meshes. The inner surface is lined by a single layer of endothelial cells. It does not contain many nerve fibres, nor is it highly vascular (Fig. 259).

2. The *dura mater cerebralis* is not only the covering of the brain, but it forms the periosteum lining the inner surface of the bones of the skull. It consists of two layers—(*a*) an *inner*, corresponding to the *dura mater spinalis*, and having a similar structure, and (*b*) an outer, corresponding to the periosteal lining of the vertebral canal. The outermost connective tissue fibres of this layer run across the innermost layer of fibres, and the outer layer is rich in blood-vessels, which enter the bones of the cranium.

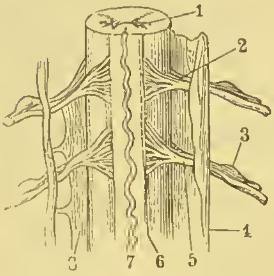

Fig. 259.—Portion of cervical spinal cord seen from before and a little above. Two-thirds natural size. 1, section of the grey matter; 2, posterior roots; 3, ganglion; 4, *dura mater*; 5, anterior root; 6, antero-lateral groove; 7, anterior spinal artery; 8, *ligamentum denticulatum*. (Krause.)

3. The *pia mater* is a saccular structure, consisting of two layers. The outer, called the *arachnoid membrane* is lined on the free surface with a single layer of endothelial cells and its outer surface is firmly connected with the *dura mater*. The inner, called the *pia mater*, is adapted to the outer surface of the brain and cord, and sends prolongations into the substance of these organs. The arachnoid and pia mater are connected by numerous little bundles of fibres or trabeculæ running from the surface of the one to the surface of the other. In the vicinity of the superior longitudinal sinus little cul-de-sacs, or hernial-like protrusions of the arachnoid bulge into the sinus, pushing before them the dura mater, which is very thin opposite these protrusions. These are the so-called *Pacchionian bodies*, at one time held to be pathological in character. The pia and arachnoid consist of very delicate connective tissue, and the outer surface of the pia and inner surface of the arachnoid and the trabeculæ already mentioned are clothed with endothelial cells.

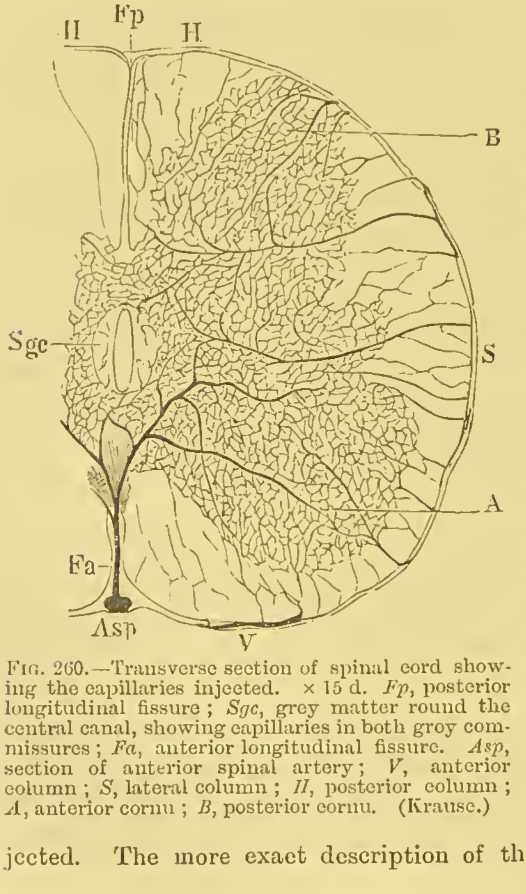

Fig. 260.—Transverse section of spinal cord showing the capillaries injected. × 15 d. *Fp*, posterior longitudinal fissure; *Sgc*, grey matter round the central canal, showing capillaries in both grey commissures; *Fa*, anterior longitudinal fissure. *Asp*, section of anterior spinal artery; *V*, anterior column; *S*, lateral column; *H*, posterior column; *A*, anterior cornu; *B*, posterior cornu. (Krause.)

The *telæ choroideæ* and *plexus choroideæ* consist of connective tissue and numerous blood-vessels bound together so as to form fringes or flaps which are pushed into the ventricles. They are covered with a single layer of cubical epithelial cells, ciliated in early life, and often containing pigmentary granules and drops of oil.

The *blood-vessels* of the central nervous organs form in the grey matter a narrow meshed reticulum of capillaries, but the meshes are much larger in the white matter. This is illustrated by Fig. 260, showing a transverse section of the spinal cord in which the vessels have been injected. The more exact description of the arrangement of the vessels in the brain and cord will be given in discussing these organs. In the meantime, it is sufficient to observe that the grey matter is much more vascular than the white matter. The wall of the venous sinuses is formed of flattened endothelial cells and the veins springing from these have their walls strengthened by connective tissue.

Lymphatic Arrangements.—1. Between the *dura mater* and the arachnoid layer there is a thin fissure or space, termed the **Sub-Dural Space.** The following lymphatic channels communicate with this space: the deep lymphatics and lymphatic glands of the neck, the lymphatic spaces surrounding the peripheral nerves, the lymphatics of the mucous membrane of the nose, the lymphatic spaces existing between the laminæ of the dura mater, and the lymphatic spaces around the Pacchionian bodies. A very small amount of serous fluid exists in the subdural space.

2. The **Sub-Arachnoid Space** is that between the two layers of the soft membranous covering, traversed by trabeculæ, as already described. It communicates with the lymphatic spaces around the peripheral nerves, with the lymphatics of the mucous membrane of the nose, with the ventricular cavities in the brain and with the central canal of the spinal cord. This space contains a considerable amount of fluid, the *liquor cerebro-spinalis.*

3. The sub-arachnoid space communicates also with the lymphatic spaces in the connective tissue coverings of the blood-vessels. Such communicating channels are termed *adventitial lymph spaces.* Several observers have shown that if a coloured injection is forced by a fine syringe into the brain substance, some of the injection appears in what resemble well-marked channels or spaces. These occur (1) around the larger ganglion cells in the *cortex cerebri*, hence termed *peri-cellular spaces*; (2) around the connective tissue sheaths of the vessels, *peri-vascular spaces*; and (3) between the *pia mater* and the brain, and therefore termed *epicerebral spaces.* It is still doubtful whether these are real lymphatic channels, or appearances accidentally produced by the forcible injection.

CHAP. III.—THE SPINAL CORD.

The spinal cord consists externally of white and internally of grey matter. The white matter forms a series of strands or columns in each half of the cord. The grey matter in the central part of the cord is arranged in two crescentic masses, and shows numerous multipolar cells connected with nerve fibres and embedded in neuroglia. The neuroglia is composed of a semi-fluid matrix, fibrils, and cells having branches, called *Deiter's cells* (Fig. 254). The nerve cells are arranged in definite groups and occupy the same relative position in successive sections, forming the ganglionic or vesicular columns of the grey matter, as follows: (1) Cells found along the whole of the anterior part of the anterior cornua, many of the processes of the nerve cells being continuous with the nerve fibres of the anterior roots of the spinal nerves. The cells are from 67 to 135 μ in diameter. This column is the *motor ganglionic column*, or the *vesicular column of the anterior cornu.* (2) A group or column of nerve cells, from 45 to 90 μ in diameter, at the mesial angle of the base of the posterior cornu, in the middle region of the cord from the third lumbar to the seventh cervical nerve. This is the *posterior vesicular column*, or *Lockhart Clarke's column.* The nerve cell processes are continuous with nerve fibres coming from the lateral column. This vesicular column is best developed where the column of the anterior cornu is least so. (3) The third column of nerve cells, termed the *intermedio-lateral column*, is in the outermost portion of the grey matter, midway between the anterior and posterior cornua (Fig. 262).

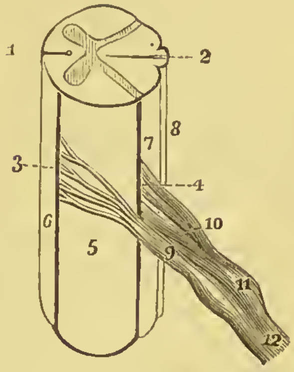

FIG. 261.—Side view of spinal cord, showing the fissures and columns. 1, anterior median fissure; 2, posterior median fissure; 3, anterior lateral fissure; 4, posterior lateral fissure; 5, lateral column; 6, anterior column; 7, posterior column; 8, posterior median column; 9, anterior root; 10, posterior root; 11, ganglion on 12, a spinal nerve.

It is important to note: (1) that the large medullated nerve fibres supplying the striated muscles arise from the cells in the anterior horn; and (2) that the efferent nerve fibres passing to the viscera originate chiefly in the cells of Clarke's column, and partly from cells in the intermedio-lateral tract and posterior horn. Gaskell has pointed out that the cells of Clarke's column give origin to the inhibitory or anabolic nerves of the muscles of the alimentary canal, and perhaps to the corresponding nerves of the vascular and glandular systems. The katabolic nerves of the vessels—vaso-constrictors—and the katabolic glandular nerves arise only in the thoracic region, and are not connected with Clarke's column. The solitary cells at the base of the posterior horn are either splanchnic sensory cells, or, as suggested by Gaskell, they are connected with the motor fibres of the muscles of the alimentary canal. The large cells in the ventral side of the intermedio-lateral tract give origin to motor fibres, supplying muscles developed from the lateral plates of the mesoblast (diaphragm, *transversalis abdominis* muscles, muscles of jaws). The smaller cells of this tract give origin to the katabolic or motor nerves of the vascular and glandular organs.[1]

At an early period in development the anterior horns are differentiated from the posterior, and the grey matter between them is the last to be formed. It has been observed by Flechsig and others that the white substance of the cord makes its appearance first in the neighbourhood of the anterior and posterior roots. The cord at a very early period consists almost entirely of grey matter, and the columns are superadded, the anterior first, the posterior last. The posterior can be traced to the cortex of the cerebellum (Fig. 264).

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[1] W. H. Gaskell on the "Cranial Nerves." *Jour. of Physiology*, vol. x. p. 153.

The anterior and posterior roots of the spinal nerves are attached along the sides of the cord, opposite to the corresponding cornua of grey matter. Some of the fibres of the anterior roots end in nerve cells in the anterior cornu. Others pass through the grey matter and cross to the other side of the cord through the anterior commissure, a layer of white matter at the bottom of the anterior median fissure. A third set passes to the anterior part of the lateral column and to the posterior cornu. A portion of the fibres of the posterior roots ends in the grey matter on the same side, but many cross to the grey matter on the opposite side. There is thus a decussation of fibres connected with both the anterior and the posterior roots.

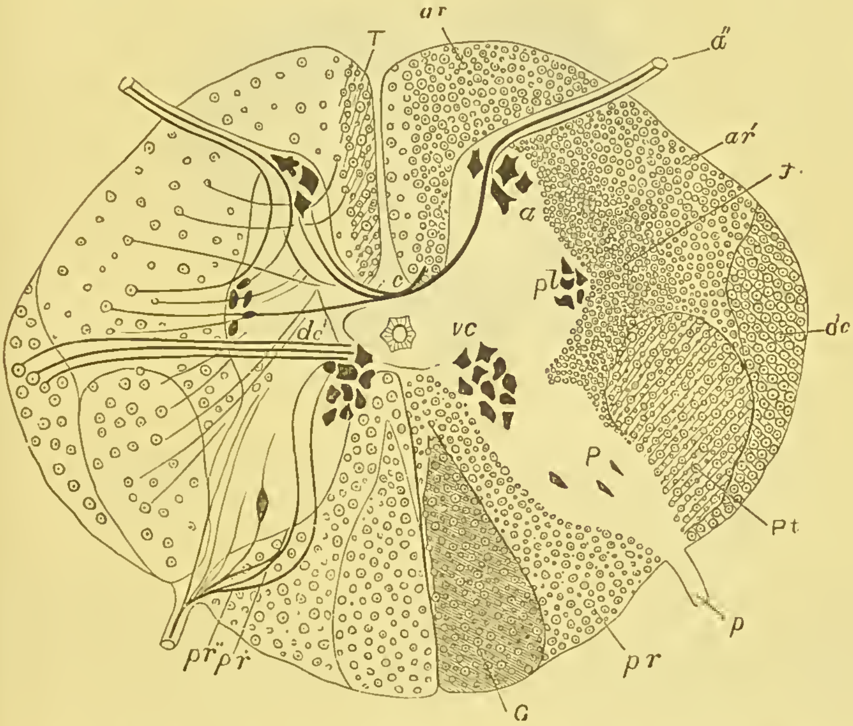

FIG. 262.—Diagram of a transverse section of the spinal cord in the upper half of the dorsal region. *C*, anterior commissure; *dc*, fibres running from the vesicular column of Lockhart Clarke, *vc*, to the direct cerebellar tract, *dc*; *P*, posterior horn; *Pt*, pyramidal tract of the lateral column; *T*, column of Türck; *dc*, direct cerebellar tract; *ar*, internal portion of anterior root zone; *ar′*, external portion of anterior root zone; *pr*, posterior root zone; *G*, Goll's columns; *fr*, reticular formation of cord; *a*, anterior grey horns; *a′*, anterior roots; *p*, *pr′*, *pr″*, posterior roots; *pl*, nerve cells. (Flechsig and Ross.)

The columns of the cord, as shown in Fig. 262, are as follows: (1) *Anterior*, on each side of the anterior median fissure, termed the *columns of Türck*, and as the fibres forming these do not decussate in the *medulla oblongata*, they are known as the *direct pyramidal tract*, *T*. They are motor in function. (2) Beyond these we have the *anterior root zones*, *ar*, so termed because the anterior roots of the spinal nerves pass through them. (3) Beyond these again, the *lateral column*, consisting of, *a*, a *descending* bundle of motor fibres, which have decussated or crossed at the anterior pyramids of the *medulla oblongata*, and hence termed the *crossed pyramida tract*, *p* ; and *b*, an ascending bundle of sensory fibres passing up to the cerebellum, and hence called the *direct cerebellar tract*, *dc*. (4) At the back of the cord we find, on each side of the postero-median fissure, sensory fibres which pass upwards without decussating, termed the *columns of Goll*, *G*. (5) Beyond the columns of Goll, there are the remaining portions of the posterior columns, known as the *columns of Burdach*, or *posterior root zones*, *pr*. They are sensory in function.

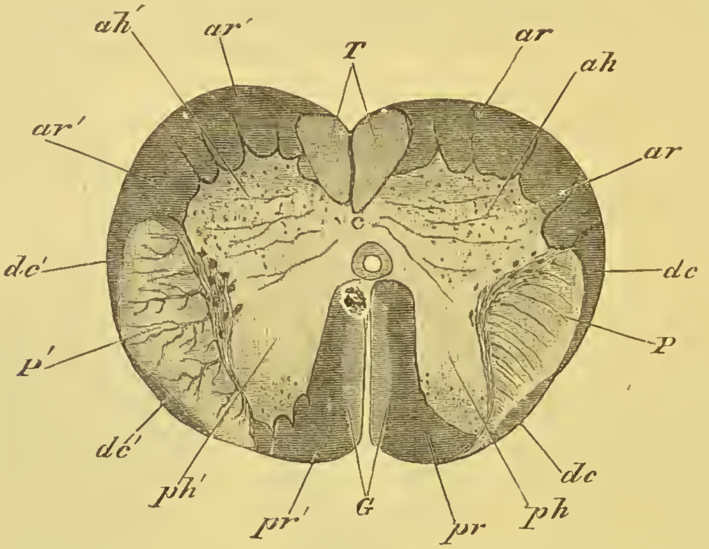

FIG. 263.—Cord of human embryo of 5 months. *ah*, *ah′*, anterior horns of grey matter; *ph*, *ph′*, posterior horns of grey matter; *ar*, *ar′*, anterior root zones; *pr*, *pr′*, posterior root zones; *P*, *P′*, pyramidal fibres of lateral columns; *T*, columns of Türek; *G*, columns of Goll; *dc*, *dc′*, direct cerebellar tract; *c*, anterior commissure. (Ross and Young.)

The spinal cord acts (1) as a transmitter of motor and sensory—or centrifugal and centripetal—impressions between the encephalon and the periphery, (2) as a reflex centre, and (3) as a trophic centre.

1. Transmission of Motor and Sensory Impressions.—Each spinal nerve, as already mentioned, is connected with the spinal cord by two roots, an anterior and a posterior. Section of a number of anterior roots causes paralysis of motion of muscles on the same side of the body, whilst irritation of the distal or peripheral end of the divided roots causes twitchings or tetanus of the muscles. Neither section nor irritation has any effect on sensation. Hence the anterior roots contain motor fibres, carrying impressions from the cord outwards. Again, section of a number of posterior roots is followed by loss of sensation of a part of the body on the same side, and, if the proximal ends of the divided roots are irritated, painful sensations are excited. The posterior roots, therefore, contain sensory fibres, carrying impressions into the cord from the periphery. As we have seen, these roots are connected with the grey and white matter of the cord, and it is practically impossible to trace all their ramifications. Recourse must therefore be had to the evidence supplied by experiment (cutting, or by the Wallerian method, p. 459) and by pathological observation. In tracing the path of fibres, what may be called the developmental method has been pursued. It has been shown by Flechsig that the white substance of Schwann of the nerve fibres is formed later along certain tracts of the white columns than in the rest of the white matter, so that in transverse sections of the cord these tracts are distinguishable by their more transparent grey appearance. The results are shown in Fig. 263.

As to effects of incisions of different portions of the cord of adult animals, the following has been ascertained :—

(1) If the *anterior* columns are cut by an incision extending into the grey matter, leaving the posterior columns intact, voluntary movements disappear in the parts below the section. Again, section of the *posterior* columns and grey matter, leaving the anterior uninjured, enfeebles but does not destroy the power of voluntary movement below the section. Finally, section of an *antero-lateral* column on one side paralyses voluntary motion on the same side. From these facts it is inferred (*a*) that the motor tracts passing from the brain to the periphery are in the antero-lateral columns, and (*b*) that the fibres forming these tracts are chiefly distributed to the same side of the body. These inferences are supported by pathological observation. In diseases where the anterior horns of grey matter are affected, paralysis ensues, with complete flaccidity of the limbs; and if, from hæmorrhage, softening, or the pressure of tumours, the anterior portion of the cord is irritated, there are spasmodic twitchings of muscles.

(2) Complete transverse section of the *posterior* columns does not abolish sensibility in the parts below; but there is a loss of the power of making co-ordinated movements. Section of the posterior columns and of the antero-lateral columns, leaving only the grey matter in the centre of the cord intact, does not abolish sensibility. Again, section of the antero-lateral columns and of the whole of the grey matter, leaving only the posterior columns uninjured, is followed by complete loss of sensibility in the parts beneath. The inference therefore is that sensory impressions pass through the grey matter. As already seen, many of the sensory fibres connected with the posterior roots decussate in the grey matter. This explains some of the results obtained by Brown-Séquard, that hemi-section of the cord, involving the grey

matter, enfeebled sensibility *on the opposite side* more and more as the section cut deeply into the grey matter; that a vertical section in the bottom of the posterior median fissure caused loss of sensibility on both sides; and that a lateral section, whilst it caused loss of sensibility (anæsthesia) on the opposite side, was followed by increase of sensibility (hyperæsthesia) on the same side,—a curious fact, explained by Brown-Séquard as being due to irritation caused by paralysis of the vessels of the cord on the side of the section.

(3) It would appear also that *tactile* impressions travel, for a certain distance at all events, in the posterior columns. This has been inferred chiefly from the fact that in certain cases of paralysis involving the posterior columns, where the sensation of touch was absent, the patient could still feel a painful sensation, as when a needle was thrust into the skin; whilst in other cases, in which these columns were not affected, the converse held good. In the disease known as *locomotor ataxia*, the patient first passes through a period in which there are disorders of general sensibility, especially lancinating pains in the limbs and back. By and bye there is unsteadiness of gait when the eyes are closed or in the dark, and to a large extent the patient loses the power of co-ordinating movement. Especially is he unable to judge of the position of the limbs without seeing them; in other words, the muscular sense is enfeebled. At last there is a stage before death in which there is almost complete paralysis. A study of this disease has thrown light on the physiology of the cord. It is known to be caused by a slow disorganization, or sclerosis, of the posterior root zones, the posterior columns—slowly passing on to affect the columns of Goll, the lateral columns, and the anterior grey horns, and ultimately involving all the cord. The disordered sensations at an early stage, the staggering gait at a later, show that the posterior part of the cord has to do with the transmission of sensory impressions. The man staggers, not because he is paralysed as regards the power of movement, but because, in consequence of the sensory tracts being involved, he does not receive those peripheral impressions which excite or indirectly regulate all well-ordered movements of locomotion.

2. **As a Reflex Centre.**—The grey matter of the lower cervical, dorsal, and lumbar regions of the cord contains reflex centres associated with the general movements of the body, whilst in the upper cervical region there are more differentiated centres corresponding to special actions. The initial excitation may commence in any sensory nerve; the effect passes to the cord, and sets up changes in the nerve cells of the grey matter, involving time, and resulting in the transmission out-

wards along motor fibres of impulses which excite particular groups of muscles. There is an exact *co-ordination*, with a given strength of stimulus, between certain areas of skin and certain groups of muscles, and thus movements may be so purpose-like as to simulate those of a conscious or voluntary character. Thus irritation near the anus of a decapitated frog will invariably cause movements of the limbs towards the irritated point. The activity of reflex centres may be *inhibited* by higher centres, or by sensory impressions reaching them directly from the periphery. Hence removal of these higher centres is followed by increased reflex excitability. Strychnia and the alkaloids of opium increase it, whilst aconite, hydrocyanic acid, ether, chloral, and chloroform have an opposite effect. In certain pathological conditions also, as in tetanus, or in some slow progressive diseases of the cord, reflex excitability may be much increased. In tetanus the slightest touch, a movement of the bedclothes, the closing of a door, the vibration caused by a footstep, may throw the patient into severe and prolonged convulsions. In tetanus, the muscles of mastication are first affected, causing lockjaw or *trismus*, and after these, in order, the muscles of the neck, of the upper extremities, of the thorax, of the abdomen, and of the lower extremities.

The earlier formed ganglionic cells are those specially concerned in reflex acts.

Special Reflex Centres exist in the cord. (1) A *cilio-spinal* centre, between the 6th cervical and 3rd dorsal nerves, associated with the movements of the iris. The fibres controlling the radiating fibres of the iris, and found in the sympathetic, originate here. Hence irritation of this region causes dilatation of the pupil, an effect not produced if the sympathetic fibres have been divided. (2) *Accelerating* centres, supplying fibres to the sympathetic which ultimately reach the heart; irritation of these centres quickens the movements of that organ. (3) *Respiratory* centres. The movements of respiration, of a reflex character, involve the action of many thoracic and abdominal muscles. Section of the cord above the 8th dorsal paralyses the abdominal muscles; above the 1st dorsal, the intercostals; above the 5th cervical, the *serratus magnus* and the pectorals; and above the 4th cervical, by paralysing the phrenics, it arrests the action of the diaphragm. (4) In the cord we also find, from above downwards, centres for the muscles of the limbs in the following order:—(*a*) centre for adduction of upper extremity; (*b*) centre for abduction of upper extremity; (*c*) centre for flexion of lower extremity; and (*d*) centre for extension of lower extremity. (5) *Genito-spinal* centre. This is in the upper part of the lumbar region. Irritation causes erection, etc.; destruction or disease is followed by loss of virile power. (6) *Ano-spinal* and *vesiculo-spinal* centres. These, connected with the movements of the *sphincter ani* and of the bladder, exist in the lower portion of the dorsal and upper portion of the lumbar regions. The vesiculo-spinal centre in the dog is near the level of the 5th lumbar vertebra. The ano-spinal is a little above this. Disease or injury involving these centres causes involuntary evacuation of the bowel and complete paralysis of the bladder, with non-retention of urine. The bladder may be full whilst the urine constantly escapes in small quantity. (7) *Sweat* centres. In the cat, at the level of the 3rd cervical vertebra for the anterior, and at the level of the 9th and 10th thoracic vertebræ for the posterior, limbs. (8) *Vaso-motor* centres. There are probably several in the cord, but the only one whose locality is known is that for the lower extremities, at the lower part of the dorsal region. (9) Centres for *lymph-hearts* of amphibia exist. In the frog, for the anterior pair, at the level of the 2nd dorsal, and for the posterior, at the level of the 7th dorsal vertebræ.

There are certain reflex actions the presence or absence of which in diseases of the cerebro-spinal centres has proved to be of great diagnostic value. These are either cutaneous reflexes or tendonous reflexes. The chief *cutaneous reflexes* are as follows:—(1) The *plantar reflex* caused by tickling or pricking the sole of the foot. A dorsal flexion of the toes and of the foot is caused or the leg may be quickly drawn to the trunk. The centre involved is the lower part of the lumbar region. (2) The *cremasteric reflex.* On pinching the inner surface of the thigh or pressing strongly on the internal condyle, there is a contraction of the cremaster muscle, raising the testicle on the side irritated. The centre is at the level of the 1st and 2nd pairs of lumbar nerves. (3) The *abdominal reflex* is a contraction of the abdominal muscles caused by a sharp push of the finger on the abdominal surface. The centre is between the 8th and 12th dorsal nerves. (4) The *epigastric reflex.* If we excite the skin between the 4th, 5th, and 6th intercostal spaces, contractions may be excited of the *rectus abdominis* on the same side. The centre is between the 4th and 8th pairs of dorsal nerves. (5) The *scapular reflex.* A sudden irritation of the skin covering the scapula may cause contraction of the muscles of the shoulder. The centre is between the 7th pair of cervical and the 2nd pair of dorsal nerves. The *tendonous reflexes* are as follows:—(1) The *knee jerk* is caused if the person crosses one leg over the other, and, while his attention is distracted, a sudden blow is made transversely on the tendon of the extensors below the patella. The leg is immediately thrown forward. (2) The reflex of the *tendo Achillis.* If we flex the leg on the thigh, and then strike transversely the *tendo Achillis* the muscles of the calf of the leg will contract so as to extend the foot. (3) The reflexes of the *ankle.* Flex the leg at the knee, extend the foot, then suddenly and strongly flex the foot, and keep hold of it. It will be again extended and there may be rhythmic movements of the muscles of the calf, causing flexions and extensions of the foot. The tendonous reflexes are diminished or weakened in various diseases in which either the centres in the cord or the afferent and efferent nerves are involved. Related to these is the *paradoxical contraction of Westphal.* Place the person on the back, flex the foot strongly as in producing the ankle reflex, and occasionally the tendon of the *tibialis anticus* starts out, keeping the foot flexed even for several minutes. This reflex is of pathological origin.

3. **As a Trophic Centre.**—The ganglion cells in the anterior cornua have a trophic or nutritive influence upon muscles. If these cells undergo atrophy or degenerative changes, the muscles, even though they may be kept periodically in a state of activity by galvanism, become

soft, and fatty changes take place. There is thus a correlation between the nutritive condition of muscle and nerve centre, and influences affecting the one affect the other also.

It has been supposed that the cells in Clarke's vesicular column form the centres in visceral innervation. They are bipolar, like those in the sympathetic, and not multipolar as in the rest of the cord, and the columns are absent in the lumbar and cervical enlargements. The cells are found where nerves come off that influence the viscera, and similar cells are found at the roots of the vagus in the medulla. (See p. 498.)

Inhibition of Reflex Actions.—The reflex actions of the spinal cord may be *inhibited* by the action of centres in the encephalon, so that pure reflex actions only occur after removal of the cerebrum, or during profound sleep, when the cerebrum is inactive. By a strong effort of the will one may refrain from scratching an irritated part of the skin, whilst the same amount of irritation would cause reflex movements if the will were in abeyance. Such power of voluntary control is limited with respect to most reflex actions, whilst some reflex acts cannot be so influenced. Any movement that may be originated by the will may be inhibited to a certain extent when the movement is of a reflex character; but, if the movement be invariably involuntary, it can never be inhibited. Thus the ejaculation of semen cannot be voluntarily induced, and the reflex act once provoked cannot be arrested. That these inhibitions of reflex actions of the cord depend on mechanisms in the brain is proved by the facts that removal of the brain is followed by an increase in the reflex excitability of the cord, and that section even of the cord permits of increased reflex excitability below the plane of section. Further, after section of the spinal cord in the cervical region, irritation of the lower end arrests reflex movements dependent on reflex centres in the lower cervical, dorsal, and lumbar regions.

CHAP. IV.—THE MEDULLA OBLONGATA.

This is the prolongation into the cranium of the spinal cord so as to unite it with the brain. Strictly speaking, the *medulla spinalis* and the *medulla oblongata* form one organ. The columns of white matter of the cord undergo changes in form, structure, and relative position when they pass into the medulla. Without again detailing the minute anatomy, it is desirable to show, in the following table, the connections of the cord and of the medulla with the rest of the brain.

Columns of the Spinal Cord.		Divided into	Continued in Medulla Oblongata as	Pass on to
Antero-lateral column.	A. Pyramidal tract.	a. Lateral, or crossed, fibres from the posterior part of the lateral column as low as the 3rd or 4th sacral nerves. (*Crossed pyramidal tract.*)	Decussate in anterior pyramids.	*The motor areas in the cortex of the cerebrum.*
		b. Anterior or uncrossed fibres from the columns of Türck. (*Direct pyramidal tract.*)	Pass under pyramid on same side, and form longitudinal fibres of the *reticularis alba* in dorsal part of mesial area. 1. Posterior longitudinal bundle in *pons*. 2. Tract of the fillet.	*Cerebrum.* *Corpora quadrigemina.*
	B. Cerebellar tract.	c. Cerebellar tract between lateral pyramidal tract and the outer surface of the cord as low as the 2nd or 3rd lumbar.	Restiform body.	*Cerebellum.*
	C. All the antero-lateral columns except A and B.	d. Principal tract of anterior column, that is, the antero-lateral column, less the fibres in b. Not continued up—probably commissural from one side of cord to the other.	....	....
		e. Fibres from anterior column.	Pass below olivary body to form part of restiform body. Sometimes called the "band of Solly"—not always present.	*Cerebellum.*
Posterior column.		a. Posterior white column, or Goll's tract from middle of dorsal region.	Restiform body.	*Cerebellum.*
		b. Posterior lateral column, between posterior median column and postero-lateral groove.	Posterior median column becoming the *funiculus gracilis*, which, with the expansion called the *clava*, becomes the posterior pyramids.	*Cerebrum.*
		c. *Funiculus* of Rolando, between the posterior lateral column, b, and postero-lateral groove higher up.	*Funiculus cuneatus*, forming, with cerebellar tract from antero-lateral column, the restiform body.	*Cerebellum.*

Each column of the cord, through the *medulla*, is thus connected both with the cerebrum and with the cerebellum. Development has shown that when the cord of a human embryo is examined at the end

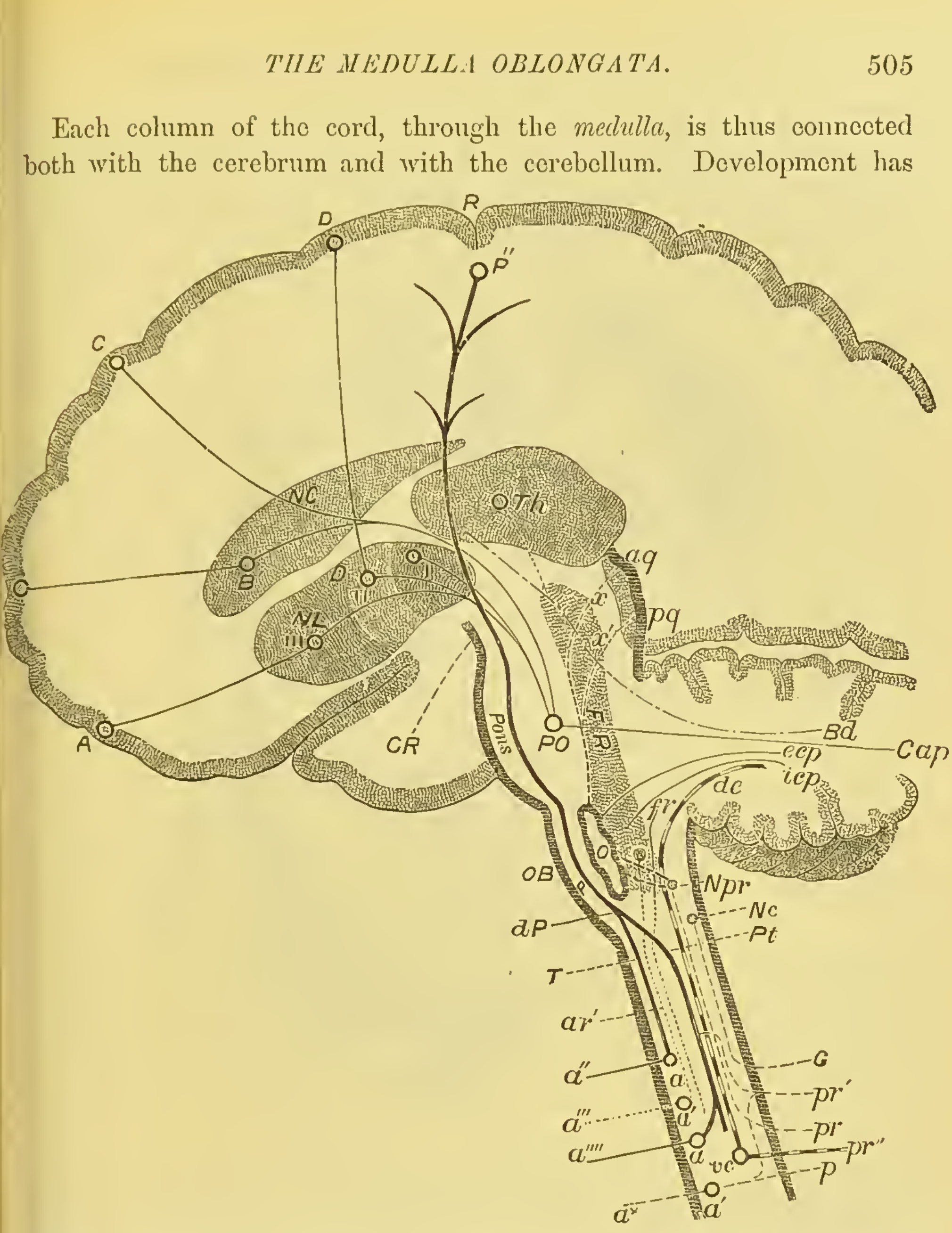

Fig. 264.—Diagram of the grey masses of the spinal cord and brain, showing the course of the conducting paths. *R*, fissure of Rolando; *P''*, *P*, *T* and *Pt*, course of the fibres of the pyramidal tract from their origin in the central convolutions to their termination in the anterior grey horns, *a a'*. I, II, III, 1st, 2nd, and 3rd portions of lenticular nucleus, *NL; NC*, caudate nucleus; *Th*, optic thalamus; *D*, *C*, *B*, *A*, fibres issuing from cortex and passing to basal ganglia and also to the grey matter of the *pons Varolii*, *PO; Bd*, fibres connecting optic thalamus and cerebellum;' *Cap*, fibres connecting cerebellum and grey matter of pons; *aq*, anterior (nates), *pq*, posterior (testes), *corpora quadrigemina*; *x*, upper, and *x'*, lower, fibres connecting olivary body and *aq*, *pq*. *FR*, *formatio reticularis* of *medulla oblongata* formed by fibres from optic thalamus; *Th*, internal portion of the inferior peduncle of cerebellum, *icp*, from spinal cord, *fr*, *ar*, and *ar'*, and probably also from clavate nucleus, *Nc*. *O*, olivary body; *ecp*, fibres of restiform bodies connecting olivary bodies with cerebellum; other fibres connect it with the triangular, *Npr*, and clavate nuclei, *Nc*; *dP*, decussation of the pyramids; *pr*, fibres of posterior roots which pass upwards or downwards into the grey matter for a short distance; *a*, *a'*, *a''*, *a'''*, *a''''*, anterior roots; *p*, *pr*, *pr'*, *pr''*, *G*, posterior roots. (Flechsig and Ross.)

of the fifth month it will be found that the pyramidal fibres of the lateral columns, the fibres of the columns of Türck, and of the columns of Goll are non-medullated, while the fibres of the anterior and posterior root zones and the cerebellar fibres of the lateral columns are medullated. It appears, therefore, that the latter are the more primitive structures, and that the former are superadded in the cords of the higher animals.

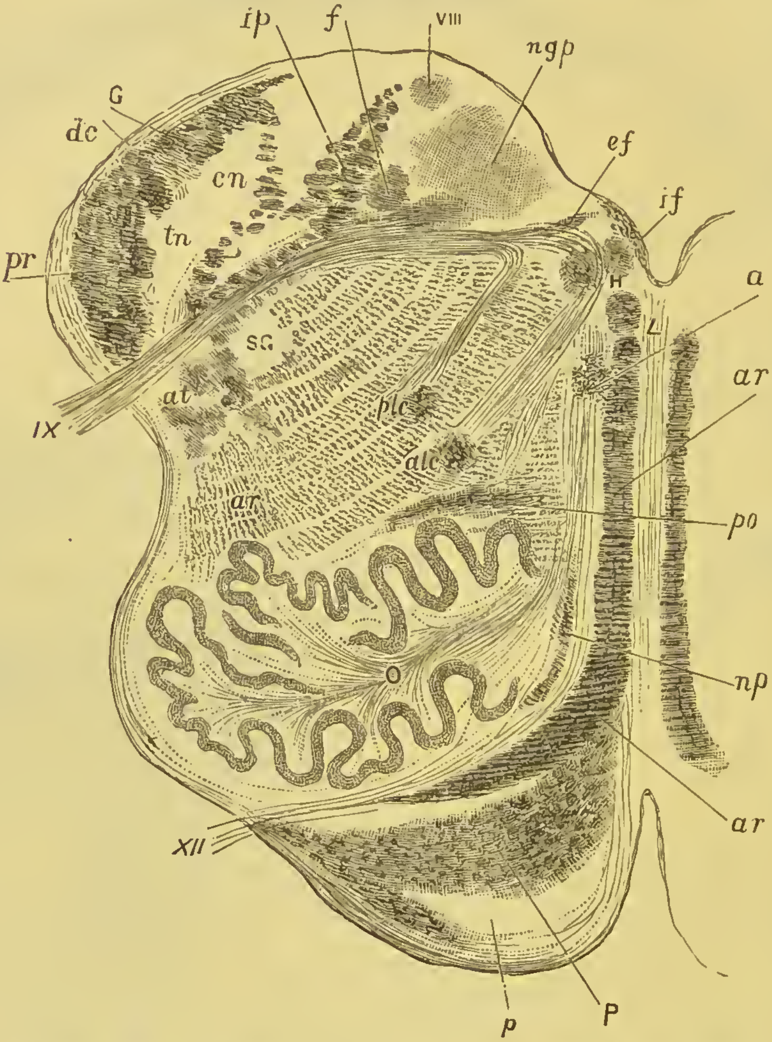

Fig. 265.—Section of the *medulla oblongata* on a level with the glosso-pharyngeal nerve. *P*, pyramid; *p*, accessory portion of the pyramid; XII, hypoglossal nerve; *H*, nucleus of hypoglossal, showing the internal, antero-lateral, and postero-lateral groups; *a*, anterior group of cells; IX, glosso-pharyngeal; *ngp*, nucleus of glosso-pharyngeal; VIII, lower part of the posterior median acoustic nucleus; *if*, internal accessory facial nuclei; *ef*, external accessory facial nuclei; *alc*, anterior nucleus of lateral column; *plc*, posterior nucleus of the lateral column; *f*, *fasciculus rotundus*; *ip*, internal division of the inferior peduncle of the cerebellum; *G*, column of Goll; *cn*, clavate nucleus; *pr*, posterior root zone; *tn*, triangular nucleus; *dc*, direct cerebellar tract on surface of posterior root zone, and the ascending root of the 5th (*trigeminus*); *at*, ascending root of the *trigeminus*; *sg*, *substantia gelatinosa*; *L*, posterior longitudinal fasciculus; *ar*, portion of *formatio reticularis*, which represents the *internal* division of the anterior root zone of the spinal cord; *ar'*, portion of *formatio reticularis* which represents the *external* division of the anterior root zone of the spinal cord; o, olivary body; *np*, nucleus of pyramid; *po*, parolivary body. (Alfred H. Young.)

The grey matter of the medulla is broken up by changes in the distribution of the white matter into nuclei or masses of nerve cells, instead of having the crescentic form seen in the spinal cord. These nuclei are connected with the roots of cranial nerves, and may be regarded as corresponding with the anterior horns of grey matter, with the posterior horns, and with the grey matter between these (Fig. 265).

The following nuclei can be found:—(1) the *hypoglossal* nucleus, for the hypoglossal nerve, the motor nerve of the tongue; (2) a *common* nucleus, for a portion of the spinal accessory, vagus, and glosso-pharyngeal nerves; (3) the *principal* or *lower auditory* nucleus, for the auditory nerve; (4) nuclei for the *sixth* or *abducent* nerve, supplying the external rectus muscle of the eye; (5) nucleus for the *fourth* nerve, supplying the superior oblique muscle of the eye; (6) the *facial* nerve, the motor nerve of the face; (7) the *corpus dentatum of the olivary body*, not directly connected with the roots of nerves, but containing nerve cells. Some fibres, both of the sensory and motor roots of the *fifth* nerve, originate also as far back as the medulla. The 3rd, 4th, 6th, and hypoglossal nerves belong to the system of *anterior motor* nerves, related to the anterior cornua, whilst the spinal accessory, vagus, glosso-pharyngeal, and 5th belong to the *mixed lateral system*—that is, they are related to the posterior cornua and intermediate grey matter.

Like the spinal cord, the *medulla* contains tracts for sensory and motor transmission, and possesses reflex centres for special movements.

1. **As a Conductor of Motor and Sensory Impressions.**—Inasmuch as the movements of the circulation, respiration, and vaso-motor action are necessary to life, destruction of the *medulla* causes almost instant death. Motor fibres coming from the brain above decussate in the anterior pyramids and run down the lateral columns of the cord, issuing to the muscles by the anterior roots of the spinal nerves. Hence, whilst section of an antero-lateral column of the cord will cause paralysis of motion on the same side, section of an anterior pyramid above the decussation causes paralysis of motion on the *opposite* side. But fibres carrying sensory impressions also decussate in the grey matter at the bottom of the posterior median fissure of the cord. It follows, therefore, that a pathological change, such as rupture of a vessel causing a clot in the brain, say in the left *corpus striatum* and left *thalamus opticus*, causes paralysis both of motion and of sensation on the opposite side—that is, in the case supposed, there would be right hemiplegia. The path of sensory impressions is probably in the grey matter, but the precise course of sensory fibres has not been traced.

2. **As a Reflex Centre.**—Numerous special centres have been referred to the *medulla oblongata.*

(1) *Respiratory* centres, two in number, expiratory and inspiratory, connected with the roots of the pneumogastric nerves. Destruction at once causes cessation of respiratory movements. (2) *Vaso-motor* centre, regulating the calibre of the

smaller blood-vessels throughout the body (see p. 291). (3) *Cardiac* centres, probably two in number—one accelerating, associated with the sympathetic; the other inhibitory, connected with the pneumogastric (see p. 225). (4) Centres for *deglutition*, associated with the sensory and motor nerves involved in this process (see p. 70). (5) Centre for *voice*, regulating to some extent, through the sterno-cleido-mastoid muscle, the emission of air through the glottis in expiration and phonation. (6) Centre influencing *glycogenesis*, probably by the action of the vaso-motor centre on the blood-vessels of the liver (see p. 375). (7) Centre directly influencing *salivary secretion*, from which originate those fibres of the facial, forming the *chorda tympani* and small superficial petrosal, distributed to the salivary glands (see p. 58). (8) Centre for the *motor fibres supplying the face and muscles of mastication*. These exist in the facial for the muscles of the face and in the motor portion of the 5th for the muscles of mastication. (9) Centre for the *sweat glands* of the head, also probably governing the spinal sweat-centres. Further, the medulla receives nervous influences from the higher centres, by which all the centres above enumerated may be more or less influenced.

CHAP. V.—THE PONS VAROLII, CEREBRAL PEDUNCLES, AND BASAL GANGLIA.

1. Pons Varolii.—The *pons Varolii* is above and in front of the *medulla oblongata*, and between the hemispheres of the cerebellum. It consists of fibres passing longitudinally, connecting the brain above with the medulla and cord below; and transversely, connecting the lateral hemispheres of the cerebellum, thus forming the middle peduncles of that organ.

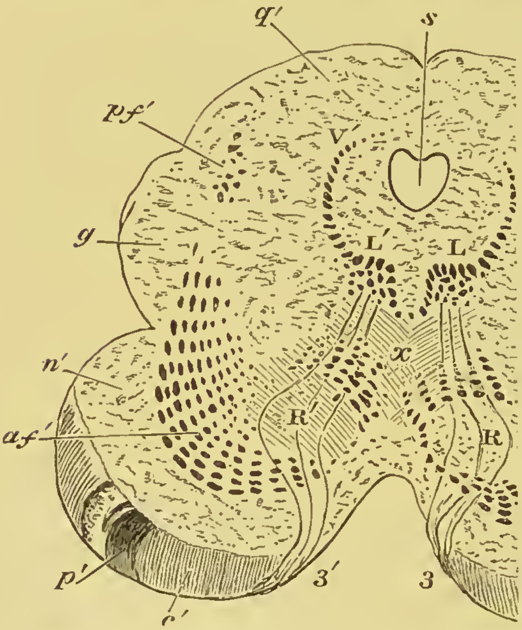

FIG. 266.—Transverse section of the *crura cerebri* on a level with the anterior part of the *corpora quadrigemina*, from a nine months' human embryo. The dark portions represent medullated fibres. *s*, aqueduct of Sylvius; *qq'*, anterior pair of *corpora quadrigemina*; *pf, pf'*, fasciculi of medullated fibres proceeding to the anterior pair of *corpora quadrigemina*; *L L'*, posterior longitudinal fasciculi; *V V'*, portions of these fasciculi which join the posterior commissure of the third ventricle; *gg'*, external geniculate bodies; *af, af'*, anterior portion of fillet; *nn'*, *substantia nigra*; *R R'*, red nuclei; *p p'*, pyramidal tract; *c c'*, *crustæ*; 3 3', 3rd pair of nerves; *x*, decussation in front of aqueduct of Sylvius, which is a part of the interlacement of the *tegmentum*. (Young.)

It contains the following bundles of fibres: (1) an *anterior*, motor, fasciculus, continuous above with the motor regions of the cortex of the brain by the middle fibres of the peduncle (*crus*), and inferiorly with the superficial part of the anterior pyramids of the *medulla oblongata* and with the crossed pyramidal tract on the opposite side of the spinal cord; (2) a *middle* fasciculus, continuous above with the frontal lobes of the cerebrum through the internal fasciculus of the *crus;* (3), a *second middle* fasciculus, close to (2), containing fibres from the external portion of the *pes* of the *crus*, and passing below to the lateral column of the cord on the same side; (4) a *posterior* fasciculus, continuous below to the columns of Türck of the cord on the same side; (5) *transverse*, or *commissural* bundles passing from one half of the cerebellum to the other half; (6) a *second posterior* fasciculus consisting of sensory fibres passing up from the *medulla* to the cerebrum.

Mixed up with these fibres are various nuclei of grey matter connected with the roots of cranial nerves.

These nuclei are—(1) the nucleus of the facial nerve; (2) the motor nucleus of the 5th nerve; (3) the upper sensory nucleus of the 5th nerve; (4) the inner or chief nucleus of the auditory nerve; (5) the outer or superior nucleus of the auditory nerve; (6) the accessory nucleus of the auditory nerve; (7) the nucleus of the 6th nerve. It will be observed that several of these nerves are also connected with nuclei in the *medulla oblongata.*

Like the cord and medulla, the *pons* is a conductor of impressions and a reflex centre. Motor transmission occurs chiefly in the anterior part. As the fibres of the facial nerve decussate in the *pons*, and then carry influences outwards, unilateral injury or disease of the lower half of the *pons* causes paralysis of the face on the same side as the disease, and paralysis of the limbs on the opposite side if the disease has affected the facial *after* its decussation in the *pons.* Usually in cases of paralysis of one side (hemiplegia) from a clot or disorganization in one *corpus striatum*, the paralysis of the face is on the same side as that of the limbs. In diseases of the *pons* loss of sensibility is a more rare result than loss of motion, and is always on the opposite side. According to Brown-Séquard, tactile, thermal, and painful impressions pass through the central part of the *pons.* The numerous centres in the *pons* are associated in complex reflex movements. Nothnagel has described it as a *convulsive centre*, because irritation caused severe cramps, but this was due to irritation of the motor strands passing through it.

2. **Cerebral Peduncles.**—These contain both sensory and motor fibres, and they establish a connection between the cerebellum and the cerebrum, and also between the ganglia at the base—*corpora striata, thalami optici*, and *corpora quadrigemina* on the one hand, and the *pons* and *medulla* on the other (Fig. 266).

Each peduncle consists of three parts:—(1) an anterior and inferior portion termed the *pes;* (2) above 1, a pigmented grey layer, the *locus niger*, and (3) posteriorly and superiorly, another layer of nerve fibres, the *tegmentum* or *calotte.* The *pes* is formed of (1) an internal part, coming from the anterior portion of the internal capsule; (2) above this a layer of fibres, *fasciculus geniculatus*, and (3) a layer of fibres, *fasciculus pyramidalis*, connected with the anterior two-thirds of the posterior part of the capsule; (4) an external portion coming from the posterior part of the internal capsule, *fasciculus sensitivus;* (5) fibres from the caudate and lenticular nuclei; (6) fibres passing to and from the *locus niger;* and (7) fibres arising from the *corpora geniculata.* The *tegmentum* is composed of two bundles of fibres:—(1) an internal, the *processus a cerebello ad testes,*—the fibres decussating below the *corpora quadrigemina,* and having in it two masses or nuclei of grey matter—(*a*) the *red nucleus,* and (*b*) the *rhomboidal nucleus;* and (2) fibres passing from the *thalamus opticus* to the posterior part of the anterior pyramid of the *medulla oblongata.*

Little is known of the functions of the peduncles except that they are conductors. Destruction of one peduncle causes the animal to move to the side opposite the lesion, describing a circle somewhat in the manner of a horse in a circus. Irritation causes pain and movements.

3. **Basal Ganglia.**—The ganglia termed the *basal ganglia,* include, from behind forwards, the *corpora quadrigemina,* the *thalami optici,* and the *corpora striata;* but in addition we find the *locus niger,* the red nucleus of the *tegmentum,* and the *corpora geniculata.* These ganglia all act along with the cerebral hemispheres, so that practically the whole mass forms one organ.

(*a*) **Corpora Quadrigemina.**—These are two pairs of rounded bodies found above the Sylvian aqueduct, which passes between the 3rd and 4th ventricles. They are situated behind the *thalami optici* and are intimately related to the *crura,* and through these to the *pons, medulla,* and cord. Homologous with the optic lobes seen in the brain of the fish, frog, and bird, their relative size to the mass of the encephalon is less in the brain of man and of the higher animals. These bodies contain grey matter, covered by a thin stratum of white matter. The two posterior bodies are connected with the cerebellum by the superior peduncles of that organ, these peduncles disappearing under the base of the *corpora quadrigemina.* The two posterior bodies are also related to the *crura cerebri* by the prominences on the sides of the *crura* known as the *corpora geniculata interna.* Both anterior and posterior bodies, more especially the anterior, are connected with the optic tracts, and finally, the two anterior bodies unite with the *thalami optici.* As shown by their anatomical connections, the *corpora quadrigemina* are part of the mechanism of vision. Destruction causes blindness. If, in a pigeon, the encephalon is removed with the exception of these bodies, the iris still continues to contract under the influence of light. On then destroying one of these bodies, the iris is immobile, and the power of accommodation is lost. As the 3rd cranial nerve (which is known to contain fibres controlling the circular fibres of the iris by which the pupil contracts, and the fibres governing the ciliary muscle by which the eye is accommodated to varying distances) originates in the grey matter of the floor of the Sylvian aqueduct, close to the *corpora quadrigemina*, it is held that these bodies are the centres of the reflex movements of the iris and of the ciliary muscle (Fig. 266, *s* and 3 3′). The *corpora quadrigemina* are also the first recipients of visual impressions. When light falls on the retina changes are there induced, which stimulate the optic nerve fibres, and these fibres carry impressions through the optic tracts to the *corpora quadrigemina*. What then occurs is matter of conjecture. Whether sensation is there excited, or whether to produce sensation it is necessary that the impulses be sent onwards to the cerebrum, or whether the impressions directly received from the retina may excite, through the *corpora quadrigemina* and adjacent ganglia, reflex movements (like those of the somnambulist, who may see so that his steps are taken rightly, but who may at the same time not see *consciously*), are all speculative questions. We know that these bodies are concerned in the movements of the iris and of the ciliary muscle, but their great proportionate size in lowly-formed brains indicates that this is probably a secondary function, and that they are largely concerned in the phenomena of consciousness of light and colour.

(*b*) **Thalami Optici.**—These are two ganglionic masses placed behind the *corpora striata* and in front of the *corpora quadrigemina*. The internal surfaces are seen in the 3rd ventricle, the upper surfaces in the same ventricle and the lateral ventricles, whilst the external and under surface of each *thalamus* is united with other parts of the brain. The under surface receives fibres from the *crus cerebri*, whilst the upper surface is covered by fibres which diverge and pass between the *thalamus* and a mass of grey matter in the extra-ventricular portion of the *corpus striatum* (lenticular nucleus), to form a white layer called the *internal capsule*. From the internal capsule, which thus contains fibres from the *thalamus opticus*, fibres radiate outwards to the surface of the cerebral hemispheres. The under surface of the *thalamus* is connected with the *tegmentum*—that is, with the layer of fibres forming the upper surface of the *crus cerebri*. They also receive fibres from the *corpora quadrigemina* and from the superior peduncles of the cerebellum. The substance of the *thalamus* contains nerve cells, scattered and also aggregated into two nuclear masses, but the relations of these to nerve tracts have not been ascertained. The *thalami* receive fibres from the back of the *crura*, and therefore are related to the posterior or sensory portion of the spinal cord.

There is still uncertainty as to the functions of the *thalami optici*. The commonly received opinion is that they are centres for the reception of peripheral impulses, which they may transmit forwards to the *corpora* *striata*, or upwards to the cerebral hemispheres. If the sensory impulses received by the *thalami optici* are sent to the *corpora striata*, and by these are transmitted downwards and outwards through the *crura cerebri*, then reflex actions may occur in which the basal ganglia are the centres; but, if the impulses are sent up, in the first place, to the cerebral hemispheres, and by these transmitted down to the *corpora striata*, then the action must include the higher mechanism of the grey matter of the hemispheres. In the former case, it is supposed by those who hold that consciousness is connected with the grey matter of the hemispheres that the action must be purely reflex and unconscious. Experiment has not thrown much light on this problem, owing to the deep-seated situation of these bodies rendering the results of operative interference untrustworthy. The little that has been done shows that injury to them does not cause paralysis of motion. Nor can it be said that such injuries cause loss of sensation, the only phenomenon observed being that the animal places its limbs in anomalous positions, and does not seem to be aware of having done so. The theory most consistent with fact, is that the *thalami optici* fulfil the same functions for tactile impressions—that is, impressions on the periphery of the body—as the *corpora quadrigemina* do for visual impressions—that is, impressions on the retina. In other words, the *thalami optici* and the *corpora quadrigemina* are the centres of the *spatial senses*, vision and touch, that is, of the senses in which the sensations are referred to positions in space. It is highly probable that in their close connections we have the organic mechanism for the fusion of tactile and visual space into indivisible space perception.

In cases of apoplexy in which these bodies are involved there are sensory disturbances on the side opposite the lesion. This would lead to the inference that the *thalami optici* are the sensory ganglia of the opposite sides of the body. They are not, however, the first ganglionic apparatus through which sensory impressions pass, but they co-ordinate centripetal impulses before these are sent to the cerebral hemispheres, where they are correlated with feeling. Further, as the old name *thalami optici* indicates, these ganglia are concerned in vision, because, if injured, blindness, or at all events disturbance of vision, is one of the results. This favours the view that they are centres intermediate between special sensory centres and the higher centres of the cerebrum.

(*c*) **Corpora Striata.**—These ganglia, sometimes termed the *ganglia of the cerebral hemispheres*, situated in front and on the outer side of the *thalami optici*, are seen in the lateral ventricles. The greater part of each is embedded in the white substance of the hemisphere, the extra-ventricular portion, whilst the part seen in the floor of the lateral ventricle is called the intra-ventricular portion. Each of these contains a nucleus of grey matter, the *nucleus caudatus*, or the *intra-ventricular*, and the *nucleus lenticularis*, or the *extra-ventricular*. (See Fig. 267, p. 520, and Fig. 268, p. 523.) The latter is separated internally from the intra-ventricular portion by a layer of white matter called the *internal capsule*, whilst on the outer side there is another layer of white matter called the *external capsule*, beyond which, again, is a lamina of grey matter, called the *claustrum*, separating the external capsule from the *island of Reil*. The internal capsule is continuous with the *crusta*, a portion of the *crus cerebri*, which, in turn, is a continuation of the pyramidal fibres of the *medulla oblongata* and the *pons*. Multipolar nerve cells are found in the *nucleus caudatus*; in the *claustrum* the cells are small and spindle-shaped. Posteriorly the *corpus striatum* is related by fibres with the *thalamus opticus*, inferiorly, through the internal capsule, with the pyramidal portion of the *medulla* and cord ; and externally and superiorly with the grey matter of the cerebrum. Each lenticular nucleus consists of three masses of grey matter, the lenticular nucleus proper most external, and within this two masses termed *globus pallidus major et minor*.

The *corpus striatum* is a centre for the co-ordination of motor impulses. It may be roused into activity by impressions reaching it directly from the *thalamus opticus*, but it usually acts in obedience to impulses coming from the cerebral hemispheres. When a clot of blood is formed in, say, the right *corpus striatum*, there is motor paralysis of the opposite side of the body, and, according to the size of the clot, and especially the portion of the internal capsule involved, the paralysis may affect more or less completely the different groups of muscles. Destruction of the two bodies destroys voluntary movement, but the animal moves forwards as in running. Destruction of the *nucleus caudatus* renders movements of progression impossible, but the animal performs movements of rotation. Nothnagel, by injecting a minute drop of a solution of chromic acid, destroyed the *nucleus lenticularis* of a rabbit, with the result of throwing the animal into complete unconsciousness. He also states that in the *corpus striatum* of the same animal there is a point, the *nodus cursorius*, the excitation of which caused the rabbit to rush forwards. This observation agrees with the statement of Magendie that, when he injured the *corpora striata*, the animal seemed to have an irresistible propulsion forwards. Ferrier states that when the *corpora striata* were stimulated by an interrupted current, convulsive movements of the opposite side of the body took place; and when the current was powerful, the side of the body opposite to the side of the brain stimulated was forcibly drawn into an arch.

Here we may give a brief summing up as to the paths of the two kinds of influences, motor and sensory:—

1. **Motor.**—An impulse, commencing with volition, passes from the cerebrum down the *crus cerebri* and the *pons Varolii* of the same side, as far as the *medulla oblongata.* Here many of the fibres decussate at the anterior pyramids, pass down the opposite side of the cord, as the *crossed pyramidal tract*, while others are continued down on the same side as the columns of Türck. It is believed that the latter also decussate in the course of their passage down the cord, forming the anterior white commissure. Thus there is a complete decussation of both sets of fibres, so that the right hemisphere of the brain is related, as regards motion, to the left side of the body, and *vice versâ.* The motor influences are carried out by the anterior roots.

2. **Sensory.**—Sensory impulses, originating, we shall say, in the skin, enter the cord by the posterior roots, run up for a variable distance on the same side, then pass into the grey matter of the posterior horn, run from ganglion cell to ganglion cell, then pass out of the grey matter, and still continue to run up on the same side of the cord, forming part of the posterior columns. They then go to the *pons Varolii*, decussate in this structure, and reach the brain on the side opposite to that from which they started. Here, however, as in the motor tracts, many of the fibres decussate in the cord itself, and then run up on the opposite side to the brain. It is still doubtful whether the largest decussation of the sensory fibres occurs in the cord itself or in the pons, but the result of the decussation, wherever it may occur, is that, as regards sensory impressions, the right brain receives those from the left side of the body, and *vice versâ.*

CHAP. VI.—THE CEREBELLUM.

The cerebellum has three peduncles: (1) the superior peduncles—*crura ad cerebrum*, or *processus ad testes*,—together with the valve of Vieussens,—connect the cerebellum to the cerebrum; (2) the inferior peduncles, or *crura ad medullam*, are the superior extremities of the restiform bodies; (3) the middle peduncles, or *crura ad pontem*, much the largest, are the lateral extremities of the transverse fibres of the *pons Varolii.* The latter are largely commissural fibres for the hemispheres of the cerebellum. These peduncles pass into the cerebellum at its fore part. In the interior of the organ there is a nucleus of grey matter, the *corpus dentatum.* The cortical substance is formed of two layers—an outer *molecular*, consisting of a delicate matrix containing a few round cells and fibres, and an inner, or *granular*, containing nucleated corpuscles closely packed together (Fig. 258, p. 495). At the junction of the granular with the molecular layer there are the large cells called *Purkinje's cells* (Fig. 174, *d*, p. 314, Vol. I.). The white centre of each lamina consists of delicate nerve fibres, the terminations of which have not been made out. Probably they end in the plexus of nerve fibres in the granular layer, or in the processes of Purkinje's cells.

Results of Experiments.—The cerebellum is insensible to mechanical excitations. Puncture causes no pain, but there may be twisting of the head to the side. Ferrier states that Faradic irritation causes movements of the eyeballs and movements indicative of vertigo. Section of the middle peduncle on one side causes the animal to roll rapidly round its longitudinal axis, the rotation being towards the side operated on.

If the cerebellum is removed gradually, by successive slices—an operation easily done in a pigeon—there is a progressive effect on locomotive actions. On taking away only the upper layer, there is weakness and a hesitation in gait. When the sections have reached the middle of the organ, the animal staggers, and assists itself by its wings in walking. The sections being continued further, it is no longer able to preserve its equilibrium without the assistance of its wings and tail; its attempts to fly or walk resemble the fruitless efforts of a nestling, and the slightest touch knocks it over. At last, when the whole cerebellum is removed, it cannot support itself even with the aid of its wings and tail; it makes violent efforts to rise, but only rolls up and down; then, fatigued with struggling, it remains for a few seconds at rest on its back or abdomen, and then again commences its vain struggles to rise and walk. Yet, all the while, sight and hearing are perfect. It attempts to escape, and appears to have all its sensations perfect. The results contrast very strongly with those of removing the cerebral lobes. "Take two pigeons," says Longet, "from one remove completely the cerebral lobes, and from the other only half the cerebellum; the next day, the first will be firm on its feet, the second will exhibit the unsteady and uncertain gait of drunkenness."

There is thus loss of the power of co-ordination, or of regulation of movement, without loss of sensibility, and hence it has been assumed that the cerebellum acts as the co-ordinator of movements.

CO-ORDINATION OF MOVEMENT.

The nervous mechanisms by which movements are co-ordinated—that is, adapted to specific ends—are not thoroughly understood, but a short description of what is known may be here given. Muscular movements may be either simple or complex. In winking, the movement of the eyelid is effected by two muscles, one bringing the lid down, the other raising it. But picking up a pen from the table, taking a dip of ink, and writing a few words, involve a complicated set of movements of the muscles of the trunk, shoulder, arm, forearm, fingers, and thumb. To perform the movements with precision, each muscle or group of muscles must act at the right time and to the proper amount. It is also clear that all this is accomplished automatically. We are not conscious of the requisite combinations; but many of these movements are first acquired by conscious efforts, and they become automatic only by repetition. Again, in walking, equilibrium is maintained by a delicate series of muscular adjustments. When we swing forward one leg, and balance the body on the other, many muscular movements occur, and with every change in the position of the centre of gravity in the body, there are corresponding adjustments. It would appear, that in all mechanisms of co-ordination, the first part of the process is the reception of sensory impressions from the periphery. These sensory impressions are derived from the skin or muscles, and are caused by variations of pressure. Thus, if we lift a heavy weight, as a large stone, by the right hand, and raise it to the bend of the elbow, we throw the body to the other side by the action of the muscles of that side, thus maintaining the equilibrium. We judge of the amount of force necessary to overcome an obstruction by the feeling of resistance we encounter. All the movements of the body give rise to feelings of varying pressures, and these feelings regulate the degree of muscular action necessary to maintain equilibrium, or to perform a requisite movement. This is at first a conscious experience, and a child has to pass through an education, often involving painful efforts, before the nervous mechanisms become automatic, and the movement is done without effort. But the ordinary sensory nerves, from skin and muscle, are not the only channels by which such guiding mechanisms, are set in action. Other sensory impressions may be brought into play.

1. *Impressions from Semicircular Canals.*—Impressions are, in all probability, derived from the canals of the ear which assist in the maintenance of equilibrium. The mechanism of such is discussed in treating of the ear. It is sufficient to state that if we take the peculiar position of the three canals into consideration, any movement in space may be appreciated, and these appreciations enter into the judgment we form of the movements. The sense of equilibrium is largely due to impressions derived from the position of the head, and muscular movements required for placing the body in definite positions are thus determined by impressions coming from the canals.

2. *Impressions from the Eye.*—Many movements are guided and controlled by the sense of vision. Simply blindfolding a bird makes it passive, and it will not attempt to walk or to fly; the same

effects, to a less degree, may be seen in a mammal, and a blindfolded man staggers in his gait. The accurate movements of the blind in walking are acquired by laborious effort, and are guided by the sensations of hearing, of touch, and of resistance. If the optic lobes of a frog are destroyed, its power of balancing is lost.

There are thus three channels by which peripheral impressions pass to the centres and guide or co-ordinate movement: (1) from the periphery, by nerves of ordinary sensibility arising in the skin, muscles, and viscera; (2) from the semicircular canals, by nerve fibres in the auditory nerve; (3) from the eye, by fibres of the optic nerve. How and where these skeins of sensitive impressions are gathered up and arranged so as to call forth the requisite movements can only be conjectured; but the cerebellum is the organ most likely to be concerned in such a mechanism. It is in connection with many of the nerve fibres conveying sensory impressions. By the restiform bodies it receives sensory fibres from the spinal cord, the auditory nerve has roots related to the cerebellum, and there are communications between the *corpora quadrigemina* and the cerebellum.

Stimulation of the cerebellum causes movements of the eyeballs, and disease of the cerebellum is sometimes attended by blindness. How the cerebellum co-ordinates movement is unknown, and the difficulty in explaining its functions is not lessened by the fact that disease of this organ may exist without any appreciable sensory or motor disturbance. There is no evidence to support the view of the founders of phrenology that the cerebellum has to do with the sexual functions.

The following peculiar movements are seen when the peduncles of the cerebellum are destroyed: (1) *mouvement de manège* (like a horse in a circus) by irritation of the *processus in cerebello ad testes* or of the back of the underlying cerebral peduncle; (2) *mouvement gyratoire*, the body rotating on a longitudinal central axis, by irritation of the middle peduncle; (3) *rotation en rayon de roue* (like the spokes of a wheel), when the body of the cerebellum is injured. A sudden irritation of one upper cerebellar peduncle may cause an animal to spring towards the injured side, and if the inferior peduncle is injured, the animal may roll like a wheel from the injured side.

Chap. VII.—THE CEREBRAL HEMISPHERES.

The white matter of the cerebrum consists of ascending or peduncular fibres, longitudinal or collateral fibres, and of transverse or commissural fibres.

1. Peduncular Fibres.—The *crustæ* of the peduncles consist of bundles of longitudinal fibres derived from the anterior pyramid of the medulla. The crusta is quadrilateral in form, but in ascending to the hemispheres it becomes flattened from above downwards, so that the fibres spread out like a fan. The fan formed by these fibres is bent into the form of an incomplete hollow cone, the convex surface of which is directed upwards and inwards. Thus the fibres pass between the *thalamus opticus* and the lenticular nucleus, forming the internal capsule. Higher up, the fibres pursue their course beneath and to the outside of the *thalamus* and the caudate nucleus, and over the lenticular nucleus. At

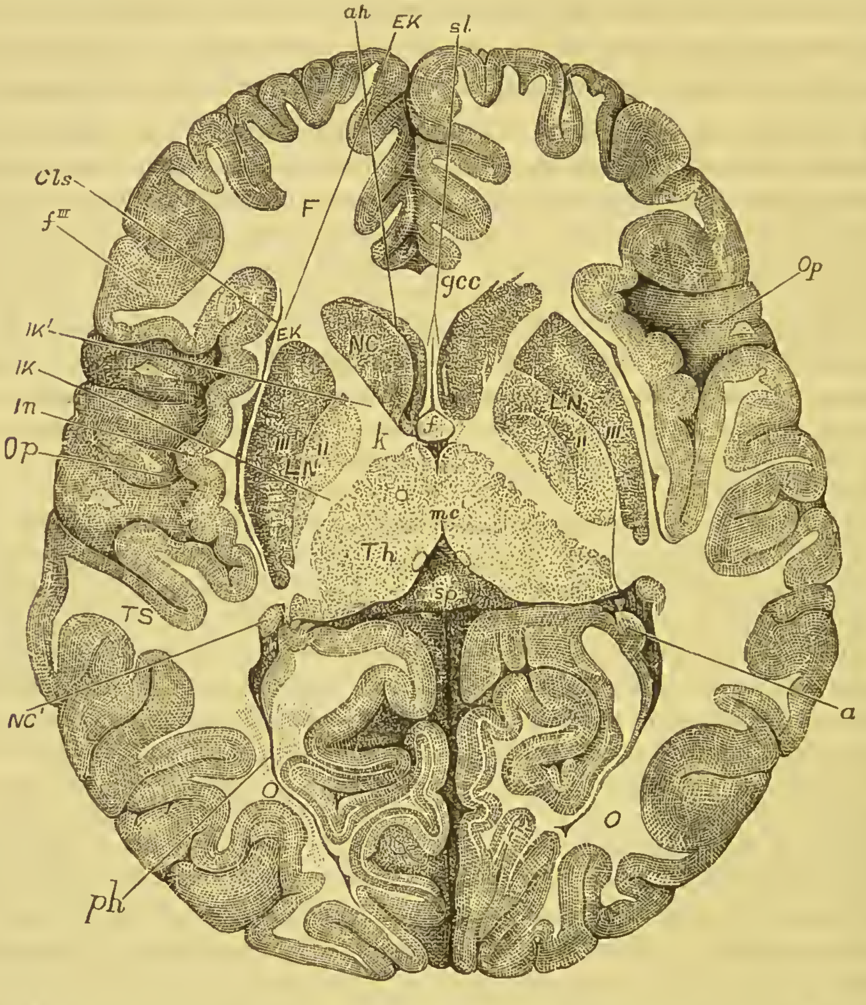

Fig. 267.—Horizontal section of brain of child nine months old, only a portion of the right side being shown. *F*, frontal, *TS*, temporo-sphenoidal, and *O*, occipital lobes ; *op*, *operculum* ; *In*, island of Reil ; *Cls*, claustrum ; *f'''*, third frontal convolution ; *Th*, *thalamus opticus* ; *NC*, caudate nucleus ; *NC'*, tail of caudate nucleus ; *LN*, lenticular nucleus ; *II*, *III*, second and third divisions of lenticular nucleus ; *EK*, external capsule ; *IK*, posterior division, *IK'*, anterior division, and *K*, knee of internal capsule ; *ah*, *ph*, anterior and posterior horns respectively of lateral ventricles ; *gcc*, knee of *corpus callosum* ; *sp*, *splenium* ; *mc*, middle commissure ; *f*, fornix ; *sl*, *septum lucidum*. (After Flechsig.)

a higher level, the internal capsule spreads out from before backwards, while the anterior half forms an obtuse angle with the posterior. The angle where the halves meet is called the *knee* (Fig. 267, *k*), while the divisions themselves are called the anterior (Fig. 267, IK′) and posterior *segments* (IK) of the internal capsule. On emerging from the basal ganglia, the fibres of the internal capsule radiate in all directions to reach the cortex of the brain, giving rise to the *corona radiata*. The following sets of fibres have been traced into connection with the cerebrum:

(*a*) Sensory peduncular fibres, derived from the posterior root zones and the columns of Goll. These are chiefly in connection with the cerebellum; but many pass up through the *pons* to reach the *crus cerebri*, occupying the posterior and external portion of the pyramidal tract. They are not connected with the *thalamus opticus* and the lenticular nucleus, but pass between them to the cortex. (*b*) Fibres from the roots of the optic nerves, reaching the brain by what have been called the *optic radiations of Gratiolet*. This bundle of fibres issues from the posterior and external border of the *thalamus opticus*, and is applied to the peduncular sensory tract in its passage through the internal capsule, and the fibres are connected with the convolutions of the occipital lobe. At least one of the roots of the optic nerve (the internal) passes into the external geniculate body, and thence into the anterior bodies of the *corpora quadrigemina*. Thus there is a path for the passage of impressions from the retina to the cortex of the brain. (*c*) Fibres from the olfactory lobes also join with the optic radiations, and pass with them to the convolutions of the cortex of the temporo-sphenoidal lobe. (*d*) The pyramidal tract passes on to form the internal capsule and the *corona radiata*, the fibres ending in the parietal lobe, the paracentral lobule, the superior extremities of the ascending frontal and parietal convolutions, the posterior extremity of the first frontal convolution, the posterior extremity of the third frontal, and the inferior extremities of the ascending frontal and parietal convolutions—in short, in the convolutions forming the middle and parietal region of the cortex. (*e*) Fibres from the external surface of the *thalamus opticus* join the internal capsule. These pass to the convolutions of the frontal and parietal lobes. (*f*) Fibres from the external surface of the caudate nucleus pass into the *corona radiata*. (*g*) Fibres from the superior and internal surface of the lenticular nucleus join the ascending fibres of the internal capsule. (*h*) Fibres ascend from the superior peduncle of the cerebellum. Some of the fibres of the superior peduncle of the cerebellum of the opposite side pass through the red nucleus and along the internal surface of the fibres of the pyramidal tract to the central convolutions. (*i*) Fibres issue from the *corpus callosum* and descend into the internal capsule. (*k*) Fibres of the external capsule ascend from the *crusta* and reach the cortex through the *corona radiata*.

In addition to the peduncular fibres above enumerated, all of which belong to what may be termed the system of the internal capsule and *corona radiata*, fibres from the *fornix*, *tænia semicircularis*, outer layer of *septum lucidum*, and the fillet of the *crus* also pass from below upwards to the cortex of the hemispheres. (Jas. Ross.)

Longitudinal or Collateral Fibres.—These are: (*a*) Fibres run immediately below the surface of the cortex, and connect the grey matter of adjacent convolutions. (*b*) Fibres in the *gyrus fornicatus*, the convolution above the *corpus callosum*. Bands of these fibres arise in the anterior perforated space, and pass round the *corpus callosum* and end in the same perforated space, and offsets of these fibres pass upwards and backwards to reach the summits of the secondary convolutions derived from the *gyrus fornicatus* near the longitudinal fissure. (*c*) Longitudinal fibres of the *corpus callosum* (*nerves of Lancisi*), connect the anterior and posterior ends of the callosal convolution. (*d*) Longitudinal septal fibres, lying on the inner surface of the *septum lucidum*, enter into the *gyrus fornicatus*. (*e*) The *fasciculus uncinatus*, passing across the bottom of the Sylvian fissure and connecting the convolutions of the frontal and temporo-sphenoidal lobes. (*f*) The longitudinal inferior fasciculus, connecting the convolutions of the occipital with those of the temporal lobe.

Transverse or Commissural Fibres.—(*a*) It is generally held that many, if not all, of the fibres of the *corpus callosum* pass transversely from one side to the other, and connect corresponding convolutions in the hemispheres; but Hamilton holds that there is no such commissural system between convolutions, and that the fibres decussating in the *corpus callosum* are not continued to convolutions on the other side, but pass downwards (Fig. 268). (*b*) The fibres of the anterior commissure wind backwards through the lenticular nuclei to reach the convolutions round the Sylvian fissure. (*c*) The fibres of the posterior commissure run through the *thalami optici*.

The following *resumé* of the arrangement of the fibres may be applied to the clinical investigation of various forms of cerebral disease:—

1. The fibres issuing from the frontal convolutions form the internal portion of the *crus cerebri* and the anterior portion of the internal capsule.
2. The fibres issuing from the lower part of the ascending frontal convolution form the knee (*genu*) of the internal capsule and the *genicule* (or bent portion) of the *crus*.
3. The fibres issuing from the upper part of the ascending frontal convolution form the anterior third of the posterior segment of the capsule and the pyramidal tract of the *crus*.
4. The fibres issuing from the lower portion of the ascending parietal convolution form the middle third of the posterior segment of the capsule, and the inner half of the external fasciculus of the *crus*.
5. The fibres issuing from the convolutions of the posterior region of the cerebrum form the posterior third of the posterior segment of the capsule, and the external part of the *crus*.
6. Fibres pass from the cerebral cortex to the lenticular nucleus, and thence into the *crus*. In like manner, fibres pass from the *thalamus opticus* to the cortex.

To put these statements more succinctly, the anterior part of the internal capsule, the knee, and the anterior two thirds of the posterior segment contain *motor* fibres issuing from the *motor region of the cortex*, and the posterior third of the posterior segment contains *sensory* fibres passing to the posterior and sensory part of the cortex.

Arrangement and Structure of Grey Matter.—This has already been described at p. 493. The grey matter of the hemisphere is associated with intelligence in its various forms. The phenomena of disease support this conclusion. Diseases producing slow changes in the layer of grey matter on the cortex are associated with mental disturbance, such as melancholia, mania, or dementia. If the grey matter is suddenly injured or com-

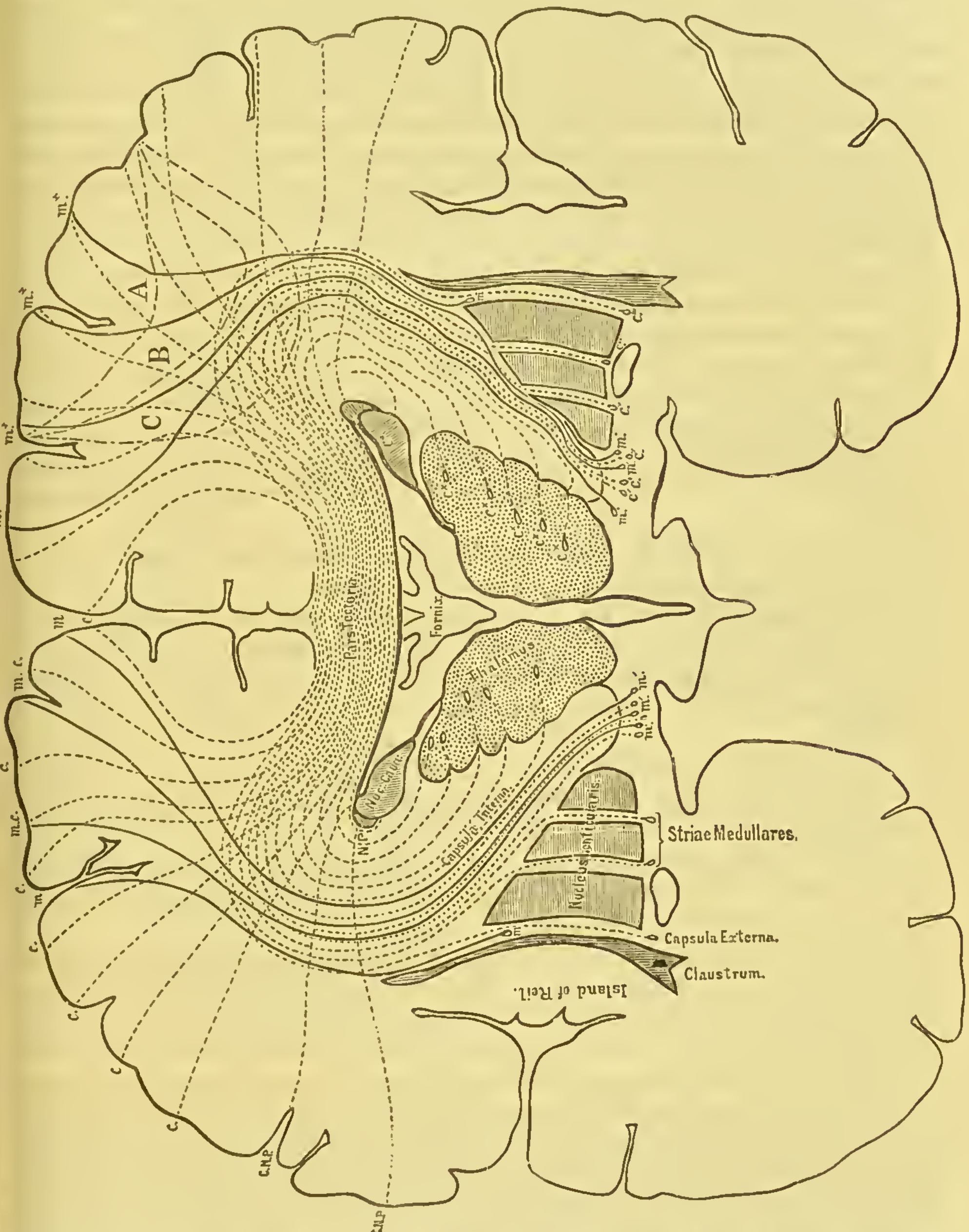

FIG. 268.—Diagrammatic scheme of a perpendicular transverse section of human brain, explaining Hamilton's view of the *corpus callosum*. *c, c, c*, callosal fibres passing into the *pars tectoria* of the *corpus callosum*, and curving downwards on opposite side into internal capsule, *striæ medullares*, c'', c'', and outer capsule c'''. Those entering the inner capsule are distributed to the caudate nucleus, C°, thalamus, $c^\times$, and to *pons* and *medulla*, c'. At *CNP* are represented the cortical fibres connected with the *nucleus plexiformis*, *NP*. The motor and other direct fibres are shown at *m*, *m*, *m*, running directly into the inner, m', m', m', and probably into the outer, capsule, m''. They are continued downwards to the medulla and cord. The dotted lines A, B, and C, show the effects of lesions of the cortex at various depths. In A the motor fibres, m', m', m', and the callosal fibres about to cross would be involved; in B, the lesion would, in addition, destroy certain of the callosal fibres which have already crossed; while in C, nearly the whole of the latter would suffer. (Drawn for this work by Professor Hamilton.)

pressed by a blow or by the effusion of fluid consequent on inflammation, unconsciousness is a certain result. So long as the pressure continues there is no consciousness; if it be removed, consciousness may soon return. On the other hand, if the disease affect the white matter of the central portions or the ganglia at the base, there may be paralysis or convulsions without consciousness being affected. The facts of pathology relating to the brain indicate that the grey matter on the surface is the organ of consciousness and of all mental operations.

FIG. 269.—Lateral view of the human brain. F, frontal lobe; P, parietal lobe; O, occipital lobe; T, temporo-sphenoidal lobe; S, fissure of Sylvius; S′, horizontal, and S″, ascending ramus of the same; c, *sulcus centralis*, or *fissure of Rolando*; A, anterior central convolution, or ascending frontal; B, posterior central convolution, or ascending parietal; F_1, superior, F_2, middle, and F_3, inferior, frontal convolutions; f_1, superior, f_2, inferior, frontal sulcus; f_3, *sulcus præcentralis*; P_1, superior parietal lobule, or postero-parietal lobule; P_2, inferior parietal lobule; P_2, *gyrus supra-marginalis*; P_2', *gyrus angularis*; ip, *sulcus intraparietalis*; cm, termination of the calloso-marginal fissure; O_1, first, O_2, second, O_3, third, occipital convolutions; po, parieto-occipital fissure; o, *sulcus occipitalis transversus*; o_2, *sulcus occipitalis longitudinalis inferior*; T_1, first, T_2, second, and T_3, third, temporo-sphenoidal convolutions; t_1, first, t_2, second, temporo-sphenoidal fissures. (Ecker.)

This statement is now an axiom of medical science, and the basis of the rational treatment of the insane and of maladies of the central nervous organs.

Two methods of experiment upon the cerebrum have usually been followed, and both have yielded important results. To understand these, we shall examine the external topography of the convolutions of the cerebrum. In the first place, observe the arrangement of the convolutions, as shown in Fig. 269, by Ecker, identifying the fissure of Rolando (cm) and the fissure of Sylvius (S), and the *rami* of the latter (S′ and S″). Next, observe the three frontal convolutions (F_1, F_2. F_3). The third (F_3) is sometimes termed *Broca's convolution*, and is itself formed of three parts, an ascending, situated behind the ascending branch of the Sylvian fissure (near S″, a middle, V-shaped, between two branches of the Sylvian fissure, and an anterior, the shaded portion above S). Observe two convolutions bounding the fissure of Rolando, in front, the ascending frontal (A) and behind the ascending parietal (B). Then we have three parietal convolutions (B, P_1, and P_2). Note the position of the angular gyrus (P_2'). Below, we find the three temporo-sphenoidal convolutions (T_1, T_2, T_3). On the inner surface of the great longitudinal fissure, and immediately above the *corpus callosum*, we find a convolution termed the *gyrus fornicatus*, and running along the margin of the longitudinal fissure as far back as the fissure of Rolando, we find the *marginal convolution* (not shown in Fig. 269).

(*a*) *Removal.*—Flourens and the older observers found that as successive slices of grey matter are removed from the surface of the cerebrum an animal becomes more dull and stupid, until at last all indications of perception and volition disappear. A pigeon in this condition if carefully fed, may live for many months.

The animal remains in a state of profound stupor, in which it is entirely inattentive to surrounding objects. It sits motionless upon its perch or stands with the eyes closed and the head sunk between the shoulders. The plumage is expanded by an erection of the feathers, so that the body appears puffed out. Occasionally the bird opens its eyes with a vacant stare, stretches its neck, shakes its bill once or twice, and then relapses into its former condition.

Similar observations have also been made on reptiles and mammals, but the latter survive the operation for only a short time. In watching such an animal it is difficult to divest one's mind of the belief that it feels and sees and hears. It rarely makes movements unless stimulated from without. Thus it may remain motionless for many hours; but if pushed, or gently touched, it moves.

(*b*) *Localisation of Function.*—If we exclude the theory of the founders of phrenology, the view held by physiologists was, up to recent times, that all parts of the cerebral cortex had the same functional value. About 1860, Broca made the observation that the affection of speech often seen in paralysis termed *aphasia* depended on pathological alterations in the third frontal convolution or island of Reil. In this condition, the patient cannot give the proper word-symbol for an object he desires or which he is requested to name. He may know the word and know the thing, he has an idea of the thing, but he cannot give correct articulate expression to the idea. This was the first step to localisation of function in the cerebral cortex. The next was taken with the aid of the method of electrical stimulation.

Magendie, Matteucci, Longet, Weber, Budge, Schiff, and others, taught that electrical irritation of the surface of the hemispheres called forth no muscular movements; and it was generally accepted that the grey matter on the cortex of the brain was entirely concerned in the phenomena of sensation, volition, and intellectual action. During the Franco-German war, in 1870, Hitzig had occasion to apply galvanism to a portion of the exposed brain of a wounded soldier, and he observed contractions of the muscles of the eyeball. When peace was restored, experiments were made on the lower animals by Hitzig and Fritsch, in which a portion of exposed brain was irritated by a continuous current, and it was observed that the phenomena of contraction took place on opening and closing the current. The observers discovered that when certain areas of grey matter were stimulated, contractions of certain muscles occurred, and they were able to map out areas for groups of muscles. Immediately afterwards, the research was taken up by Ferrier, who, using a Faradic instead of a continuous current, greatly extended the field of inquiry, and obtained many important results. The motor areas, as determined by Ferrier in the monkey, are shown in Fig. 270. Ferrier has also indicated the corresponding motor areas in man by carefully comparing the convolutions with those of the monkey (Figs. 271 and 272, pp. 527-8). An inspection of the figures shows that the areas which, when stimulated, give rise to definite movements are distributed only over a part of the cortex. As stimulation gives rise to no movements over other regions of the brain, the latter have been assumed to be connected with psychical states, such as sensation, volition, etc. Much controversy has arisen as to the real nature of these so-called *motor areas*, or *psycho-motor areas* or *centres*. It has been ascertained that the effects are not due to diffusion of the electric currents influencing other parts of the brain. That there is to some extent such diffusion between the elec-

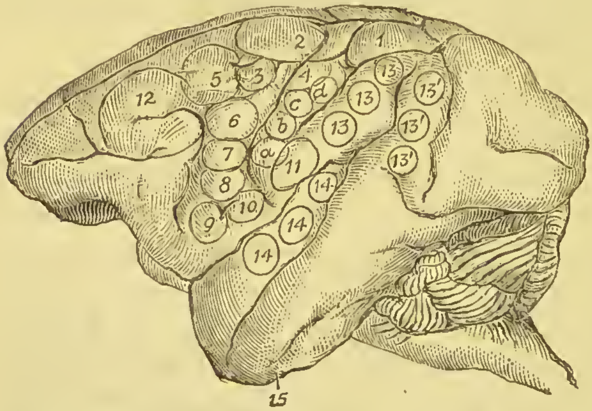

Fig. 270.—Left hemisphere of monkey. For an account of the phenomena following irritation of these areas see description of Figs. 271 and 272. (Ferrier.)

trodes there can be no doubt, but the exact correspondence between the area stimulated and the movements produced, and the fact that shifting the electrodes a very short distance to one side or another is followed by different results, show that the effect is owing to changes excited by the electric current in that particular area of grey matter. Hitzig, Ferrier, and others, have also found that removal of the layer of grey matter of a motor centre is followed by enfeeblement of the movements assigned to the area, but in the course of a few days the paralytic symptoms disappear. The latter effect cannot be due to the corresponding centre on the opposite side taking up the work, as subsequent destruction of the latter produced the usual paralysis on the side opposite to the lesion, but did not cause a repetition of the paralysis on the side opposed to the first lesion. It would appear, therefore, that after destruction of a centre on one side some other part of the same hemisphere may take up the functions of the destroyed part.

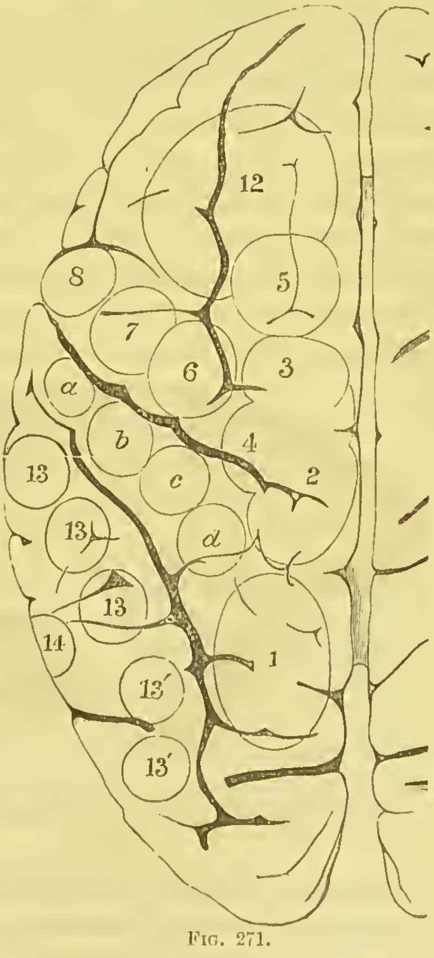

Fig. 271.

Figs. 271 and 272.—Upper and side view of the cortex of the human brain. The figures have been constructed by marking on a human brain, in their respective situations, the motor areas determined on the monkey's brain. The following description of the effects of stimulating the various areas refers, of course, to the brain of the monkey.

1. *On the postero-parietal lobe.* Advance of the opposite hind leg as in walking.

2, 3, 4. *On the upper extremity of the fissure of Rolando.* Complex movements of the opposite leg and arm, and of the trunk, as in swimming.

a, b, c, d. On the ascending parietal convolution. Individual and combined movements of the fingers and wrist of the opposite hand. Prehensile movements.

5. *On the posterior extremity of the superior frontal convolution.* Extension forward of the opposite arm and hand.

6. *On the upper part of the ascending frontal convolution.* Supination and flexion of the opposite fore-arm.

7. *On the median portion of the ascending frontal convolution.* Retraction and elevation of the opposite angle of the mouth by means of the zygomatic muscles.

8. *Lower down on the same convolution.* Elevation of the ala nasi and upper lip with depression of the lower lip on the opposite side.

9, 10. *At the inferior extremity of the ascending frontal and posterior extremity of the third frontal convolution.* Opening of the mouth with (9) protrusion and (10) retraction of the tongue. (*Region of aphasia.*)

11. *At the inferior extremity of the ascending parietal convolution.* Retraction of the opposite angle of the mouth, the head turned slightly to one side.

12. *On the posterior portions of the superior and middle frontal convolutions.* Eyes opening widely, pupils dilating, and the head and eyes turning towards the opposite side.

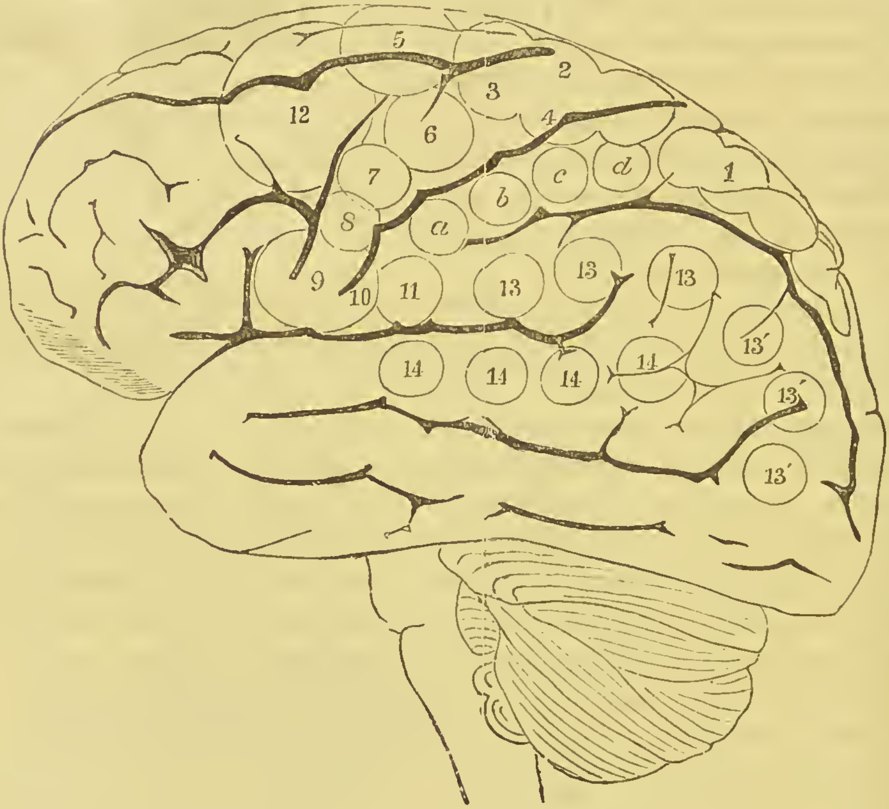

FIG. 272.

13, 13′. *On the supra-marginal lobule and angular gyrus.* The eyes moving towards the opposite side with an upward (13) or downward (13′) deviation. Pupils generally contracting. (*Centre of vision.*)

14. *On the infra-marginal or superior temporo-sphenoidal convolution.* Pricking up of the opposite ear, head and eyes turning to the opposite side, and pupils dilating largely. (*Centre of hearing.*)

The centres of *taste* and *smell* are at the *extremity of the temporo-sphenoidal lobe*, and that of *touch* in the *gyrus uncinatus and hippocampus major.* (Ferrier.)

Goltz has removed large portions of the grey cortex (even to the extent of almost the whole of one hemisphere) by a jet of water, so as to avoid hæmorrhage, and still recovery of motor power took place after a time, although there remained "clumsiness in the execution of certain movements." His opinion is that the paralytic phenomena are caused by the injury exciting an inhibitory action on lower centres. This view, substantially that advocated by Brown-Séquard, does not explain why it is that gentle irritation of the centre by a weak Faradic current calls forth movements of a definite character, and the denial of cerebral localisation is negatived by the fact discovered by Horsley and Schäfer that a function so widely diffused over the body as tactile sensibility has a specific centre in the *gyrus fornicatus.* The evidence is complete that there are definite motor areas of grey matter on the cortex—that is, in ordinary circumstances, these areas are related to specific muscles or groups of muscles. It is possible that each group of muscles does not depend on one area alone, but on several, whilst it is more intimately related to one than to the others. This would account for the fact that movements of a group of muscles may be excited by stimulation of other areas than those mapped out by Ferrier. Areas associated with definite movements of the thorax, abdomen, and pelvis, have also been discovered, and thus all muscular mechanisms have been connected with cerebral convolutions.

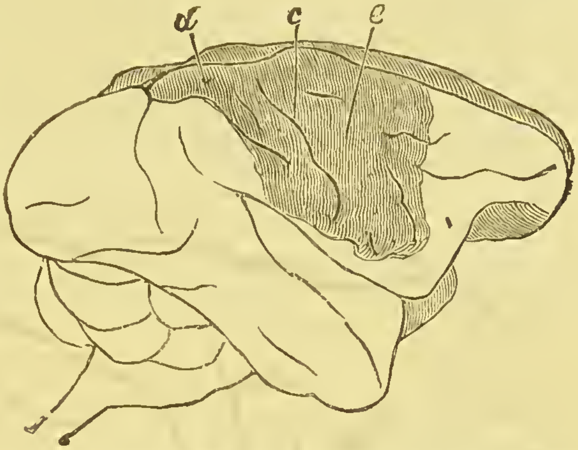

FIG. 273.—Lesion of the grey matter of the right hemisphere of a monkey's brain, causing complete hemiplegia (loss of motor power) of the opposite side without affection of sensation. c, Fissure of Rolando; *d*, postero-parietal lobule; *e*, ascending frontal convolution. (Ferrier.)

The following is a *resumé* of the subject of the location of motor centres :—1. The centre for the movements of the *head and neck* is the posterior part of the first frontal convolution. (2) For the movements of the *facial muscles*, the posterior part of the second frontal convolution. (3) For the movements of the *tongue, jaws, lips*, or *the mechanism of articulation of words*, the upper part of the third left frontal convolution, near the end of the ascending frontal. This centre is near that of the facial muscles. (4) For the *arm*, the middle of the ascending convolutions, more especially the ascending frontal. (5) For the *leg*, the upper part of the ascending convolutions, especially the ascending parietal, and the paracentral lobule, near the fissure of Rolando. (6) For the *eyes*, the posterior portions of first and second frontal, the supra-marginal lobule and the angular gyrus. (7) For the muscles of the *trunk*, the marginal convolution and the convolution of the *corpus callosum.* The centre of *sight* is in the occipital lobe, and that for hearing (especially the hearing of words) is in the first temporo-sphenoidal. *General* *sensibility* is referred to the occipital lobe and the posterior portions of the parietal and temporo-sphenoidal lobes.

The whole subject of localisation has been re-investigated by Horsley and Schäfer,[1] and they point out that there are no lines of demarcation between the centres, and that the areas overlap to a greater or less extent. According to these observers, the *arm area* occupies most of the upper half of the ascending parietal and ascending frontal convolutions from the level of the sagittal part of the precentral fissure below to the margin of the hemisphere above. It also bends round to the mesial surface, and is continued into the marginal convolution. The shoulder muscles are related to the upper limit of the area, those of the fore-arm and wrist to the centre of the area, and those of the wrist and fingers to the posterior border. The *face area* occupies all the ascending parietal and frontal convolutions *below* the arm area, down to the Sylvian fissure. The upper part of the area is related to closure of the eyelids, raising of the ala of the nose, and retraction and elevation of the mouth. The lower part is concerned in movements of the jaw and tongue, as in mastication, and irritation of its posterior part causes retraction, while irritation of its anterior part is followed by protrusion of the tongue. The lowest part of the face area is connected with retraction of the tongue and lower lip and bending of the head to the side. The lower part of the ascending frontal convolution is related to the muscular arrangements for closing the vocal cords in phonation (Felix Semon). The *head area*, or *area for visual direction*, is an oblong part of the surface of the frontal lobe, bounded posteriorly by the arm area, and anteriorly by the non-excitable part of the frontal lobe. Irritation causes opening of the eyes, dilatation of the pupils, and turning of the head to the opposite side, with conjugate deviation of the eyes to that side. The *leg area* is situated on the

FIG. 274.—Diagram of monkey's brain, showing motor areas on outer surface. 1, trunk area; 2, flexion of thigh and leg; 3, movements of toes and foot; 4, arm area; 5, head; 6, wrist; 7, fingers; 8, upper face muscles; 9, lower face muscles; 10, mouth and larynx; 11, fissure of Rolando; 12, fissure of Sylvius; 13, junction of interparietal (anterior) and external parieto-occipital fissures. (Reduced from Horsley and Schäfer.)

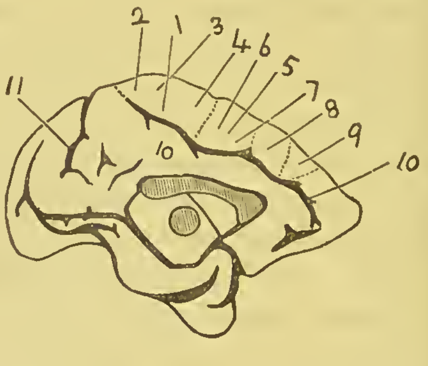

FIG. 275.—Diagram of inner surface of monkey's brain. Observe section of *corpus callosum*. 1, leg area; 2, movements of toes and foot; 3, flexion at knee (hamstring muscles); 4, extension at hip (glutei muscles); 5, trunk area; 6, movements of tail and pelvis; 7, rotation and lateral movements of spine; 8, movements of shoulder and arm; 9, head area; 10, calloso-marginal fissure; 11, internal parieto-occipital fissure. (Reduced from Horsley and Schäfer.)

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[1] Horsley and Schäfer on the "Functions of the Cerebral Cortex." *Trans. of Royal Society*, 1888, B.

mesial surface of the hemisphere, extending over the margin, and occupying a part of the external surface, from the parieto-occipital fissure forwards as far as the anterior end of the trunk area. Externally it is related to the arm area. The portion of this area behind the upper end of the fissure of Rolando is associated with the ankle and digits. More anteriorly, it is connected with flexion of the leg at the knee, and most anteriorly with flexion at the hip. The *trunk area* is almost entirely in the marginal convolution. Irritation of the pre-frontal part of this convolution gives no result, but immediately above the anterior end of the *corpus callosum*, irritation sometimes causes movements similar to those following irritation of the head area, showing that this area occupies a part of the marginal convolution. Behind this, there is an area related to the shoulder and arm, still farther back an area for the upper dorsal part of the trunk, causing rotation and arching of the spine, still farther back, an area for the muscles of the lower pelvic part of the trunk, still farther, an area for the movements of the leg at the hip, still farther, for those moving the lower leg at the knee, and most posteriorly, an area for the muscles of the foot and toes.

Ferrier has also differentiated *sensory centres.* On stimulating the *angular gyrus* he obtained movements of the eye and associated movements of the head, and he regarded the phenomena as being "merely reflex movements on the excitation of subjective visual sensation." He then found that, "when the angular gyrus of the left hemisphere was destroyed, the animal was blind on the right eye soon after the operation, but recovered sight completely on the following day" (Fig. 276). On destroying the angular gyri of both hemispheres, an animal became permanently blind in both eyes. In neither case was there motor paralysis. By similar experiments he placed the *auditory* centre in the superior temporo-sphenoidal convolution, the centres of *taste* and *smell* at the extremity of the temporo-sphenoidal lobe, and that of touch in the *gyrus uncinatus* and *hippocampus major*.

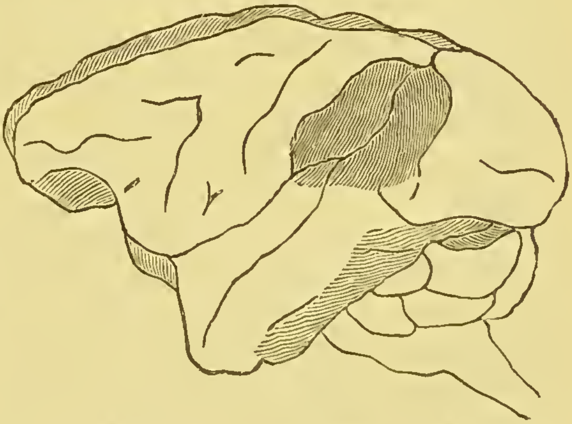

FIG. 276.—Monkey's brain. Destruction of the left angular gyrus, causing temporary blindness of the right eye, according to Ferrier. The position of the part destroyed is indicated by shading.

As regards sensation, Horsley and Schäfer have found that removal of the occipital lobe on one side causes hemiopia, that is blindness in the lateral half of each retina corresponding to the side of the brain injured, and they have arrived at the conclusion that the angular gyri and the occipital lobes are concerned with visual perceptions in such a way that each occipital region is connected with the corresponding lateral half of each retina. They have been unable to substantiate the statement of Ferrier as to the localisation of auditory impressions in the superior temporo-sphenoidal gyrus. The evidence on this point is very conflicting, and the matter cannot be regarded as settled. By removal of the temporo-sphenoidal lobe, it is possible to reach the hippocampus and the uncinate gyrus. This was first done by Ferrier and Yeo, and these observers detected hemianæsthesia after destruction of these parts. This has been corroborated so far by Horsley and Schäfer, but they doubt the statement that this region is exclusively connected with painful and tactile sensibility. Sensibility they locate in the *gyrus fornicatus*, which is continuous with the *gyrus hippocampi*, as they find that injury to the former is followed by hemianæsthesia.

On the other hand, Goltz asserts that even after removal of a considerable part of the cortex, the animal is not actually blind, but suffers from an imperfection of sight; and he states that he "can no more obtain distinct evidence of localisation in reference to vision or other sensations than in reference to movements." Ferrier's view is supported by the observations of Munk, who finds that destruction of a considerable portion of the occipital lobes causes blindness. Munk has made the distinction that there may be blindness in the sense of total deprivation of vision, and "psychical blindness," or the "inability to form an intelligent comprehension of the visual impressions received"; and he supposes that the grey matter of the cortex over the occipital lobes has to do with the elaboration of simple visual impressions into perceptions. In like manner, he concludes that other parts of the cortex may have to do with the elaboration of tactile, olfactory, gustatory, and auditory sensations.

Munk agrees with Schiff in contending that the same cortical area contains nerve cells from which originate motor impulses for special muscles, and other nerve cells which receive sensory impressions from these same muscles, that is to say, that motor power and the sensibility to variations of pressure are in the same area. The supporters of this statement have supposed that the small superficial cells of the cortex are sensory, while the larger and more deeply-placed cells are motor. Against this view, it may be contended that if we can destroy one area and produce paresis of a group of muscles, without affecting the sensibility of these muscles, and if, on the other hand, we can destroy another area, in a different part of the brain, and produce loss of sensibility in the muscles without paralysis of motor power, it is clear that the one area is devoted to the one function, and the other area to the other function.

It may be stated generally that the posterior portion of the brain has to do chiefly with the reception of sensory impressions, and the middle and lateral regions with the transmission outwards of motor impulses. But there still remains the anterior portion. Electrical irritation of the præ-frontal region of the cortex in the monkey causes no motor reaction. Complete destruction causes no paralysis of motion and no sensory disturbance. Dr. Ferrier states :—

> "Removal or destruction by the cautery of the antero-frontal lobes is not followed by any definite physiological results. The animals retain their appetites and instincts, and are capable of exhibiting emotional feeling. The sensory faculties —sight, hearing, touch, taste, and smell—remain unimpaired. The powers of voluntary motion are retained in their integrity, and there is little to indicate the presence of such an extensive lesion or a removal of so large a part of the brain. And yet, notwithstanding this apparent absence of physiological symptoms, I could perceive a very decided alteration in the animal's character and behaviour, though it is difficult to state in precise terms the nature of the change. The animals operated on were selected on account of their intelligent character. After the operation, though they might seem to one who had not compared their present with the past fairly up to the average of monkey intelligence, they had undergone a considerable psychological alteration. Instead of, as before, being actively interested in their surroundings, and curiously prying into all that came within the field of their observation, they remained apathetic or dull, or dosed off to sleep, responding only to sensations or impressions of the moment, or varying their listlessness with restless and purposeless wanderings to and fro. While not actually deprived of intelligence, they had lost to all appearance the faculty of attentive and intelligent observation." [1]

Thus the frontal lobes have to do with cognition and intellectual action. If so, the grey matter on the surface of the brain may be mapped out into three great areas—an area concerned in cognitions and volitions in front, a motor or ideo-motor area in the middle, and a sensory area behind. These distinctions are no doubt to a considerable extent arbitrary ; but, if they are retained as the expressions of a working hypothesis, they are of service. Long ago, and prior to these researches, Hughlings Jackson pointed out that disease of certain areas of grey matter on the cortex of the hemispheres may occasion epileptiform convulsions, affecting groups of muscles. The theory of the localisation of motor functions has been of service in the diagnosis of such diseases (illustrated by Fig. 277).

By studying the diagram in Fig. 278, the effects of various lesions of the central nervous system may be observed. Thus we may shortly note the effects of lesions, on the supposition that the lesion is always on the *right* side. At 1, by interrupting the motor fibres coming from *a*, the centres for the face and tongue, a lesion causes paralysis of the face and of the tongue (lesion in the

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[1] D. Ferrier, *Functions of the Brain*, 1st ed. p. 231.

cerebral cortex). At 2, by interrupting the motor fibres from *b*, the centres for the limbs, we would have paralysis of the arm on the opposite side (lesion in the cerebral cortex). At 3, by cutting the motor fibres from *a* and *b*, there would be hemiplegia on the opposite side, that is, paralysis of the muscles of the face, tongue, arm, and leg (lesion in the fibres below the cerebral cortex). At 4 (above and to the right), by cutting the fibres from *b* and *c* (centre for *motores oculorum*) there would be incomplete hemiplegia, that is, paralysis of the 3rd pair, causing deviation of the eye and ptosis, along with paralysis of the arm and leg (lesion in fibres below cerebral cortex). At 5, by dividing the sensory fibres from the eye and from the body, there would be left hemianæsthesia, with right hemianopsia and deafness on the same side (lesion about posterior portion of internal capsule). At 6, by dividing all motor and sensory fibres, there would be complete hemiplegia and hemianæsthesia (lesion involving internal capsule). At 7, by dividing all the motor fibres, including those from *c*, there would be complete left hemiplegia and hemianæsthesia, along with paralysis of the 3rd on the right (lesion below internal capsule—involving peduncles). At 8, by dividing the motor fibres from *a* and *b*, and also the sensory fibres from the body, there would be complete hemiplegia and hemianæsthesia on the left (lesion in *pons*). At 9, by cutting the motor fibres from *a* and *b*, and also the fibres of the facial, there would be crossed hemiplegia, that is to say, paralysis of the muscles of the leg and arm on the left and of the muscles of the face on the right (lesion

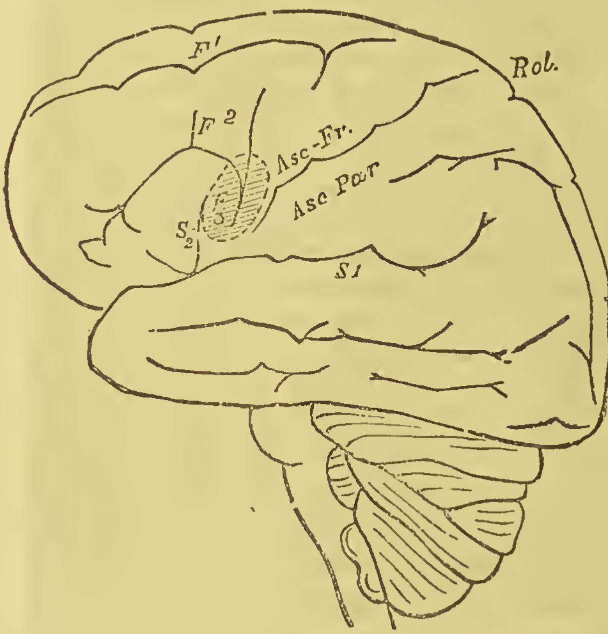

FIG. 277.—Brain of a boy, aged 10, who was seized with right hemiplegia, chiefly brachio-facial, and aphasia. From this he apparently recovered at the end of a month. Three months after he was seized with left brachio-facial monoplegia. From this time there was not only aphasia, but paralysis of all voluntary movements of the face and tongue. Sensation not affected. On post-mortem examination, a lesion (yellow-softening) was found in each hemisphere in exactly corresponding situations. The region involved was the lower end of the ascending frontal, and the hinder end of the middle and inferior frontal, convolutions. (Barlow, quoted by Bastian.)

in the *pons*). At 10, by cutting the same fibres as at 9 and also the sensory fibres from the body, there would be complete crossed hemiplegia, that is to say, involving the muscles of the arm and leg on the left, and the face, tongue, eye

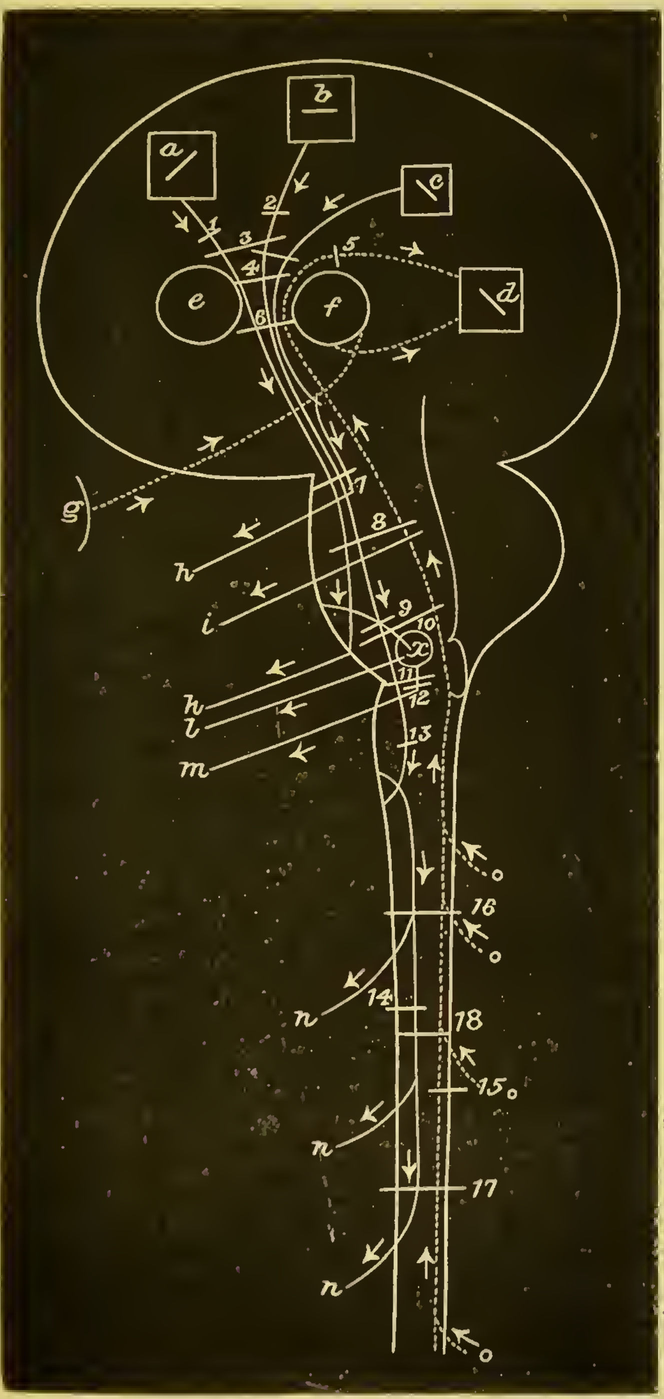

FIG. 273.—Diagram showing the effects of lesions of the central nervous system. The motor fibres are represented by straight, and the sensory by dotted lines. *a*, the three frontal convolutions containing the centres for speech and for the face; *b*, the ascending convolutions containing the centres for the limbs; *c*, centre for the origin of the 3rd cranial nerves (movements of the eye); *d*, centres for general and special sensibility; *e*, the *corpus striatum*; *f*, the *thalamus opticus*. Between these is the position of the internal capsule. *g*, optic nerve; upper *h*, 3rd nerve; *i*, the motor portion of the 5th; lower *h*, 6th or *abducens* for *rectus externus* of eye; *l*, facial nerve; *m*, hypoglossal; *n*, anterior roots of spinal nerves; *o*, posterior roots of spinal nerves. The lines, ——, with figures represent the positions of lesions.

(*motor oculi*), and auditory nerve on the right (lesion in the *pons*). At 11, by cutting the motor fibres of the hypoglossal, facial, and vagus (laryngeal nerves), in both halves of the bulb, there would be labio-glosso-laryngeal paralysis (lesion in the *medulla oblongata*). At 12, by interrupting the fibres of the hypoglossal there would be paralysis of the tongue on the right (lesion in the *medulla oblongata*). At 13, by cutting the motor decussating fibres in the *medulla* there would be hemiplegia. At 14, by destroying the motor fibres in the anterior part of the cord on one side, there would be paralysis of muscles on the same side (lesion in the anterior part of cord). At 15, by destroying the sensory fibres in the posterior part of the cord on one side there would be anæsthesia on the opposite side, in consequence of the decussation of the sensory fibres in the cord. At 16, by disease of the cord in the lower cervical and upper dorsal regions, involving both sides, there would be paraplegia, with increase of reflexes in the paralysed limbs and anæsthesia below the lesion. At 17, in the lumbar region, there would be paralysis with abolition of reflexes and anæsthesia. At 18, supposing the lesion to involve one lateral half of the cord, there would be paralysis of the right leg and anæsthesia of the left leg.

Chap. VIII.—THE NERVOUS SYSTEM AS A WHOLE.

The functions of the nervous system have now been described; but they are so complicated and so closely related to each other as to make it no easy matter to form a conception of the system working as a whole. The progress of discovery naturally tends to differentiation, and to the attaching of undue importance to one organ as compared with the others, so that we are in danger of losing sight of the solidarity of the whole nervous system. Probably every nervous action, however minute and evanescent, affects more or less the entire system, and thus there may be an under-current of nervous action streaming into and out of the nerve centres, along with a series of interactions in the centres themselves, contributing to, and accounting for, the apparent continuity of conscious experience. No one doubts that consciousness has an anatomical substratum, but the problem of the relation between the two is as far from solution as in the days when little was known of the physiology of the nervous system. Consciousness has been driven step by step upwards until now it takes refuge in a few thousand nerve cells in a portion of the grey matter of the cortex of the brain. The ancients believed that the body participated in the feelings of the mind. As science advanced, consciousness took refuge in the brain, first in the *medulla* and lastly in the cortex. But supposing we were able to understand all the phenomena—chemical, physical, physiological—of this intricate ganglionic mechanism we should be no nearer a solution of the problem of the connection between the objective and subjective aspects of the phenomena. It is no solution to resolve a statement of the phenomena into mental terms or expressions and to be content with the idealistic theory of cognition; nor is it any better to resolve all the phenomena of mind into terms describing physical conditions, as is done by those who support the materialistic hypothesis. A philosophy that recognizes both sets of phenomena, mutually adjusted and ever interacting, recognizes facts, and does not delude the mind by offering a solution which is no solution at all. The difficulty is somewhat lessened if we assume that behind all physical and mental phenomena there is a metaphysical essence, conscious or unconscious, and that those phenomena we term physical and mental are only different sides of the same thing. Such an essence can never be known to science, and the discussion of its possible existence and of its properties belongs to the province of philosophy.[1]

Apart from the ultimate question, however, there is the important one whether physiologists are right in relegating consciousness entirely to the grey matter of the brain. The facts of comparative physiology are against such an exclusive notion, because we cannot deny consciousness to many animals having rudimentary nervous systems. As already said, research in anatomy and physiology and the observation of disease have driven physiologists to adopt the view that the brain is the organ of sensation. This is no doubt true in the sense that it ultimately receives all those nervous impressions that result in consciousness; but the parts transmitting the nervous impressions are in another sense as much concerned in the production of conscious states as the brain. This view of the matter was urged by Cleland in 1870,[2] and is consistent with the facts of nervous physiology. It presents fewer difficulties than the one generally held, which drives consciousness into the recesses of the nerve cells in the cortex of the cerebral hemispheres. It keeps clear of the prevailing error in the philosophy of modern physiology—that of regarding the body and even the nervous system as a vast series of almost independent organs, losing sight of community of function and interdependence of parts.

The simplest morphological nervous unit is a cell, A, with a fibre passing to it from a specialized cell, B, on the surface of the body, and another fibre passing from it to a contractile cell, C. A stimulus applied to B causes molecular changes in it, which result in the transmission of an impulse to A, in which molecular changes again occur, resulting in

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[1] Von Hartmann, *Philosophy of the Unconscious*, especially vol. iii.

[2] Cleland on *Evolution, Expression, and Sensation*, Glasgow, 1881, p. 106.

the transmission of an impulse to C. Suppose the same kind and degree of stimulus be applied to A many thousand times in succession, we can imagine that its molecular structure will become so modified that it will gradually become more and more responsive to stimuli of this kind, the simple mechanism becoming attuned to the movements of the outer world. Here we have then a molecular condition associated with the first dawn of consciousness, and the attuned condition of the structure is the beginning of memory. No doubt it is impossible here, as in dealing with complex brain structure, to form any conception of the nature of consciousness. It evidently cannot be the result, in any physical sense, of the molecular changes in the cell, because even although we were cognizant of all the molecular changes, we could not detect a conscious state, as this can only be recognized by some outward manifestation in the form of movement. Suppose a, b, c, d, e, etc., to represent links in the chain of physical phenomena between the irritation of the cell, B, and the movement of C, and that consciousness is an attribute of A, which we may call x, it will be impossible to find a place for x in the chain, in the same sense as the movement of C is the last link of the chain. It cannot come in between a and b, as a is the physical antecedent of b, nor, for a similar reason, between b and c, or c and d, d and e, etc. The condition x is therefore outside the physical chain, and yet it is related to it, so that if the chain a, b, c, d, e, etc., did not exist, neither would x exist. Nor do we get any farther into the mystery if we suppose that even dead matter has in some way associated with it units of consciousness, because it is equally impossible there to understand the nexus between the material particles and consciousness. The condition of the conscious state may therefore be better represented by two parallel curves, infinitely close in contact, the one representing the chain of physical phenomena, the other the chain of conscious states. Any variation in the one occurs along with a variation in the other, but no explanation can be given of how the one influences the other. To assert that the one is the cause of the other is simply to beg the whole question. If we say that the chain of physical phenomena is the cause of the conscious states in the same sense as the physical phenomena in a hepatic cell are the cause of the secretion of bile, we introduce into the chain an immaterial something and break the physical continuity of the various links, and if we think to escape the difficulty by translating the physical links themselves into states of consciousness, and practically deny the existence of the physical substratum, we are deceived by a jargon of words and reach no solution. Again, to regard consciousness as a mode of energy is absurd. Energy, in the physical sense, is nothing more than the power any material system has of doing work, owing to the relative positions of its component parts. If the position of these parts be altered, the distribution of energy in the system will also be altered. It follows from this that energy may be manifested by various kinds of movements—heat, light, electricity, gravitation, etc—and one form may be resolved into another. But when motion produces heat, there is a quantitative conversion of energy from motion to heat, which is, in turn, another mode of motion. If we now assume molecular changes to be the cause of consciousness, these molecular changes also produce heat, molecular movements associated with chemical action, and perhaps movement, but the sum of these resultant forms of energy is equal to the energy at first existent in the physical system, which we assume to be also the seat of consciousness. Consequently consciousness does not come into the dynamical chain : it cannot be measured, it cannot be derived from the physical energies, nor can it be resolved into them. It is outside the chain. Movements of matter, therefore, cannot be resolved into consciousness, or in other words, consciousness is not a form of energy. We are thus face to face with an insoluble problem, even when we discuss it in its simplest form, and it becomes infinitely more complicated when we consider the manifold phases of consciousness connected with the mechanism of the brain of man. If, however, we begin with the morphological unit of a simple reflex mechanism, along with its associated conscious state, we find that the complex functions of the fully developed brain are really aggregations of the simple mechanism we have considered, and that what we term consciousness is a condition which is the sum of the conscious states of the individual nerve cells, or aggregations of nervous matter, constituting the brain. We can form no conception of the nature of the consciousness of a ganglionic nerve cell any more than we can of the consciousness of a sea anemone or a worm, but we must assume the existence of consciousness in a ganglionic nerve cell, otherwise it is impossible to understand how consciousness is associated with an aggregation of such cells, constituting a brain. To deny consciousness to such a cell would be equivalent to denying consciousness to the brain, which would be absurd. Whilst, therefore, we give up the explanation of consciousness as an insoluble problem, it is possible to obtain some insight into the general mode of action of the brain. For example :—

Suppose we irritate the skin of the sole of the foot, an impression is carried by nerves to cells in the posterior horns of grey matter in the spinal cord, in which molecular processes are excited. From these, impressions are carried by fibres in the cord to cells in the anterior horn, in which, again, molecular processes occur, resulting in the transmission of nervous impulses along motor nerves to the muscles of the limb, and the limb is drawn away by a sudden contraction of the muscles. This is a reflex movement, not connected with volition, not connected with consciousness, so far as the activity of the brain is concerned, but still we may assume that these molecular changes in the cells of the cord are associated with a lower form of consciousness, such as exists in animals having a nervous system of this simple type. But the cells in the grey matter of the cord are connected with cells in the masses of grey matter of the upper centres, and, in particular, we have every reason to believe that each unit area of sensitive surface of the body has a corresponding unit area in the cerebral cortex, that is to say, from each unit area (the size of which varies much in different parts of the body), nerve filaments pass, which carry impressions to a corresponding unit area in the cortex. This does not mean that individual nerve fibres pass from unit area of surface to unit area of cortex, but that impressions are so related. If so, the irritation of the skin of the foot, in the experiment we are considering, may cause impressions to travel to the brain, and the result will be a feeling of pain. Here the sensation of pain is associated with molecular changes in the cells of the cortex, and, as a rule, these changes cause the reflex transmission of impressions outwards to other nerve centres, which, and in turn, call forth various movements. . Thus, they may be carried to the cells in the grey matter of the medulla, which is the seat of the nerves governing the movements involved in crying, contraction of the muscles of the face, or to the cells in the grey matter of the cord, calling forth movements of the limbs for drawing the limb away from the irritation, or for defending it from attack. Again, the irritation may call forth involuntary exclamations, in the form of words, such as "Oh! that is painful," etc., and in this case the centre for articulate speech has been involved. Impressions may also be carried from the sensory centre in the cortex to the parts of the brain concerned in volition, and the reflex and involuntary movements we have considered will be added to, or supplanted by, direct voluntary movements. Even voluntary movements, however, are essentially reflex in character, inasmuch as they are called forth by stimulations which have been applied either immediately before the voluntary act, or which have been applied, it may be, long before. In the latter case, the effects of the stimulation have been left in certain groups of nerve cells, as a kind of memory, so that when they are roused into activity, the voluntary act will follow, as it did in the first instance. Finally, the irritating body applied to the foot may be *seen*, and the effects of the image formed optically on the retina are carried by the optic nerve to the *corpora quadrigemina*, and by these to the optical centres in the cortex. Again, a memory of this impression may remain, and may be called into action by nervous impressions coming from other parts of the brain, so that a vision of the irritating body may afterwards arise into consciousness, so vividly as to call forth movements similar in character, although, probably, not so intense, as those which occurred in the first instance.

Sensory impressions, however, may not only be carried to the cerebral cortex, there awakening consciousness, but it is highly probable they may be conveyed to the cerebellum, and in this organ they may set into action the physiological mechanism that results in co-ordinated movements. It is not improbable that the sensory areas of the body have corresponding areas on the grey surface of the cerebellar convolutions, just as they have areas on the grey matter of the cerebral convolutions. Thus we may imagine the cerebellum to be the organ of all the movements of the limbs that are rhythmic in character, and that it is only when those movements become associated with sensation or are voluntary that the cerebrum comes into play.

If an external object acts at the same time on different organs of sense, the various sensations thus related to molecular movements in different parts of the cortex are combined by the action of the numerous fibres passing from centre to centre, and the result is a consciousness of the thing as a whole. These fibres may be termed *fibres of association*, because they combine impressions that have reached various cortical centres. It is evident that such a combination of impressions may also give rise to various movements of the limbs, or of the muscles of expression, and that the impressions will be more or less vivid, as the exciting causes are strong or weak. If the impressions are vivid, or, in other words, if the molecular changes in the nerve cells of particular parts of the cortex of the brain are intense, they will have both a tendency to last after the exciting cause has been removed, and a tendency to be renewed by a slighter stimulus than was at first necessary to produce them. This is an organic foundation for what we term memory, and also for the mental process known as the association of ideas. Again, if such molecular processes, by long repetition, become so intimately related to the structure of particular parts of the cerebral cortex, as to be transmitted according to the laws of heredity, then we have a physiological basis for so-called intuitions, or intuitive tendencies. One brain differs from another in this respect. The greater the number and variety of impressions made on an individual, the greater will be the number and variety of the molecular movements in the cells of the cortex, and the greater the number and variety of resulting reflex phenomena. So intense may these processes be that they may be called into action by a stimulus from another part of the brain, as when irritation of the *corpora quadrigemina* by Indian hemp awakens in the cells of the visual centres of the cortex those changes which are associated in the mind with long forgotten visual impressions, and the person sees passing before him a phantasmagoria of brilliantly-coloured images. They may also arise apparently spontaneously. Spontaneity, however, is probably dependent on a stimulus so feeble as to escape notice, as when the sight of an object suddenly and almost unconsciously awakens memories of past events, and brings before the mind's eye forms and colours that long before produced impressions on the organs of sense.

It is important to observe that many nervous phenomena are at first in a sense voluntary, and that by and bye they become more and more reflex, and less and less associated with the higher consciousness. Thus the child acquires powers of walking by repeated efforts involving volition, judgment, and perception of different impressions, but the movements of walking may be unconsciously performed by an adult. Familiar examples also are seen in the unconscious dexterity of movement of a skilful performer on a musical instrument, or in the deft movements of a cunning artificer. So is it even with psychical operations involving the action of the brain, and the brain cortex may, as in unconscious cerebration, pass through molecular processes which result in the unconscious performance of what would be termed mental processes, if the person were conscious. Many instinctive actions are probably unconscious in this sense. There can be no doubt that even in man the brain may work unconsciously, and the product may suddenly start out into consciousness.[1]

Facility of mental acquirement means a certain receptiveness for particular kinds of molecular movement. Other personal factors come into operation, such as the power of choice of particular impressions, the degree of attention paid to them at the time, the degree of stability of the molecular movements after they have been excited, and the power of association of different impressions. Each of these factors has a physiological basis peculiar to each individual. They are susceptible of being extended and strengthened by exercise, and just as muscular exercise causes a

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[1] Maudsley, *Physiology of Mind.* See also Von Hartmann, *op. cit.* vol. iii. p. 253.

development of muscular fibre, so regulated mental exercise will develop and strengthen the tissue (cell and fibre) of the brain. To sum up, we hold that one man differs from another in the primitive constitution of his nervous centres. This determines his degree of intelligence, power of accurate judgment, and aptitude for special kinds of work. These qualities seem to be determined chiefly by inheritance from ancestors who have thus given their descendant a groundwork of mental character. In the next place, the influence of a man's environment develops to a greater or less extent this and that faculty. This is the rational basis of all educative processes. Again, the degree of excitability of the nerve centres varies considerably among individuals, and it also may be influenced by exercise. On this depends the aptitude for reflex acts of all kinds. Lastly, there may be a greater or less influence exerted by the higher over the lower centres, or, in other words, a greater or less degree of inhibitory power. The power of the will, which may also be strengthened by exercise, depends on this factor.

The aberrations of an insane mind also rest on a physiological basis. Nothing is more certain than that mental disorders are always associated either with organic changes in the brain or with perverted functions. Hæmorrhages, softenings, degenerations, affect the mind in all its phases, producing the torpor, difficulty of comprehension, slowness of response, incoherence and depression of the melancholic, or the wild delirium, hallucinations, and delusions of the maniac. It may not always be easy to detect the morbid changes in the brains of the insane, but the progress of cerebral pathology has shown that these can be detected if the methods are adapted to the object in view. No doubt it is true that little, if any, correlation can at present be established between the particular form of mental derangement and the pathological lesion, but this does not vitiate the statement that all forms of mental disease are invariably associated either with organic alterations in brain structure or with perversion of function, or, in other words, with the normal nutrition of the cerebral elements.

CHAP. IX.—THE CIRCULATION IN THE BRAIN.

A due supply of healthy arterial blood and the removal of venous blood are essential to cerebral activity. The brain is contained in an osseous case of which the total capacity is variable. The cerebral substance undergoes almost insignificant changes of volume even under a pressure of 180 mm. of mercury. The quantity of blood in the cranium may vary, but it rarely exceeds 1 or 2 per cent. of the total quantity of blood in the body. If a small round window be made in the cranium and a suitable piece of glass fitted into it, the veins of the *pia mater* may be observed to dilate or contract if intermittent pressure be made on the veins of the neck. There is evidently, then, within the cranium some arrangement by which such variations become possible. This is probably accomplished by the anatomical arrangements of the sub-arachnoid spaces. These spaces, containing fluid, communicate freely with each other and with the space surrounding the spinal cord, so that when the quantity of blood increases in the cranium a corresponding quantity of fluid escapes into the spinal space, the walls of which are not inextensible like those of the cranium. In young children, before the fontanelles are closed, the variations of circulation and blood pressure cause pulsations, of which there are two kinds—those coinciding with the ventricular systole, produced by the pulsation of the arteries at the base of the brain, and those coinciding with inspiration and expiration. During inspiration, the fontanelle rises, and during expiration it falls, in consequence of the rise and fall of blood pressure in these movements respectively (see Fig. 259, p. 397, Vol. I.). About 100 grms. of *cerebro-spinal fluid* may be obtained from an adult. The fluid during life is under a pressure greater than atmospheric pressure, so that after trephining a portion of the skull and removing the underlying *dura mater*, there is a hernial-like protrusion of the arachnoid at the orifice. Pressure on the brain substance beyond a certain limit leads to paralysis, unconsciousness, and death. The large sinuses assist in equalizing internal pressure, and, as inspiration favours the flow of blood from the sinuses, too great distension of these is also avoided. An insufficient supply of blood to the brain causes fainting, weakness, sickness, and *tinnitus aurium*. If these symptoms occur in a weakly person while standing, they may disappear when he takes the recumbent position, owing to more blood flowing to the brain. Ligature of both carotids and both vertebrals causes epileptiform convulsions, similar in character to those of profuse hæmorrhage. These are due to increased venosity of the blood. Vaso-motor nerves regulate the calibre of the arterioles of the brain, but we know nothing of the conditions affecting the nerves. Nor do we know how the waste products of the brain are got rid of. There are no lymphatic vessels, but there are spaces around many of the blood-vessels. These probably communicate with the cavities in the membrane containing the cerebro-spinal fluid, the value of which depends more on its physiological properties as lymph than on its hydrostatic properties as a fluid.

The brain receives blood from the vertebral and internal carotid arteries. The two vertebral arteries unite to form the basilar artery, which in turn gives off the two posterior cerebrals. The internal carotid, close to the outer side of the optic commissure, divides into the anterior and middle cerebral arteries, and the circle of Willis is completed by the posterior communicating arteries passing from the anterior to the posterior cerebral arteries. The middle cerebral, shown in Fig. 280, is of special importance, inasmuch as by its perforating branches, it supplies blood to the *corpus striatum* and to the anterior part of the *thalamus opticus.* The main artery divides into secondary and tertiary branches, ramifying on the *pia mater* till they become of very minute calibre, when they pass into the grey matter of the cortex, as shown in Fig. 279. Some of these so called *medullary* arteries enter on the free surface of a convolution, while others pass obliquely into the sides of the convolution, each showing from 12 to 15 arteries. In addition to these, still more minute vessels (*cortical nutritive arteries*) pass from the *pia mater*, a short distance into the most superficial web of grey matter. The nature of the plexus is shown in the Figure.

Fig. 279.—Injected convolution of cerebrum. 1, 1, medullary arteries; 1′, group of medullary arteries in fissure between two neighbouring convolutions; 1″, arteries of system of arcuate fibres; 2, 2, 2, arteries of grey substance of cortex; *a*, large-meshed capillary network situated under *pia mater*; *b*, smaller-meshed capillary network situated in middle layers of cortex; *c*, somewhat larger network in internal layers adjoining white substance; *d*, capillary network of white substance. (Duret.)

The arteries carrying blood into the central parts of the brain come from the trunks of the chief cerebral vessels at the base, and they pass vertically upwards. As shown by Charcot, a circle 20 mm. from the vessels forming the circle of Willis surrounds all these vessels, and the space enclosed in the circle is the *vascular ganglionic area.* Some of these vessels are shown in Fig. 280.

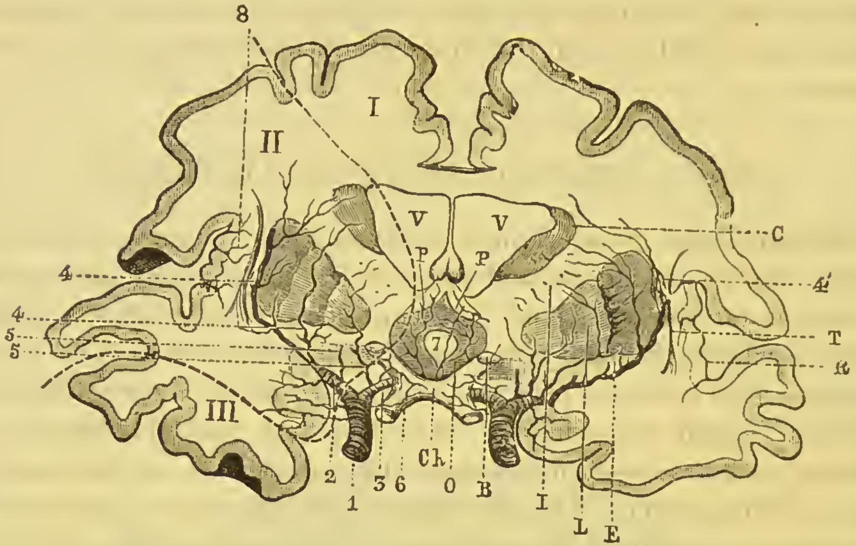

FIG. 280.—Transverse section of the cerebral hemispheres, about 10 mm. behind the optic commissure, showing the position of the vessels. *Arteries of the corpus striatum.* Ch, *chiasma*; B, section of optic tract; L, lenticular nucleus; I, internal capsule; C, caudate nucleus; E, external capsule; T, *claustrum*; R, island of Reil; V, V, section of the lateral ventricle; P, P, anterior pillars of *fornix*; O, grey substance of the third ventricle.

Vascular areas. I, anterior cerebral area; II, middle cerebral area; III, posterior cerebral area. 1, internal carotid artery; 2, Sylvian artery; 3, anterior cerebral artery; 4, 4, external arteries of the *corpus striatum*, or the lenticulo-striate artery; 5, 5, internal arteries of the *corpus striatum*, or the lenticular arteries. (Duret.)

The more important of these are derived from the middle cerebral as follows:— 1) The *lenticulo-striate* artery runs along the outer surface of the lenticular nucleus, supplies the anterior part of the internal capsule, and passes into the caudate nucleus (Fig. 280, 4, 4). A rupture of this vessel is frequently the cause of cerebral hæmorrhage, when a clot forms between the lenticular nucleus and the external capsule, and Charcot has named it *l'artère de l'hémorragie cérébrale.* (2) The *lenticulo-optic* artery, like the one first described, passes along the outer surface of the lenticular nucleus, supplies the posterior part of the internal capsule, and ends in the *thalamus opticus.* (3) *Lenticular* branches (Fig. 280, 5, 5) are minute vessels entering the lenticular nucleus, sending twigs also to the caudate nucleus. (4) The *inferior* arteries of the *thalamus opticus* are minute vessels, supplying the inner surface of the *thalamus* and the walls of the third ventricle, and they are ruptured when blood is found in this cavity. (5) The *posterior* arteries of the *thalamus opticus* enter the thalamus near the inner border of the cerebral peduncle, and are ruptured when hæmorrhage occurs on the peduncle.

E.—THE FUNCTIONS OF THE PERIPHERAL NERVES.

Nerves originate from centres in the spinal cord and brain, and ramify throughout the body. To distinguish them from the nervous tracts which unite portions of the nerve centres, they are termed *peripheral*, and are classed as spinal, cranial, and sympathetic. In many classifications, the sympathetic nerves are kept distinct from the cerebrospinal; but it will be seen that there are intimate connections between the two.

CHAP. I.—FUNCTIONS OF THE SPINAL NERVES.

The spinal cord gives origin to thirty-one pairs of nerves, each nerve having two roots, *anterior* and *posterior*, the latter being distinguished by its greater thickness, and by the presence of a ganglionic enlargement, in which are found numerous bi-polar nerve cells. The fibres of the two roots unite to form the common trunk of a nerve at a short distance beyond the ganglion. The discovery that the fibres of the anterior root are *motor* and those of the posterior *sensory* was made by Charles Bell in 1811. This discovery was founded upon an experiment in which he ascertained that irritation of the anterior roots of the spinal nerves in an animal shortly after death caused contractions of muscles, whilst irritation of the posterior roots produced no effect. In 1822, Magendie showed that irritation of the posterior roots caused pain. Irritation of the peripheral end of the anterior root, however, may also cause pain. These indications of pain may continue after division of the mixed nerve beyond the fusion of the roots, but they cease at once on division of the posterior root. From this it has been inferred that a few sensory fibres coming from the posterior root form a loop into the anterior root, and then pass along the mixed nerve. By applying the method of Waller, these looped fibres have been traced by degeneration occurring after separation from the ganglion.

The posterior root contains afferent fibres, both somatic and splanchnic, and the ganglion is stationary and always near the central nervous system; and the anterior root contains (1) efferent non-ganglionic, splanchnic, and somatic fibres, and (2) fine efferent ganglionated splanchnic fibres, the ganglion of which may be a considerable distance from the central nervous system (Gaskell).

CHAP. II.—FUNCTIONS OF THE CRANIAL NERVES.

These are so named from their passing through foramina in the base of the cranium. They are arranged according to different systems, as follows:—

Willis.		Physiological Name.	Soemmering.
First pair,		Olfactory,	First pair.
Second ,,		Optic,	Second ,,
Third ,,		Oculo-motor,	Third ,,
Fourth ,,		Pathetic,	Fourth ,,
Fifth, ,,		Trifacial,	Fifth ,,
Sixth ,,		Abducent-ocular,	Sixth ,,
Seventh ,,	*portio dura*	Facial,	Seventh ,,
	portio mollis	Auditory,	Eighth ,,
Eighth, ,,		Glosso-pharyngeal,	Ninth ,,
		Pneumogastric or vagus,	Tenth ,,
		Spinal-accessory,	Eleventh,,
Ninth ,,		Hypoglossal,	Twelfth ,,

Of these, three are exclusively connected with special sensation, namely, the olfactory, optic, and auditory. Two are nerves of common, and partly also of special, sensation, and are combined with motor fibres close to their origin, namely, the 5th and 8th; the 5th having a motor root of its own, and the 8th receiving motor fibres from the spinal-accessory and from the roots of the pneumogastrics. The remaining nerves are all nearly exclusively motor, but some, more especially the facial, are combined with sensory fibres in the course of their distribution.

Gaskell divides these nerves into two groups:—(1) Four fully developed segmental nerves which have lost some of their original components, the parts supplied by the missing portions having ceased to be of functional importance. These are—the 3rd, 4th, 6th, and motor part of 5th, and the 7th. (2) Five segmental nerves, which have become split into various parts to make good the loss of the parts, the absence of which caused a degeneration of nerves in the first group. These are the 9th, 10th, 11th, and 12th, and the sensory part of the 5th. This group has a wide distribution, having both somatic and splanchnic peripheral nerves. Excluding the optic, olfactory, and auditory, the cranial nerves constitute a series of segmental nerves on the same type as those of the spinal region.[1]

1. **The Olfactory Nerve.**—This structure originates by three roots coming from the frontal lobe, the anterior white commissure, and the sphenoidal lobe. From the olfactory bulb, branches pass through the cribriform plate of the ethmoid bone to ramify in the mucous membrane of the nasal fossæ. The olfactory is the nerve of smell. After its destruction the animal cannot perceive odours, but it is still sensible to irritating vapours such as ammonia.

2. **The Second or Optic Nerve.**—The optic has three roots: (1) an *anterior*, coming from the posterior part of the *thalamus opticus*, termed the *pulvinar*; (2) a *middle*, from the *corpus geniculatum ex-*

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[1] Gaskell, "The Cranial Nerves." *Jl. of Physiology*, April, 1889.

ternum, and the anterior body of the *corpora quadrigemina;* and (3) a posterior, from the *corpus geniculatum internum* and the posterior body of the *corpora quadrigemina.* The three roots form the *optic tract*, and the two optic tracts, unite to form a commissure, the *optic commissure.* This is the nerve of vision. Section is followed by blindness. Irritations of any kind excite luminous sensations. The fibres are insensible to the direct action of light, and only respond to impressions received from the retina.

3. **The Third or Oculo-Motor Nerve.**—The oculo-motor, or third, arises from the grey matter immediately above the aqueduct of Sylvius (*iter a tertio*, etc.), near the origin of the 4th. It passes from the inner border of the peduncle, at the level of the *locus niger*, and, towards its termination, ends in two branches: (1) an *upper*, supplying the *rectus superior* and the *levator palpebræ superioris;* and (2) a *lower*, supplying the *rectus internus*, the *rectus inferior*, the *obliquus inferior*, the circular fibres of the iris, and the ciliary muscle. The lower branch sends a nerve to the ciliary ganglion. The 3rd nerve is also related to the posterior part of the parietal lobule on the opposite side. It is a motor nerve, supplying filaments to all the muscles of the eyeball, with the exception of the *rectus internus* and *obliquus superior.* It also supplies the circular fibres of the iris (*sphincter iridis*), and the ciliary muscle. Division of the nerve at its root causes paralysis of the muscles supplied by it; the upper eyelid hangs down and cannot be raised in consequence of paralysis of the *levator palpebræ superioris*, and the eyeball is drawn downwards and outwards by the action of the *rectus externus* and *obliquus superior.* There is also dilatation and immobility of the pupil. The power of accommodating the eye is also lost. When the two nerves are intact, the optic axes converge so as to secure binocular vision; paralysis causes divergence of the optic axis on the paralysed side, and there is double vision, the image on the affected side being higher than on the other, and crossing it.

4. **The Fourth or Pathetic Nerve.**—This nerve originates near the root of the 3rd, already described. Its fibres cross and appear on the upper peduncles of the cerebellum. It supplies the *obliquus superior*, and it determines the rotation of the eye by which the pupil is carried downwards and outwards. In paralysis of this nerve the head is turned obliquely and to the paralysed side, to obviate the effects of squinting. After division, the pupil is directed upwards and to the side by the *obliquus inferior.* In these circumstances there is double vision.

5. **The Sixth or Abducens Nerve.**—This nerve originates about the middle of the floor of the 4th ventricle, and it emerges between

the *medulla oblongata* and the *pons Varolii.* It supplies the *rectus externus* alone. When the nerve is divided the eye is pulled inwards, and irritation of the nerve causes the eye to be rotated, so that the pupil is directed obliquely outwards.

We may here consider the relation of the 3rd, 4th, and 6th nerves to the movements of the eyeball. The eyeball is supplied by six muscles, as shown in Figs. 281 and 282, the four *recti* and the two *obliqui*, and the upper eyelid is raised by the *levator palpebræ superioris.* Including the eyeball, no fewer than seven pairs of nerves are concerned in the optical apparatus.

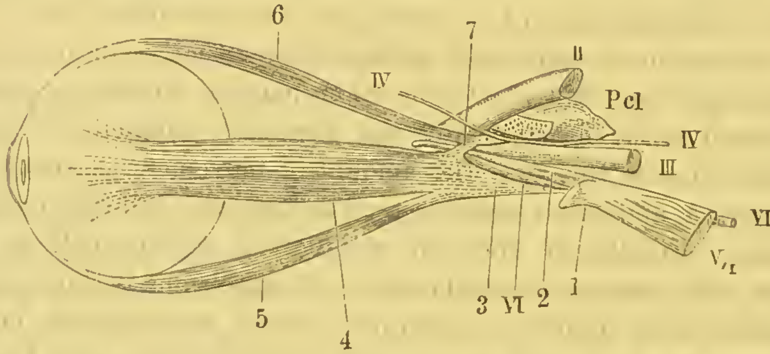

FIG. 281.—Muscles of the left eyeball seen from the side. Natural size. II, optic; III, oculo-motor; IV, the pathetic or 4th; V_1, ophthalmic; VI, abducens or 6th; Pcl, anterior clinoid process of sphenoid; 1, supra orbital nerve divided; 2, naso-ciliary nerve; 3, tendinous expansion to which the inferior and external recti are attached; 4, external rectus muscle; 5, inferior rectus muscle; 6, superior rectus; 7, one of tendons of external rectus. (Krause.)

(1) *The Eyelids.*—The lids are closed by the action of the *orbicularis palpebrarum*, supplied by the facial or 7th, and if this muscle is paralysed, the eye is partially open, even in sleep (*lagophthalmos*). If there is no other paralysis, the lesion is probably in the cortical origin of the facial on the opposite side; but if there is also paralysis of the other muscles of the face on one side, the trunk of the facial is probably involved. Again, if we have at the same time hemiplegia, the inference is that the fibres of the internal capsule are involved. If the eyelids are half open, from a drooping of the upper lid over the globe, the condition is termed *ptosis*, and it indicates paralysis of the *levator palpebræ superioris,* the 3rd nerve being affected. At the same time,

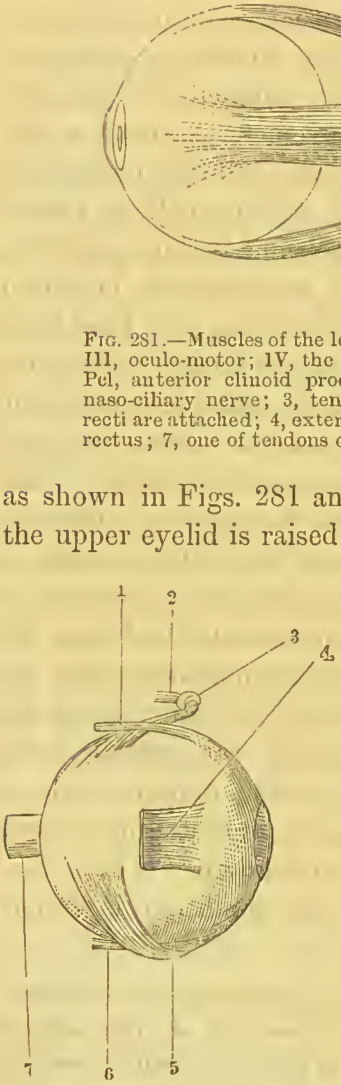

FIG. 282.—Right eyeball seen from the side. Natural size. 1, rectus superior; 2, tendon of the superior oblique; 3, trochlea or pulley; 4 external rectus; 5, inferior oblique; 6, inferior rectus; 7, optic nerve. (Krause.)

the eyeball will be pulled to the right by the *rectus externus*. In this case, the lesion is in the upper and back part of the parietal lobe.

(2) *The Eyeball.*—As the 3rd nerve supplies all the muscles, except the *rectus externus* and the *obliquus superior*, the action of the muscles supplied by it is to rotate the eyeball internally and upwards. The eyeball is directed downwards and outwards by the *obliquus superior* supplied by the 4th; and outwards by the *rectus externus* supplied by the 6th. If, then, the 3rd be paralysed, the eyeball will be directed more or less downwards and outwards, and there will be divergent strabismus, or squinting. On the other hand, if the 4th is paralysed, the eyeball is carried upwards and inwards, producing convergent strabismus, but in this case the amount of movement is small, as the *rectus inferior* and *rectus externus* tend to keep the ball downwards and outwards. Finally, if the 6th is involved, the eyeball is turned inwards, with convergent strabismus. If strabismus is thus produced, the person sees double, a condition termed *diplopia*, and he either endeavours to avoid this inconvenience by so moving the head as to bring the images on the corresponding points of the retinæ, or he shuts one eye. When both eyes are open, the gait in walking is uncertain and may be accompanied by giddiness. Sometimes a person may turn both eyes either to one side or the other (*conjugated deviation*). This condition is caused, in lesions of the cerebral hemisphere, either by paralysis of certain of the centres of the nerves of the ocular muscles, or by their irritation. If the cause is irritation, as from a tumour or hæmorrhage, the eyes are turned to the side opposite to the lesion, but if it is paralysis, as from extensive cerebral hæmorrhage, they are turned to the same side. On the other hand, if the lesion be in the basal ganglia, we have the reverse arrangement, the eyeballs being turned to the same side in excitation and to the opposite side in paralysis. The oculo-motor centre, governing the associated movements of the eyeballs, is in the ascending frontal convolution. When there are quivering movements of the eyeballs the condition is termed *nystagmus*.

The condition of a person affected by strabismus, caused by cerebral disease, may be investigated by the following experiment: Place a bit of violet-coloured glass before the normal eye, and cause the person to look at a candle flame, at a distance of several yards. He will see two flames, one of which is coloured violet. Ask him to indicate the position of the two flames. With the violet glass placed before the right eye, if the violet image is also to the right of the other image, the images are *homonymous*, and there is convergent strabismus of the left eye; but if the violet flame is to the left of the other, the images have crossed, and there is divergent strabismus of the left eye. In both divergent and convergent strabismus, the separation of the two images increases as we carry the candle in the direction in which the eyeball would have been moved by the paralysed muscle, so that in convergent strabismus the separation increases by carrying the candle towards the paralysed side, while in divergent strabismus it increases as we carry the candle to the sound side. When the diplopia is due to the paralysis of the 4th, the two images are never seen below the horizontal, but they are seen everywhere in the field of vision when the paralysis is of the 6th nerve. (Spehl.)

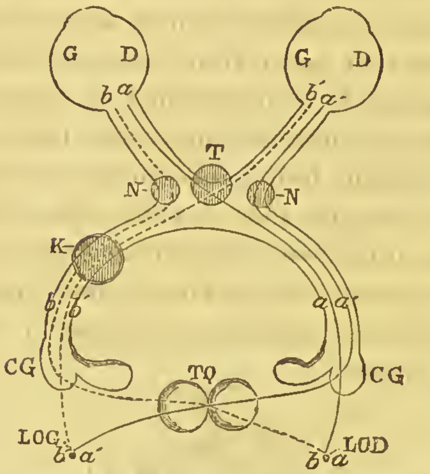

Fig. 283.—Diagram of the decussation of the optic tracts. T, semidecussation in the optic *chiasma*; TQ, decussation posterior to the *corpora geniculata*; CG, *corpora geniculata*; a', b, fibres which do not decussate in the *chiasma*; b'a, fibres which undergo decussation in the *chiasma*; b', a', fibres coming from the right eye which meet in the left hemisphere, LOG; LOD, right hemisphere; K, lesion of the left optic tract, producing right lateral hemiopia; LOG, a lesion at this point, producing right amblyopia; T, lesion producing temporal hemiopia; NN, lesion producing nasal hemiopia. (Charcot.)

Closely connected with the movements of the eyeballs, we have certain conditions of the retina that may be here shortly discussed. If a portion of an optic nerve be the seat of a lesion, there will be blindness of a corresponding part of the retina, and if the nerve were entirely destroyed, there would be complete blindness of the eye supplied by it. Blindness of one half of the retina is termed *hemiopia*, or *hemianopsia*, and it may be monocular or binocular, and internal (nasal) or external (temporal). Thus, an injury to the external half of the right optic nerve would produce right external hemiopia, and so on (Fig. 283). If, however, the lesion were in the middle of the optic commissure, so as to affect only the decussating fibres, the internal half of each retina would be affected, producing binocular nasal hemiopia—a rare condition. The condition is then termed *heteronymous*, that is, non-corresponding parts of the retinæ are affected.

Suppose, again, the lesion to affect the entire optic tract on one side (say the left), there would be blindness of the temporal side of the left eye and the nasal side of the right eye. The affection is then said to be *homonymous*, that is to say, corresponding parts of the two retinæ are affected. If the lesion affected the fibres which had not decussated in the *chiasma* (as at T Q), the external or temporal regions of both retinæ would be affected, the condition being binocular temporal hemiopia. Finally, if the lesion occurred in the cortical centre of vision (say, on the right side), the effect would be the loss of vision on the temporal side of the right eye and the nasal side of the left eye, or homonymous hemiopia. This condition always indicates a central lesion of the hemisphere on the side corresponding to the outer half of the retina that has lost sensibility. According to Charcot's diagram shown in Fig. 283, all the fibres of the left eye reach the right hemisphere and *vice versâ*. Lesion of the cerebral centre causes complete blindness of the opposite eye, while lesions of the *corpora quadrigemina*, *corpora geniculata*, or optic tracts, cause partial blindness or hemiopia. As pointed out by Ferrier, however, the arrangement suggested by Charcot is not in accordance with clinical and experimental evidence, which show that hemiopia (and not complete blindness) may occur from lesions of the optical centre in the cortex. It appears to be established by clinical observers that a lesion of the cortex may produce amblyopia, that is, blindness of one eye on the side opposite the lesion and dimness of the visual field on the same side. Each occipital lobe is thus related to both retinæ, to the half of each retina on its own side, and each angular gyrus is related to the centre of the opposite eye by fibres which have decussated in the optic chiasma, or by fibres which have crossed in the *corpora quadrigemina* (see p. 531). (Ferrier.)

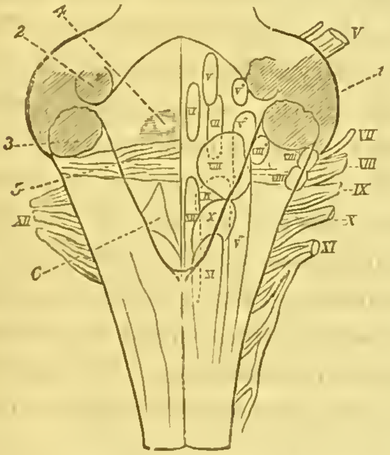

Fig. 284.—Posterior surface of medulla or floor of the 4th ventricle. The numerals indicate the positions of the nuclei from which the cranial nerves originate. *V*, motor nucleus of 5th; *V′*, median, and *V″*, inferior, sensory nuclei of 5th; *VI*, abducens, or 6th; *VII*, facial; *VIII*, posterior median root of auditory, or 8th; *VIII′*, anterior median, *VIII″*, posterior lateral, *VIII‴*, anterior lateral, nuclei of auditory, or 8th; *IX*, glosso-pharyngeal; *X*, *XI*, and *XII*, nuclei of vagus, spinal accessory, and hypoglossal. Nerve roots are indicated at the side by their respective numbers. (Erb.)

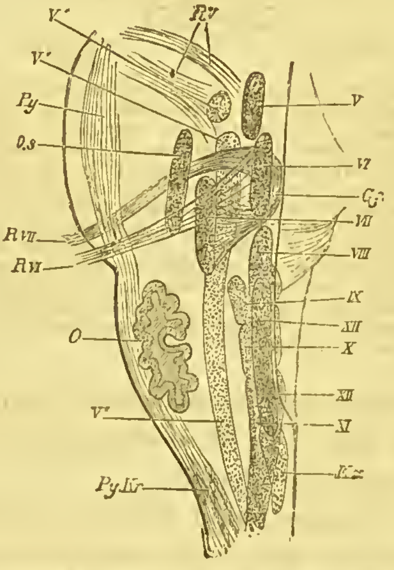

Fig. 285.—Lateral view of medulla, the right half being seen as if it were transparent, and the parts nearest to the right half are most deeply shaded. *Py*, pyramidal tract; *Py*, *Kr*, decussation of pyramids; *O*, olivary body; *Os*, upper olivary body. Numerals represent the roots of the cranial nerves, according to their number. *Gf*, genu facialis, or bend of fibres of the 7th. (Erb.)

6. The Fifth or Trifacial Nerve.—The trifacial originates by two roots, a large sensory root springing from the grey matter in the *medulla*, representing the posterior cornua of the cord, and a short motor root, coming from nuclei of grey matter, representing the anterior cornua (Figs. 284 and 285). This nerve consists, at its origin from the side of the *pons Varolii*, of two portions of unequal size, the smaller being the motor portion, whilst the larger, having on it the Gasserian ganglion, is sensory. The smaller or motor root unites with one of the three large branches given off by the posterior root, so that of the three main divisions which separate from each other beyond the ganglion, the ophthalmic and superior maxillary division are sensory, whilst the inferior maxillary part is senso-motor. Section of the larger root causes loss of sensation in the cutaneous and mucous surfaces of the head and face, in the salivary and lachrymal glands and teeth, and loss of taste as well as loss of tactile sensibility on the tip of the tongue. After section, an animal has difficulty in mastication from loss of sensibility.

The three branches are :—(A) The *ophthalmic* division, or *nerve of Willis*, is sensory and supplies (*a*) the skin of the forehead, the eyebrow, the upper eyelid, the root and lobule of the nose ; (*b*) the palpebral and ocular conjunctiva, the mucous membrane of the lachrymal passages, the frontal sinuses, the upper part of the nasal mucous membrane ; (*c*) the cornea, the iris, the choroid, and the sclerotic ; (*d*) the periosteum and bones of the frontal, orbital, and nasal regions ; and (*e*) muscular sensibility to the intra-orbital muscles. It also influences the secretion of the lachrymal gland. It contains the fibres from the sympathetic governing the radiating fibres of the iris, and also the vaso-motor fibres for the iris, choroid, and retina. It is associated with the otic ganglion. (B) The *superior maxillary* division of the 5th furnishes sensory branches to (*a*) the skin of the lower eyelid, alæ of the nose, upper lip, and skin covering the malar bone; (*b*) the mucous membrane of the nasal, pharyngeal, and palatine regions, the maxillary sinuses, the gums, the upper lip, and the Eustachian tube ; (*c*) the periosteum of the bones corresponding to its distribution ; and (*d*) the teeth of the upper jaw. It furnishes filaments to the nasal and palatine glands, and probably to the glands of the *velum palati*. It contains vaso-motor fibres from the sympathetic for the vessels, and is associated with the spheno-palatine ganglion. (C) The *inferior maxillary* divison of the 5th contains sensory branches to (*a*) the skin of the cheeks, temples, lower lip, chin, front part of the ear, and external auditory canal ; (*b*) the mucous membrane of the cheeks, lips, gums, front part of the tongue, the mucous membrane of the tympanum, and the mastoid cells ; (*c*) the periosteum of the lower jaw and temporal bones ; (*d*) the teeth of the lower jaw ; (*e*) the temporo-maxillary articulation ; and (*f*) the muscles in the neighbourhood (muscular sensibility). It thus exercises an influence on taste, hearing, and secretion. It contains vaso-motor fibres for the blood-vessels.

The fibres of the small root of the 5th innervate the temporal, masseter, two pterygoids, the anterior belly of the digastric, the mylo-hyoid, and *circumflexus palati*. A filament passes also from the otic ganglion to the *tensor tympani*.

Section of the nerve on one side causes the jaw to be pulled to the sound side, so that the superior and inferior teeth do not correspond.

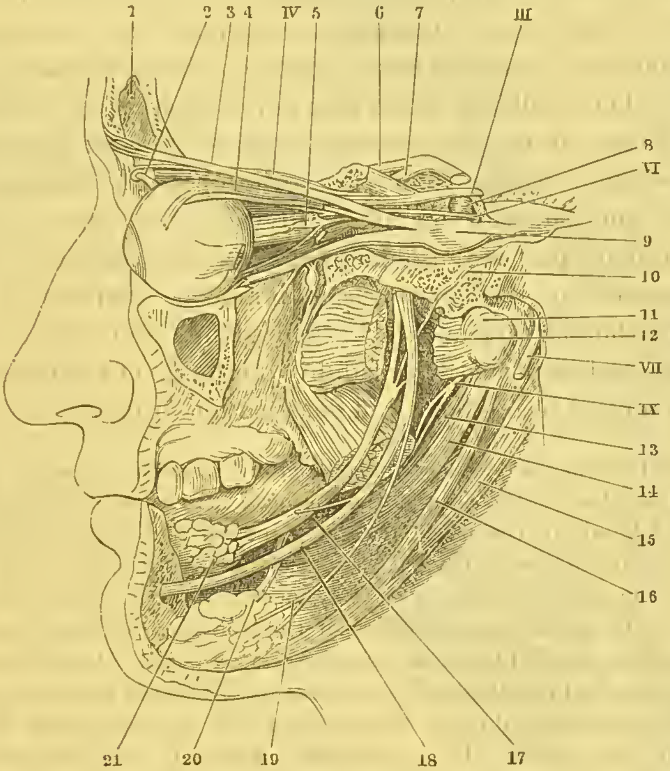

FIG. 286.—The fifth nerve. Half natural size. 1, frontal sinus; 2, tendon of superior oblique muscle passing round the pulley; 3, frontal nerve, the naso-ciliary branch has been cut; 4, levator palpebræ superioris muscle; IV., trochlear nerve; 5, ciliary ganglion, showing ciliary nerves running from it forwards; 6, right optic nerve; 7, left optic nerve, uniting with 6 at the chiasma or commissure; III., oculo-motor or 3rd nerve; 8, internal carotid artery; VI., abducens nerve, or 6th; 9, Gasserian ganglion; 10, chorda tympani, passing to the lingual branch of 5th; 11, condyle of lower jaw; 12, external pterygoid muscle cut so as to expose the chorda and the inferior maxillary nerve; VII., facial nerve, or 7th; IX., glosso-pharyngeal nerve; 13, stylo-pharyngeus muscle; 14, stylo-glossus muscle; 15, posterior belly of digastric muscle passing through 16, the stylo-hyoid muscle; 17, lingual branch of the 5th nerve; 18, inferior maxillary nerve; 19, branch of mylo-hyoid nerve to submaxillary gland; 20, duct of submaxillary gland; 21, sublingual gland. (Krause.)

(*d*) *The Ganglia.*—These are the *ophthalmic*, the *spheno-palatine or Meckel's*, the *otic*, and the *submaxillary*. (*a*) *The Ophthalmic.*—Destruction causes insensibility of the cornea and dilatation of the pupil. The motor fibres supplying the circular fibres of the iris come from the 3rd; the sympathetic also supplies motor branches which act on the radiating fibres of the iris; whilst the 5th furnishes all the sensory fibres. The filaments for the ciliary muscle, in connection with accommodation, also come from the 3rd. (*b*) *The Spheno-palatine* is in connection with the superior maxillary. Extirpation does not cause pain, nor is it followed by alteration in nutrition, nor by modifications in the vascularity of the nasal mucous membrane; smell and taste are also unaffected. The motor fibres


A
VII
H.c.
A.c.i.
A.o.
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F.r.
M.mi
Am
V.III
M.p.i.
XI.
IX
XII.
X
A c.e.
A.p.b.
R.sbm.
A.m.c.
A.l.
A.th.s.
A.c.c.
B
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4
28
31
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IX
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X
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Fig. 287.

of the ganglion are derived from the facial by the great superficial petrosal and the vidian; the sensory filaments come from the 5th; and it also contains sympathetic fibres received from the carotid plexus. (*c*) The *Otic* ganglion is connected with the inferior maxillary. Doubt has arisen as to the origin of its motor root: according to Hyrtl, the motor fibres come from a branch of the inferior maxillary supplying the internal pterygoid muscle; whilst Longet has stated that they are filaments of the facial passing through the small superficial petrosal nerve. The sensory fibres are derived from the glosso-pharyngeal by Jacobson's nerve; and the sympathetic filaments come from the plexus surrounding the middle meningeal artery. The secretory fibres of the parotid gland come from this ganglion, reaching it from the facial through the small superficial petrosal nerve. (*d*) The *Submaxillary* (see p. 58).

7. **The Seventh Pair.**—The seventh pair consists of two nerves, the auditory and the facial. The *auditory* springs from the grey matter in the floor of the 4th ventricle, and it is also connected with the cerebellum. The functions will be considered in connection with hearing. The function of the *facial* is motor. It originates in the deep part of the *pons*, in the *formatio reticularis* at the level of the nucleus of the 6th. The upper end of the nucleus is close to the nucleus of the 5th. The fibres run backwards and inwards to the floor of the 4th ventricle. They curve outwards, passing over the nucleus of the 6th, so as to be external to it, and they then make a sharp bend and pass outwards and forwards to appear at the lower border of the *pons*. The fibres thus decussate in the middle line. Section of the nerve at its root is followed by paralysis of the muscles of the face; the countenance

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FIG. 287.—Diagram showing the sympathetic nervous system in the head. III., oculo-motor nerve; VI., abducens; IV., trochlearis; 1, frontal; 2, infra-trochlear; 3, long internal ciliary nerves from the naso-ciliary nerve; 4, ciliary ganglion, showing the short ciliary nerves passing from it in front and giving a branch to the lachrymal nerve, 7. Observe also the long root from the naso-ciliary, and the median root from the internal carotid plexus, and the short root (motor) from the 3rd (III); 5, short ciliary; 6, long external ciliary; 7, lachrymal; 8, infra-orbital; 9, spheno-palatine ganglion; 10, middle superior dental; 11, superior dental; 12, supra-maxillary plexus; 13, naso-palatine plexus; 14, naso-palatine; 15, middle posterior nasal; 16, inferior posterior nasal; 17, anterior palatine; 18, middle and lateral palatine; 19, lingual; 20, submaxillary ganglion; 21, motor branch of 5th; R.sbm., submaxillary branch of external maxillary artery; A.m.c., external maxillary artery; A.c.o., external carotid artery; A.p.b., pharyngo-basilar artery; A.l., lingual artery; A.th.s, superior thyroid artery; A.c.c., common carotid artery; M.p.i., internal pterygoid muscle; 22, auriculo-temporal nerve; V.III., inferior maxillary division of 5th; 23, otic ganglion; 24, internal sphenoidal; 25, external sphenoidal; V.II., superior maxillary division of 5th; 26, branch from the carotid plexus to *tentorium cerebelli*; 27, carotid ganglion; 28, middle root of ciliary ganglion; 29, branches of internal carotid plexus to the Gasserian ganglion; H.c., *hypophysis cerebri* or pituitary body; A.c.i., internal carotid artery; A.o., ophthalmic artery; VII., facial nerve; 30, geniculate ganglion; 31, great superficial petrosal; 32, small superficial petrosal; 33, inferior branch of small superficial petrosal, passing to the tympanic nerve which supplies the *fenestra rotunda*, *fenestra ovalis*, and Eustachian tube; M.mi., *tensor tympani* muscle; F.o., fenestra ovalis: F.r., fenestra rotunda; 34, branch of small superficial petrosal to Eustachian tube; 35, small deep petrosal; 36, stapedius nerve; 37, *chorda tympani*; 38, tympanic nerve, connected with petrosal ganglion; 39, inferior carotico-tympanic nerve; IX., glosso-pharyngeal; XI., spinal accessory; XII., hypoglossal; 40, superior pharyngeal nerve; 41, gangliform plexus of vagus; 42, superior cervical ganglion; 43, superior laryngeal; 44, descendens noni; 45, superior cardiac; 46, trunk of sympathetic; 47, intercarotid gland. B. 9, spheno-palatine ganglion; 24, internal sphenoidal nerve; 28, middle root of ciliary ganglion; 30, geniculate ganglion; 31, great superficial petrosal; 32, small superficial petrosal; 38, tympanic; IX., glosso-pharyngeal; 39, inferior carotico-tympanic; 41, gangliform plexus of vagus; X., vagus; 42, superior cervical ganglion; 48, great deep petrosal. The diagram B is intended to show the relationships of the various ganglia. (Krause.)

is devoid of expression on the affected side; the features are dragged towards the sound side; the mouth is oblique. The affected half of the face is more prominent than the sound half, which is wrinkled and contracted. The eyelids are wide open, and the eye appears larger than its fellow. The muscles moving the jaws are obedient to volition; mastication is performed, and substances can be held between the teeth. The lips on one side are paralysed, food collects between the gum and the cheek, and sometimes escapes from the mouth. The pronunciation of labials such as *b* and *p*, and of *o*, is imperfect. There is also paralysis of the *velum palati* on the side of the lesion, diminution in the secretion of saliva (*chorda*), a deviation of the tongue from paralysis of the *stylo-hyoideus*, difficulty in deglutition, and sometimes deficient hearing, owing to the innervation of the tympanum by the small petrosal nerve being interfered with. There is no loss of sensibility (see p. 511).

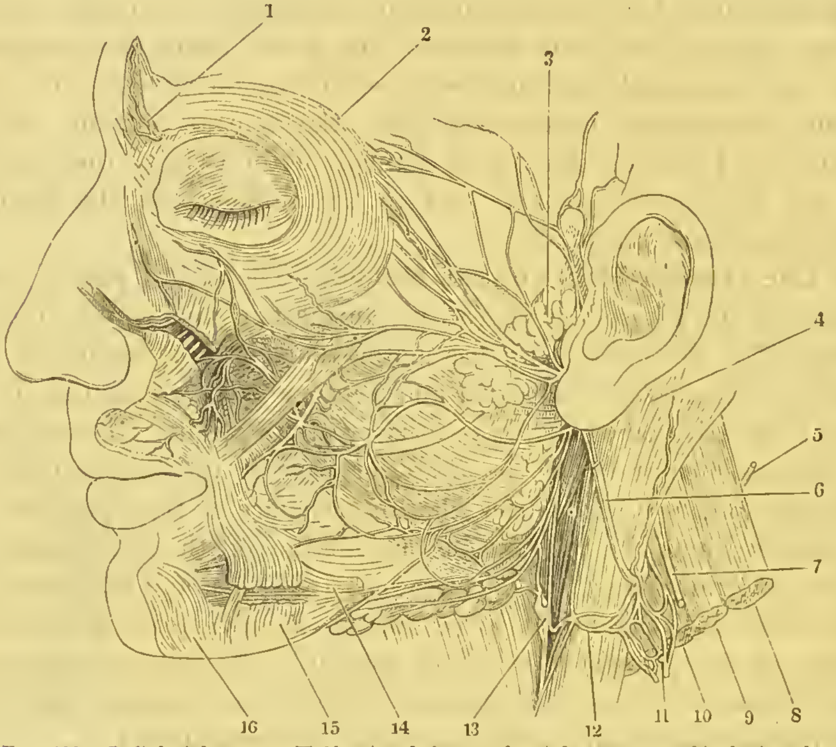

FIG. 288.—Left facial nerve. Half natural size. 1, frontal nerve; 2, *orbicularis palpebrarum*; 3, portion of parotid gland, showing Steno's duct passing from it; 4, *sterno-cleido-mastoideus*; 5, great occipital nerve; 6, great auricular nerve; 7, spinal accessory nerve; 8, *splenius capitis*; 9, *splenius cervicis*; 10, *levator anguli scapulæ;* 11, posterior supra-clavicular nerves; 12, inferior subcutaneous nerve of neck; 13, 4th cervical nerve; 14, *risorius*, cut; 15, *depressor anguli oris*, showing twig of nerve to chin; 16, *depressor labii inferioris*. (Krause.)

The facial is the special nerve of expression. At its root there is a small filament connecting it with the auditory; when the nerve enters the aqueduct of Fallopius, it swells into the geniculate ganglion, where it is connected with the spheno-palatine ganglion by the great superficial petrosal nerve, and with the otic ganglion by the small superficial petrosal nerve; and lastly, it receives filaments from the vagus by the auricular branch of that nerve, joining the posterior auricular branch of the facial. The facial is insensible at its origin, but it is slightly sensitive after its issue from the stylo-mastoid foramen. Its sensitiveness has been acquired by anastomosis with other nerves. Bernard showed that after section of the nerve below its anastomosis with the vagus, both cut ends were sensitive; on dividing the vagus branch, sensitiveness disappeared from the central portion. In the aqueduct of Fallopius it gives off a small motor twig to the *stapedius*, and also the *chorda tympani*. As to the influence of the facial on salivary secretion, see p. 58.

8. **The Glosso-Pharyngeal Nerve.**—The eighth pair of nerves consists of the glosso-pharyngeal, pneumogastric, and spinal accessory nerves. *The glosso-pharyngeal* has motor roots originating in the grey matter of the *medulla oblongata*, and sensory roots originating in the floor of the 4th ventricle. It is sensory at its origin. It supplies (*a*) the mucous membrane of the posterior part of the tongue (nerve of taste), the pillars of the fauces, the anterior face of the epiglottis, and the tonsils; and (*b*) the mucous membrane of the tympanum, the *fenestra ovalis* and *fenestra rotunda*, the mastoid cells, and the Eustachian tube along with the 5th. It is said to supply motor fibres to the muscles of the pharynx, but this is doubtful. It contains vaso-dilator fibres for the vessels of the posterior third of the tongue. (See p. 70, as to its functions in deglutition, and 357, in respiration.)

9. **The Pneumogastric or Vagus Nerve.**—The vagus nerve arises from the *medulla oblongata*, below the last nerve; and the deep fibres may be traced into the grey matter near the floor of the 4th ventricle. Two ganglia are situated on its roots; the upper one, small and rounded, in the *foramen lacerum;* the lower, elongated and plexiform, at the place of origin of the superior laryngeal branch of the nerve. Nearly all the fibres of the roots of the nerve pass through one or other of these ganglia; a few of those arising lowest down from the *medulla* pass the ganglia without being involved in them. The vagus is joined, between the ganglia, by the internal portion of the spinal accessory, constituting a bundle of fibres which may be traced past the lower ganglion, and which contributes mainly to form the motor part of the vagus. The vagus is connected near its root with the sympathetic, glosso-pharnygeal, hypoglossal, and some of the upper spinal nerves.

The functions of the pneumogastric have already been partially described in relation to the nervous arrangement of the heart, lungs, stomach, and liver; but the following is a brief *resumé*:—

The *pneumogastric* or *vagus nerve* has many complicated actions. (I.) It is sensitive to (*a*) the mucous membrane of all the respiratory passages, including specially the larynx; (*b*) the heart; (*c*) a portion of the digestive tube, namely, the base of the tongue, the velum palati, the pharynx, œsophagus, stomach, and probably the duodenum; (*d*) it confers muscular sensibility on the muscles to which it is distributed; (*e*) the mucous membrane of the biliary passages; (*f*) a part of the dura mater corresponding to the transverse and occipital sinuses; (*g*) the posterior part of the auditory canal. By the laryngeal branches it specially stimulates expiratory movements. (II.) It is motor to (*a*) many of the muscles of the palate; (*b*) the constrictors of the pharynx; (*c*) the œsophagus; (*d*) the larynx by (α) the superior laryngeal to the crico-thyroid muscle and a portion of the arytenoid, and by (β) the inferior or recurrent laryngeal to the rest of the muscles of the larynx; and (*e*) to the muscular fibres of the bronchial tubes. (III.) It contains inhibitory fibres for the heart. In connection with this organ the vagus also contains fibres belonging to the *depressor* system. (IV.) It influences secretion in the stomach, but it is doubtful whether it has any action on the renal secretion. (V.) It influences the production of glycogen in the liver.

10. **The Spinal Accessory.**—This nerve springs from nuclei in the *medulla oblongata* and also from the spinal cord by six or eight roots from the anterior horn, extending as low down as the 5th pair of cervical nerves. It is motor. Its external branch, derived from the cord, supplies the *sterno-cleido-mastoideus* along with branches of the cervical plexus; its internal branch, springing from the *medulla oblongata*, gives motor fibres to the vagus which supply the muscles of the larynx through the recurrent laryngeal. In phonation, this nerve acts, by its internal branch, chiefly upon the glottis,—the organ producing sound by the vibration of the vocal cords in a state of tension, whilst through its external branch, by regulating the action of the *sterno-mastoideus* and *trapezius*, it controls the amount of air expelled during the emission of sound. It also supplies the vagus with the inhibitory cardiac fibres.

11. **The Hypoglossal or Ninth Nerve.**—This nerve originates in the lower part of the floor of the 4th ventricle. It is distributed entirely to muscles: these are the *hyo-glossus*, *stylo-glossus*, *genio-glossus*, *lingualis;* and by its descending branch, along with the parts of the 3rd and 4th cervical nerves with which it is united, to the *thyro-hyoideus*, *sterno-hyoideus*, *sterno-thyroideus*, and *omo-hyoideus* muscles. At its root, it is entirely motor. Irritation of the root does not cause pain; but when applied to the branches of the nerve it may do so, probably owing to anastomoses with sensory nerves. Section paralyses the

muscles of the tongue, and renders articulation in speech, and the first act of deglutition, difficult. In paralysis of the hypoglossal, the tip of the tongue is turned towards the paralysed side.

CHAP. III.—FUNCTIONS OF THE SYMPATHETIC NERVES.

The fibres of the sympathetic system consist of two kinds—(1) of grey or gelatinous fibres, destitute of the white substance of Schwann; and (2) of medullated fibres similar to those met with in the cerebro-spinal centres. The grey fibres originate in the ganglia so prevalent in the sympathetic system, whilst the medullated fibres come from the cerebro-spinal system. Gaskell has shown that medullated fibres in passing through ganglia lose the white substance, and issue as non-medullated fibres. The trunk of the sympathetic nerve consists of a chain of swellings or ganglia, connected by intermediate cords of grey nerve fibres, and extending symmetrically on each side of the vertebral column, from the base of the cranium to the coccyx. On this part of the nerve 24 ganglia are placed on each side. This trunk, as it passes along the spine, is connected with the spinal nerves, the connecting fibres being of the two kinds already described. The grey fibres dominate in the sympathetic nerves, and the medullated in the cerebro-spinal, and these two elements are mixed in various proportions in both of the great divisions of the nervous system. At their lower extremities, the main trunks of opposite sides generally unite in the middle line; and at the upper ends each trunk, after being connected with the 8th and 9th cranial nerves, extends to the cranium, passes into that cavity along with the internal carotid artery, and there, as well as in other situations, comes into connection with all the remaining cranial nerves, except the olfactory, auditory, and optic. This conjunction may be effected directly, as with the 4th, 6th, and 9th nerves; or through a ganglion, as the *ophthalmic*, with the 3rd and 5th; the *spheno-palatine*, *otic*, and *submaxillary*, with the 5th and 7th, or facial; the *geniculate*, with the 7th or facial; the *jugular*, with the glosso-pharyngeal; and with the vagus, through one of its own ganglia. On the fibres of the sympathetic distributed to the viscera numerous ganglia, or plexuses in which ganglia exist, are met with, and frequently there is a plexus following the course of each vessel.

Certain of the results obtained by cutting or irritating the sympathetic nerve have been stated in describing the innervation of the heart, stomach, etc. It has been shown that if the sympathetic is cut in the neck, there is a dilatation of the vessels, both superficial and deep, on the affected side, an increased supply of blood, elevation of temperature, contraction of the pupil, and an increase of all the secretions, as shown by sweating and the secretion of tears. These results were first revealed by Petit in 1727, and afterwards discussed by Dupuy in 1816, by Brachet in 1837, and by John Reid in 1838; but it was not until 1852 that their significance was shown, their cause accounted for, and the discovery of the increase of temperature was made, by Claude Bernard. Soon afterwards, Brown-Séquard demonstrated that irritation of the cephalic end of the divided nerve was followed by the gradual disappearance of these effects, thus completing the experimental demonstration of the influence of the sympathetic on vessels. These investigations led to the recognition of the sympathetic as the nerve supplying the contractile coats of vessels, so as to keep them in partial contraction. Cut the nerve, and the vessels dilate; stimulate the end next the vessels, and they contract. Such nerves are known as *vaso-motor*, or constrictor nerves of the vessel (see p. 291).

(*a*) The vaso-motor fibres of the *head* are supplied by the cervical portion of the sympathetic, and originate in the cervical region of the cord, proceeding from it by the anterior roots of the lower cervical and upper dorsal nerves. The motor fibres supplying the radiating fibres of the iris also originate in the same region, so that section of the sympathetic in the neck paralyses these fibres, the result being contraction of the pupil, from the influence of the 3rd nerve, supplying the circular fibres, being unopposed.

(*b*) The vaso-motors of the *upper limbs* and of the *thorax* come—(1) from the inferior cervical and superior thoracic ganglia, and (2) from the cord, by communicating branches between the 3rd and 7th dorsal vertebræ.

(*c*) The vaso-motors of the *lower limbs* come from the cord through the sciatic and crural nerves; whilst those of the *pelvic organs* are derived from the abdominal ganglia of the sympathetic.

(*d*) The vaso-motors of the *abdominal viscera* exist chiefly in the splanchnic nerves; but some fibres supplying the stomach appear to be derived from the pneumogastric.

The Functions of the Splanchnic Nerves.—These nerves, three in number—the greater, the less, and the smallest—arise in man from the thoracic ganglia of the sympathetic, from the 5th to the 9th (greater), 10th and 11th (the less), and 12th (smallest) thoracic ganglia of the sympathetic. The first two supply the stomach, liver, spleen, pancreas, and intestines; whilst the second and the third disappear in the plexus passing to the kidneys. When exposed and divided in the lower animals, the abdominal viscera become engorged with blood—there is consequently greatly diminished blood pressure in other portions of the circulation. Irritation of the distal end causes contraction of vessels and an elevation of blood pressure generally. The splanchnics are thus the vaso-motor nerves of the abdominal viscera; but it is likely they also contain fibres which influence secretion. Irritation of the nerves inhibits or restrains intestinal movements. (See p. 104.)

The Vaso-Motor Fibres of the Extremities.—These are contained in the ordinary nervous trunks. Section of the sciatic nerve causes dilatation of the vessels of the affected limb and swelling. A similar effect has been seen in the limbs of man during paralysis from the influence of extreme cold.

Relation of the Vaso-motor Filaments to the Cerebro-Spinal System.—In 1832, Nasse showed that there was an elevation of temperature in the limbs after section of the spinal cord; and in 1852, Brown-Séquard discovered that section of one half of the cord, in the dorsal region, was followed by an increase of temperature in the opposite posterior extremity. The rise in temperature is coincident with an increase in the calibre of the vessels. On stimulating the distal end of the cord, the vessels contract and the temperature falls. These facts indicate that at least a portion of vaso-motor filaments comes from the cord, and the next point to be ascertained is, do they come from several segments, or from one more than another? Here there are great differences of opinion among observers. Some think that vaso-motor centres are scattered throughout the cord; whilst others are of opinion that the chief centre at all events is in the *medulla oblongata*, as stated at p. 291. The latter view is supported by the experiments of Ludwig and Owsjannikow, which show that when a particular part of the *medulla oblongata* is severed, there is at once a dilatation of the smaller vessels throughout the body, and a consequent fall of pressure in the larger vessels.

SECTION XII.

TERMINAL ORGANS AND THE SENSES.

GENERAL CONDITIONS OF SENSORY IMPRESSIONS.

By a sensory impression is understood the effect produced by the action of excitants on an organ of sense. The perception of the impression, and its reproduction as a mental image, are psychical acts.

The various kinds of sensory impressions are (1) touch; (2) taste; (3) smell; (4) vision; and (5) hearing. All of these are produced by a process which may be divided into (1) the action of an external stimulus on a terminal organ connected with the fibres forming the nerve of special sense; (2) transmission along the nerve of a change termed the nerve current; and (3) the reception of the impression in the brain, the result being a consciousness of the impression, that is to say, a sensation.

Chap I.—MECHANISM OF SENSORY IMPRESSIONS.

The essential conditions are (1) a *terminal apparatus*, for the reception of the excitant; (2) a *nerve*, for conducting impressions to the brain; and (3) a *brain*, or *central ganglion*, for the reception of these impressions. We may regard the nerve as a conductor. It is the bond of union between the terminal organ and the ganglion. Such nerves are known as *nerves of special sensation*, because the impressions conducted by them are always interpreted by the mind in a particular way. The doctrine that irritations of nerves of special sense always cause sensations of the same kind was first advanced by Johannes Müller, and is termed *Müller's law of the specific energy* of sensory nerves. Thus, the auditory nerve may be stimulated by various excitants, such as pressure, or cutting, or by its normal stimulus from the terminal organ in the ear; but when the impression reaches the brain, it always gives rise to a sensation of sound. This fact, however, does not imply that the fibres of the auditory nerve are necessarily different from those of any other nerve; but only that the central mechanism so acts as to produce this particular kind of sensation. Such nerves are not capable of being excited directly by the stimulus which acts upon their terminal organ. For example, the fibres of the optic nerve are insensible to the action of light, and those of the auditory nerve to sound. A terminal organ is required to receive the outer stimulus, and to excite the conducting filaments of the nerve. Each organ of sense has a terminal apparatus adapted for the reception of a special kind of stimulus. The retina is adapted for the action of light, the vibratory apparatus in the ear for the motions of sound, and the modified epithelial structures on the tongue and in the nose for the specific action of soluble substances and odoriferous particles.

A sensory transmission does not pass directly to the cerebral hemispheres, the seat of conscious perceptions; but there is a recipient centre, which in the first instance receives these impressions, and which may or may not transmit them to the perceptive centre. This arrangement is most evident in connection with the mechanism of vision, where we find the *corpora quadrigemina* interposed between the cerebral hemispheres and the optic tracts. These may be regarded as centres for the reception of impressions transmitted by the optic fibres from the retina. As the physical stimulus acting on the retina is a mode of motion in the form of waves of light, it is evident that its action will be intermittent, and that these intermittent impulses, following each other with great rapidity, will be transmitted along the optic fibres. It is not improbable that such impulses may be fused together in the receptive centre, and transmitted as a whole to the cerebrum. The *corpora quadrigemina* may act in some such way, and luminous effects may be stored up in these organs, ready to be transmitted to the brain This view might account for the vividness of ocular illusions experienced whilst under the influence of Indian hemp or felt by the insane. To a mind thus receiving old impressions which had long remained latent, the sensations would have all the vividness of reality, and would be just as truly referred to the outer world as if they had been immediately caused by the direct action of light on the retina, or of waves of sound on the ear, *because they reached the perceptive centre along the same channels.*

Such subsidiary cerebral centres also no doubt fulfil the purpose of linking the organs of sense, and the impressions they produce, with motor phenomena. Facts bearing upon this question have already been alluded to in treating of the *corpora quadrigemina* (see p. 512).

CHAP II.—TIME IN SENSORY IMPRESSIONS.

It has been ascertained by experiment that sensory impressions, and nervous phenomena of a kindred nature, occurring in terminal organs and in nerve centres, involve expenditure of time. Various methods have been adopted to determine the time with accuracy.

The most convenient apparatus for the purpose is a chronograph made by König. It consists of a large tuning fork vibrating 200 periods per second. This is placed in an upright position, and is kept in constant vibration by an electro-magnet placed on the outer side of each limb. In front of a marker placed on one of the limbs of the recording tuning fork, a thin strip of blackened paper is drawn vertically over a pulley. On each side of the tuning fork there is an electro-magnetic marker or signal, also arranged to record their movements on the strip of blackened paper. One of these electro-magnetic markers, A, is placed in a circuit, in which also is interposed an apparatus, say, for giving a shock, or producing a sound or a flash of light, so that when a key is closed, and the current established, the stimulus is produced, and the moment of its occurrence is recorded on the strip of blackened paper. The other electro-magnetic marker, B, is also in a circuit in which a key is interposed, so that, by closing the key and establishing the current, an observer of the event produced by A records the instant of producing it on the blackened paper. When the apparatus has been arranged, the band of smoked paper is rolled rapidly in front of the markers by a weight being allowed to fall to the ground; the key is closed, the observer feels the shock (or perceives the phenomenon—say a flash of light or a sound), closes the key, and the time of the phenomenon is recorded on the paper, as shown in Fig. 289. (See also p. 470.)

Fig. 289. — Tracing obtained with chronograph.

It is evident that an interval of time must elapse between the moment the shock is given and the moment the observer signals that he felt it. Suppose in the tracing shown in Fig. 289, that time is recorded by the fork's vibrations in the line *C*; that the instant the shock was given is indicated by the line *A* being drawn inwards by the electro-magnetic signal at *a*, and that the instant the impression is recorded is indicated by the inflection of the line *B* at *b*; the interval of time between the moment of the stimulus and the moment of signalling that it was felt is shown by the length of the line *a b*, found by drawing the dotted horizontal lines. By counting the number of the fork's vibrations in that distance, the time may be ascertained; thus, in the diagram, $\frac{8}{200}$ sec. $=\frac{1}{25}$. During the time so registered various phenomena occur. The shock irritates sensory structures in the skin of the hand. The influence so excited travels along the sensory nerves with a certain velocity, there is a distribution of nervous impulses to various centres, sensation and perception occur in the brain; then follows a volitional impulse, an impression travels along the motor nerves to the muscles of the arm, and, finally, time is occupied by the contractions of those muscles. The time occupied in the brain by the transformation of the sensory into the motor impulse is termed *psycho-physical* time.

The sense organs differ from each other as to the number of separate excitations they can receive in a second, each excitation causing a sensation. This question may be determined by observing when the number of excitations becomes so great that the separate sensations are fused into one. Thus, for the skin, Von Wittich found that the sensation was not uniform even when 1,000 separate excitations of the skin were made per second. The noises of two electric sparks have been heard by the ear when they were separated by an interval of ·00205 sec., that is about 500 per sec. could be observed. Mach reduces the interval to even less than $\frac{1}{500}$th sec. As to sensations of light, if two images of electric sparks are allowed to fall ·011 mm. apart on the retina, at an interval of ·044 sec., it can be told which occurs first. Again, if one stimulus strikes the *fovea centralis* and the other a point 6 mm. off, the interval for distinct perception is increased to ·076 sec. This fact is summed up in *Talbot's law* as follows:—If any point of the retina is periodically excited with light of a given intensity, for a given time a, and left unexcited for a given time b, then if $a+b$ be less than ·04 sec. the sensation becomes continuous, with a strength corresponding to the excitation $\frac{a}{a+b}$ (Fick).

The time between the instant when an end organ of sense is stimulated and the instant when motion occurs as the result of the conscious perception of the stimulus is termed the *reaction time.* Taking the average of observations made by eight observers, this time, for light, is ·189 sec., for hearing ·146, and for touch ·146. Von Wittich and others found for taste about ·16. Thus the reaction time may be as short as ·1 sec., while it rarely is as much as ·2 sec. With the weakest stimulations, the reaction time for the different senses approximates. Very strong stimulations diminish the reaction time. It is also diminished by expectation of the stimulus being applied, but if the quality of the stimulus is known while its intensity is unknown, the reaction time is increased. Thus the reaction time for a feeble sound intercalated in a series of loud sounds may reach ·4 to ·5 sec.

When the clear discernment of perceived objects is involved in the mental process, a certain time is required. Thus time is necessary for the discernment of a colour and for deciding in what part of the visual field it is located. This time may be termed *perception time.* It varies from ·011 to ·024 sec. It is a little less, as regards touch, for the dorsal aspect of the limbs than for the palmar aspect; it is shortened for a tone of high pitch as compared with one of low pitch; it is very short for localising the direction of a spark by direct vision (·005 to ·029 sec.); it is much increased when numerous objects require to be discriminated. Mendenhall found the time required to decide between red and white to be ·443 sec., and to decide between a triangle and a circle, ·494 sec., and S. P. Langley found in 1,000 observations of the disappearance of a very faint light (20 times brighter than the faintest perceptible), ·507 sec. Distinct vision therefore requires ·5 sec. with faint light, and with ordinary brightness ·25 sec. Lastly, if an effort of will takes place, as when it is resolved that if two stimuli of an organ of sense follow each other, only one shall be signalled and not the other, what is termed *will time* is required. In 10 persons, Merkel found this to amount to ·024 to ·155 sec. Kollert found that the sensitiveness to minute intervals of time varies for different persons from ·7 to ·8 sec. It was also found that the appreciation of a short time made the next longer and *vice versâ*. In all the time relations of mental phenomena, practice and attention diminish psycho-physical time while fatigue increases it.

Chap. III.—PSYCHICAL PHENOMENA OF SENSORY IMPRESSIONS.

1. Relation between the Stimulus and the Impression.—The stimuli which act on our sense organs are movements. Thus, light is caused by vibrations of ether, sound by movements of the air, and touch is due to variations of pressure caused by oscillations. In all periodic movements of the character of wave motion, three points are to be noted: (1) the *length* of the wave, determining the number of waves in a unit of time, affecting the *pitch;* (2) the *amplitude* of the wave, affecting the *intensity* of the impression; and (3) the *form* of the wave which influences the *quality* of the sensation.

2. Relation between the Stimulus and the Sensation.—(1) *Intensity of Sensation.*—Suppose a mode of energy, such as sound or light, to act on a terminal organ, the stimulus may be so weak as to produce no sensation; by increasing the strength of the stimulus to a certain point, a very feeble sensation may be experienced—that is to say, a *lower limit* (*or threshold*) *of excitation* has been reached. On further increasing the intensity of the stimulus, it will be found that the intensity of the sensation is also increased, according to a law which has been thus formulated in general terms by Weber (*Weber's law*): When the strength of the stimulus ascends in geometrical proportion, the strength of the sensation increases in arithmetical proportion. This law may be expressed in another way. The *intensity* of a sensation depends on two conditions: (1) the intensity of the excitation, and (2) the degree of excitability of the sensitive organ at the moment of excitation. It has been found that the intensity of the sensation does not increase proportionately to the intensity of the excitation. Thus, we have a luminous sensation of a certain intensity if a lighted candle is brought into a dark room, but the introduction of a second candle does not double the intensity of the sensation, but increases it only to a slight extent, whilst a third candle may produce no appreciable effect. By varying the absolute amount of the stimulus, and noting the corresponding strength of the sensation, it will be found that when the stimulus is doubled, tripled, quadrupled, etc., the sensation does not increase correspondingly, but *it increases as the logarithm of the stimulus.* Thus, suppose the excitation to be 10, 100, 1000 times increased, the sensation becomes only 1, 2, or 3 times more strong. Another illustration may be given. Let L equal the intensity of light in ½ of a white field, and $\frac{L}{100}$ the smallest amount of stimulus added to L that will be observed—then $L + \frac{L}{100} =$ the intensity of the other half of the field. Let $S =$ sensation of L; $S + s =$ the sensation caused by $L + \frac{L}{100}$; s being the least observed difference. Then $L = S$; $L + \frac{L}{100}$ or $\frac{101}{100}L = S + s$; $\frac{101}{100}L + \frac{\frac{101}{100}L}{100}$, or $\frac{101}{100} \cdot \frac{101}{100}L = S + s + s$, and so on. That is, if s is of the same magnitude, then L must be multiplied by the same magnitude (Ladd).

In sensory impressions we have: (1) a *minimum of excitation*, that is, the smallest excitation capable of producing a sensation; (2) a *maximum of excitation*, beyond which no increase in the amount of the stimulus augments the intensity of the sensation; (3) a *constant proportion or ratio* between the intensity of the excitant and the intensity of the sensation, which governs sensory impressions between the lower and the upper limits (*Fechner's law*).[1] The constant ratios for each sensa-

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[1] Fechner's law is as follows: Let $s =$ magnitude of sensation caused by stimulus Σ and Δs, the smallest perceptible difference caused by increase of stimulus $= \Delta\Sigma$. Let c be a constant, dependent on values of s and Σ. Then $\Delta s = \frac{C\Delta\Sigma}{\Sigma}$. Let it be assumed that Δs is constant whatever values for s and $\Delta\Sigma$ are assumed, then

tion also express the *least perceptible difference* between two sensations. Thus, if the addition of n to stimulus S, is the smallest that will cause a change in the mental state x, so that it passes into x', greater in quantity of sensation than x, then $x' - x = \Delta$, the least perceptible difference. Suppose, with the eyes blindfolded, a weight of 10 grms. is placed in the palm of the right hand, there is a sensation of weight of a certain intensity; to alter this sensation, by diminishing it, 3·3 grms. will have to be removed before a difference is perceptible, or, by increasing it, 3·3 grms. must be added to it. Again, with 100 grms., 33·3 grms., and with 1000 grms, 333·3 grms. must be added before appreciable differences will be observed—that is to say, the added or subtracted weight will be in the ratio of 1 : 3 with the primitive weight. The ratio 1 : 3 = the *constant proportion.* The constant proportion for each sense is:—Tactile sensations, 1 : 3; sensations of temperature. 1 : 3; auditory sensations, 1 : 3; muscular sensations, 6 : 100; visual sensations, 1 : 100.

The following are the values of the *minimum of excitation* for the different senses:—

Sensation of touch: pressure of ·002 grm. to ·05 grm. (*Aubert.*)

Sensation of temperature: $\frac{1}{8}$ of a degree C., the temperature of the skin being about 18·4° C. (*Weber.*)

Sensation of movement: shortening, to the extent of ·044 mm., of the internal rectus of the eye. (*Wundt.*)

Sensation of sound: a ball of pith, 1 milligramme in weight, falling 1 mm. in height, upon a glass plate, may be heard at a distance of 91 mm. from the ear. (*Schafhäutl.*) The compression of the air at the end of an organ pipe of 181 vibs. per sec. has been measured. The ear is affected by vibrations of molecules of the air not more in amplitude than ·00004 mm. at the ear, or ·1 of the wave length of green light, and the energy of such a vibration on the drum-head is not more than $\frac{1}{543}$ billionth kilogrammetre, or $\frac{1}{17}$th of that done upon the same surface of the pupil by a single candle at the same distance. (*Boltzmann* and *Töpler.*)

Sensation of light: an intensity of light about 300 times more feeble than that of the full moon. (*Aubert.*) As we can look at the sun for ·5 sec., the eye can perceive lights whose intensities vary in the ratio of 1 : $(10)^{15}$. It has also been ascertained that the *vis viva* of the light waves, whose length is ·75 μ, when arrested by the retina, represents work done in giving rise to a sensation of crimson of ·001 of an erg, while green can be caused by ·000,000,01 of an erg (*S. P. Langley.*)

$ds = C\frac{d\Sigma}{\Sigma}$, and by integration $s = c \log. \Sigma$. If two sensations are different, then $s - s' = C (\log. \Sigma - \log. \Sigma')$, or *the difference in the intensity of two sensations is proportional to the logarithm of the quotient of the magnitudes of their stimuli.* (For a criticism of the bearing of Fechner's law, and the speculations based by him thereon, see Ladd's *Elements of Physiological Psychology*, chap. v.)

Sensation of taste: 1 of salt in 426 of water, 1 of sulphuric acid in 100,000 of water, 1 of extract of aloes in 900,000 of water, and 1 of sulphate of quinine in 1,000,000 of water. (*Valentin.*)

Sensation of smell: 1 of bromine in 200,000 of air, 1 of sulphuretted hydrogen in 1,700,000 of air, and $\frac{1}{2000000}$th of a milligramme of alcoholic extract of musk. (*Valentin.*)

3. **Quality of Sensation.**—We assign different qualities either to sensations of different senses, or to sensations of the same sense caused by different forms of excitation. Thus the quality of an auditory, is different from that of a visual, sensation, and the quality of the sound of a piano is different from that of the human voice. The contrast between auditory and luminous impressions, as regards their respective excitants, is striking. Both are caused by movements, but the lowest sound audible as a musical tone is caused by 16 vibrations per sec.; the highest sound audible to the ear by 46,000; while the sensation of red at one end of the spectrum corresponds to 450,000,000,000,000 (450 billions), and that of violet at the other end to 785 billions of vibrations per sec. Sensations of temperature are caused by vibrations which come in far above the range of audible sounds, and approach, and blend with, the lower limits of those causing luminous impressions. It is not possible to make definite statements as to the molecular movements causing touch, taste, and smell.

4. **Objectivity of Sensory Impressions.**—When a nervous impression from a terminal organ reaches the brain, it excites in it changes which result in a *sensation;* and if the sensation is referred to some cause outside of the body, there arises what may be termed an *idea.* The link between the sensation, considered in its simplest form, and the idea, may be spoken of as a *perception.* Regarding the mechanism of these processes we know nothing. They may all result from the same kind of nervous activity, but of different degrees of intensity, or they may be related to broader areas of grey matter. Thus a feeble stimulus may produce such actions as result in mere sensation; a strong stimulus may cause perception; whilst a third may result in an idea of the cause of the stimulus. The term sensation has been applied to very different conditions; we need a word which will express that lower form of nervous activity which results in automatic movements, or which, in other circumstances, may be associated with conscious perception.

Sensations of sight, of hearing, and to a feebler extent, of smell, are projected into the external world, whilst those of touch and taste are referred to the periphery of the body. Sometimes exciting causes operate in the organ itself, so as to give rise to sensations, which are referred to the exterior. Such are the dots sometimes seen dancing before the eye, and the blowing, buzzing, and ringing sounds which distress the ear during disease. The projection of visual and auditory sensations is due to reasoning processes by which phenomena are connected with their causes. The organic effects of such processes are accumulated by hereditary transmission.

The five senses may be divided into two groups: (1) those depending on fine *molecular movements*, similar to those concerned in chemical action, namely, taste, smell, and vision; and (2) those depending on variations of *mechanical pressure* on the terminal organ, namely, touch and hearing. We will adopt this classification. In addition to the five senses, we have internal sensations or general feelings, such as the sensations of pain, of tickling, shuddering, nausea, voluptuousness, hunger, thirst, fatigue, breathing of pure fresh air, etc. These latter indicate states of our own body as distinguished from phenomena in the outer world, and are due to vague impressions reaching the brain from the mucous membranes and possibly from the tissues.

A.—The Sense of Taste.

The tongue is the organ of taste, but the upper part of the anterior surface of the soft palate, and probably the anterior pillar of the fauces, are endowed with gustatory sensibility to a feeble extent. The nerves connected with this sense are (1) the glosso-pharyngeal supplied to the posterior third; (2) the lingual branch of the fifth distributed to the anterior two-thirds; and (3), according to some authorities, filaments in the *chorda tympani*. These nerves are distributed to the papillæ on the surface of the tongue, of which there are three varieties—the simple or filiform, the fungiform, and the circumvallate (p. 45).

1. **Structure of the Taste Organs.**—The terminal branches of the glosso-pharyngeal nerve contain both medullated and non-medullated fibres. The medullated anastomose and ramify in the connective tissue, terminating in *end bulbs*, while the non-medullated penetrate the epithelial layer and, after forming a network, either end free, or in special terminal organs, the *taste buds* or *taste goblets* (Figs. 290 and 291). These are oval bodies, 80 μ long by 40 μ broad, embedded in the epithelial layer. Their bases rest on the *tunica propria* and their upper end passes to the upper surface of the epithelium. The end next the surface shows a minute, funnel-shaped opening, termed the *taste pore*. Each taste body is formed of two kinds of elongated epithelial cells, one equal in breadth from end to end, something like the staves of a cask, and the other, smaller, and narrow, or bifurcated at the basal end, while the outer end

is a fine pointed filament. The outer cells, forming the chief part of the goblet, and termed cover cells, serve as supporting structures to the taste cells which are the proper sensory epithelia. The taste cells are narrow and slightly thickened in the middle, where there is a nucleus.

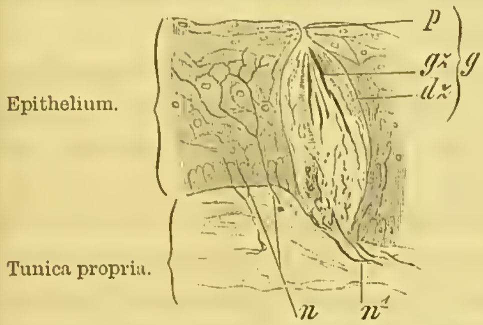

FIG. 290.—From a vertical section through a circumvallate papilla of a monkey (Hypale). × 240 d. *n*, free-ending nerve fibres; *n′*, nerve fibres passing into taste goblet; *gz*, taste cells; *dz*, cells forming goblet; *p*, taste pore. (Method No. 92, Appendix).

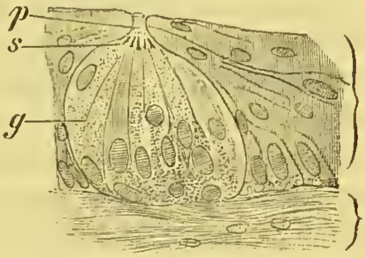

FIG. 291.—From a vertical section through the *papilla foliata* of a rabbit. × 560 d. *g*, taste goblet; *s*, fine ends of taste cells; *p*, taste pore. (Method No. 93, Appendix).

The upper half, above the nucleus, is first cylindrical, higher up conical, and it bears on the free end a bright refractive particle, which is cuticular in nature. The lower half is more slender and shows nodular swellings, and it is highly probable that this part is connected with the nerve endings, although the actual connection has not yet been seen. The taste goblets occur chiefly on the sides of the *papillæ circumvallatæ*, and in the secondary folds of the *papillæ foliatæ* (Fig. 292). They also occur in small numbers on the *papillæ fungiformes*, on the soft palate, and on the surface of the epiglottis.

The taste bodies are found in immense numbers; as many as 1760 have been counted on one circumvallate papilla in the ox. They are absent in reptiles and birds. In the *papillæ foliatæ* of the rabbit there are from 14,000 to 15,000 taste bulbs, in the papillæ of the sheep and pig 9,500, and in the ox as many as 30,000. The proofs that the taste bulbs are the

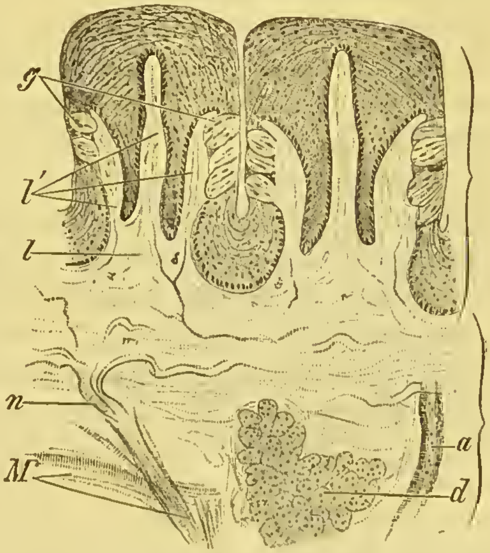

FIG. 292.—Vertical section through two folds of the *papilla foliata* of a rabbit. × 80 d. Each fold, *l*, has secondary folds, *l′*; *g*, taste goblets; *n*, medullated fibres; *d*, a serous gland; *a*, duct; *m*, muscular fibres of tongue. (Method No. 94, Appendix).

terminal organs of taste rest on observations which have shown: (1) that taste is only experienced when the sapid substance is allowed to come into contact with the taste body, and that the sense is absent or much weakened in those areas of mucous membrane where these are deficient; (2) that they are most abundant where the sense is most acute; and (3) that section of the glosso-pharyngeal nerve, which is known to be distributed to the areas of mucous membrane where taste is present, is followed by degeneration of the taste bodies. Taste is allied to smell; hence, in invertebrates, organs are found that may be referred to either of the senses.

2. **Physical and Physiological Causes of Taste.** — To excite the sensation, substances must be soluble in the fluid of the mouth. Insoluble substances give rise to sensations of touch or of temperature, but excite no taste. The specific mode of action of sapid substances is unknown. The extent of surface acted on increases the *massiveness* of the sensation, whilst the *intensity* is affected by the degree of concentration of the solution of the sapid substance. If solutions of various substances are gradually diluted with water until no taste is experienced, Valentin found that the sensations of taste disappeared in the following order—syrup, sugar, common salt, aloes, quinine, sulphuric acid; and Camerer found that the taste of quinine continued although diluted with twenty times more water than common salt. Von Vintschgau found that the time required to excite taste after the sapid substance was placed on the tongue varied. Thus saline matters are tasted more rapidly (·17 sec.), then sweet, acid, and bitter (·258 sec.). This is probably due to the activity of diffusion of the substance. There are many curious examples of substances of very different chemical constitutions having similar tastes. For example, sugar, acetate of lead, and the vapour of chloroform have all a sweetish taste.

Tastes may be conveniently classified as *sweet*, *bitter*, *salt*, *sour*, and *alkaline*. Sour tastes generally characterize acids, the alkalies have a soap-like taste, salts vary much, from the bitter of sulphate of magnesia to the sweet of neutral acetate of lead, alkaloids are usually bitter, and the higher alcohols are sweet, until we reach the sugars.

A temperature of from 10° to 32° C. is the most favourable to the sense, water above or below this temperature either masking or temporarily paralysing it.

Taste is often associated with smell, giving rise to a sensation of *flavour*, and we are frequently in the habit of confounding the one sensation with the other. Chloroform excites taste alone, whilst garlic, assafœtida, and vanilla excite only smell. Taste may be educated to a remarkable extent; and careful observation, along with the practice of avoiding all substances having a very pronounced taste or having an irritating effect, enables tea tasters and wine tasters to detect slight differences of taste, more especially when combined with odour so as to produce flavour, which would be quite inappreciable to an ordinary palate. As to the action of electrical currents on taste, observers have arrived at uncertain results. So long ago as 1752, Sülzer stated that a constant current caused, more especially at the moments of opening and of closing the current, a sensation of acidity at the anode (+ pole) and of alkalinity at the kathode (– pole). This is due to electrolysis, the decomposition products exciting the taste bodies.

Disease of the tongue causing unnatural dryness may interfere with taste. Substances circulating in the blood may give rise to subjective sensations of taste. Thus santonin, morphia, and biliary products (as in jaundice) cause a bitter sensation whilst the sufferer from diabetes is distressed by a persistent sweetish taste. The insane frequently have subjective tastes, which are real to the patient, and frequently cause much distress. In such cases, the sensation is excited by changes in the taste centres of the brain. Rare cases occur where there is a subjective taste not associated with insanity nor with the circulation of any known sweetish matters in the blood, possibly caused by irritation of the gustatory nerves or by changes in the nerve centres.

B.—Sense of Smell.

The organ of the sense of smell is the mucous membrane lining a part of the nasal cavities supplied with nerves from the *olfactory* bulbs. Attached to the side walls of each nasal cavity are two scroll-like bones, called *turbinated* bones, which to a great extent divide each cavity into three spaces, or *meatuses*, lying one above the other. The uppermost two of these constitute the olfactory chambers, whilst the lowest passage is merely used for respiratory purposes. The whole of this bony framework is covered by moist mucous membrane, having embedded in it flat elongated cells attached to the ramifications of the olfactory nerves (Fig. 293). By

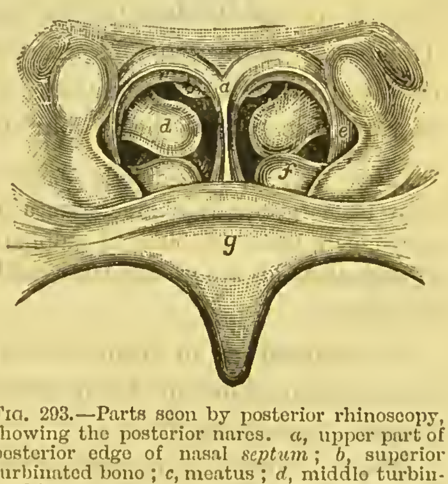

Fig. 293.—Parts seen by posterior rhinoscopy, showing the posterior nares. *a*, upper part of posterior edge of nasal *septum*; *b*, superior turbinated bone; *c*, meatus; *d*, middle turbinated bone; *e*, opening of Eustachian tube; *f*, inferior turbinated bone; *g*, soft palate. (Urbantschitsch.)

the contact of certain substances with these, a sensation of smell is produced.

1. **Structure of Olfactory Organ.**—The portion of mucous membrane connected with smell is limited to the anterior two-thirds of the superior *meatus*, the middle *meatus*, and to the corresponding part of the nasal *septum*. The greater part of the rest of the membrane, including that of the sinuses, covers the respiratory passage. The membrane lining the movable part of the nose is different in character from both of those just mentioned, as it is developed from an infolding of the skin. It is termed the vestibular portion.

(1) *Regio Vestibularis.*—The mucous membrane consists of stratified squamous epithelium, covering a *tunica propria* bearing papillæ. It contains numerous sebaceous glands, and hair follicles from which stiff strong hairs, named *vibrissæ*, are developed.

(2) *Regio Respiratoria.*—The membrane consists of stratified cylindrical ciliated epithelium (Vol. I. Fig. 147, p. 301 and p. 318), and a few goblet cells. The *tunica propria* in the inferior *meatus* is 4 mm. in thickness and is formed of fibrillated connective tissue. Numerous leucocytes exist in the meshes, and in some places groups of these form lymphatic nodules. Migratory leucocytes pass through the epithelium into the nasal cavity. In the *tunica propria* we also find small racemose glands, some of the acini of which are serous and others mucous. The ducts of these often open into funnel-shaped depressions in the vestibular portion. In the sinuses the epithelial layer is thinner, ·02 mm., and few glands exist.

Fig. 294.—Vertical section through the mucous membrane of the nasal septum of man, showing the *regio respiratoria*. × 20 d. *d*, glands, with duct opening into funnel-shaped depression, *t*; *a*, artery; *v*, veins. (Method No. 95, Appendix.)

(3) *Regio Olfactoria.*—This portion has a yellowish brown colour, contrasting with the reddish hue of the other regions. It consists of an epithelial layer, the olfactory epithelium, resting on a *tunica propria*.

Two forms of cells are found. (*a*) The one (Fig. 295, *st*) is in the upper half, cylindrical, and contains yellowish pigment and minute granules arranged in rows running longitudinally. The upper or free border appears to be covered with a cuticular layer, according to some observers; others state that short stiff cilia exist here, and others have figured what they regarded as small conical drops of a mucoid substance issuing from the cell (Fig. 295, *s*). The lower half is narrower, has indented margins, and the lower, or attached, end is forked, the prongs of the fork anastomosing with those of adjacent cells so as to form a network. These cells are known as *supporting cells.* They possess an oval nucleus projecting from the cell and the rows of nuclei, *r*, seen in section, appear as a narrow zone, the *zone of oval nuclei.* (*b*) The second form of cells (Fig. 295, *r*) have protoplasm chiefly round the nucleus. From this there passes to the surface a narrow cylindrical filament, bearing a single *cilium* on its free end, and towards the deeper tissue a very minute thread-like protoplasmic filament may be traced. These are the *olfactory cells.* The round nuclei have nucleoli, and in section they form a zone, the *zone of round nuclei* (Fig. 296, *zr*). Cells of intermediate form exist. We also find in the boundary of the epithelium and the connective tissue a protoplasmic network of cells, having nuclei, and termed *basal cells* (Fig. 296, *b*). The *tunica propria* is a loose feltwork, composed of connective tissue with a few elastic fibres, and in many animals, in the cat for example, the elastic fibres are condensed to form a structureless membrane next the epithelium. Numerous glands, known as *Bowman's glands*, exist in the *tunica propria.* These are either simple, or, as in man, they are branched tubes, in

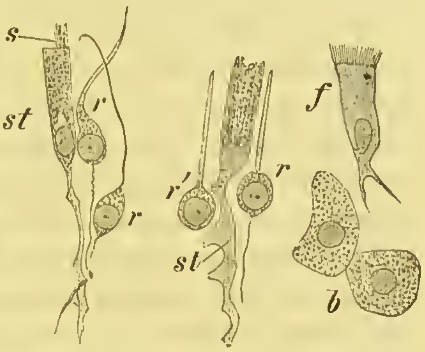

Fig. 295.—Isolated cells from *regio olfactoria* of rabbit. × 560 d. *st*, supporting cells; *s*, cones of mucus, resembling cilia; *r*, olfactory cells. At *r'*, lower process torn off; *f*, ciliary cell; *b*, cells of Bowman's glands. (Method No. 96, Appendix.)

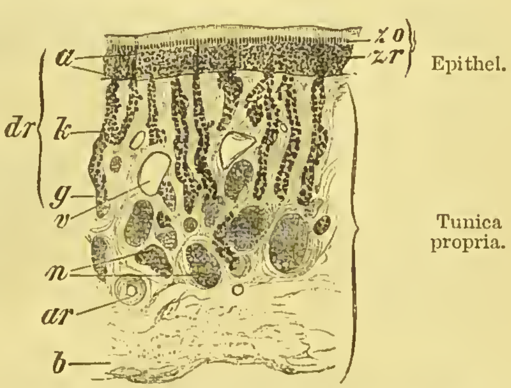

Fig. 296.—Vertical section of *regio olfactoria* of rabbit. × 50 d. *zo*, zone of oval nuclei; *zr*, zone of round nuclei; *dr*, Bowman's glands; *a*, duct; *k*, the body, and *g*, the bottom of the acinus; *n*, transverse sections of the olfactory nerve; *v*, veins; *ar*, artery; *b*, bundles of connective tissue cut transversely. (Method No. 97, Appendix.)

which we observe a duct (Fig. 296, *a*) passing through the epithelial layer, a body, and a fundus. The cells in the body are pigmented. They are mucous glands. In the *tunica propria* also we find ramifications of the olfactory nerve. The larger branches have sheaths derived from the *dura mater*, and they consist of non-medullated nerve fibres, splitting up readily into fibrils. The fibrils proceed in a curved way towards the epithelium, in which they end in a manner not yet explained. According to some, they end in the fine filaments of the olfactory cells, and according to others, they end in the network of basal cells, from which filaments pass which are connected with both the supporting and the olfactory cells. The latter view favours the opinion that both kinds of cells are olfactory in function.

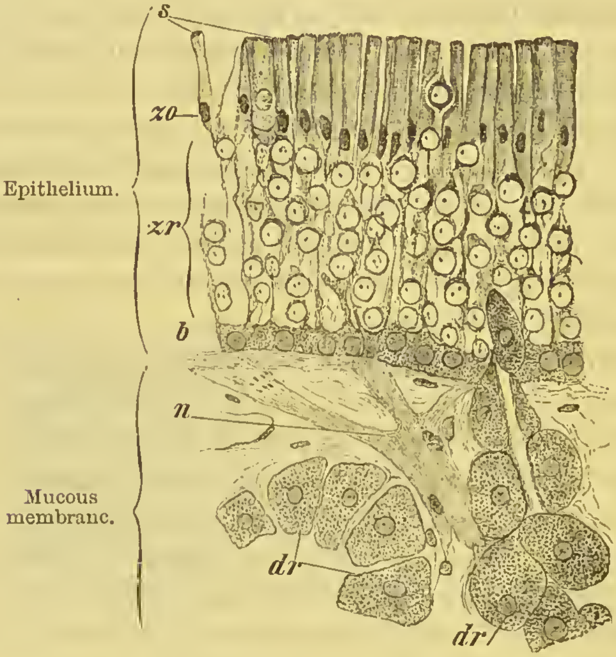

FIG. 297.—Vertical section through *regio olfactoria* of a rabbit. × 560 d. *s*, border; *zo*, zone of the oval, *zr*, zone of the round, nuclei; *b*, basal cells; *dr*, portions of Bowman's glands. The lower part of the duct is seen on the right. *n*, branch of olfactory nerve. (Method No. 98, Appendix.)

From the *blood-vessels* of the nasal mucous membrane small arterioles run into the deeper strata of the *tunica propria*, and end in a capillary network below the epithelial layer. The veins are well developed and in the posterior end of the inferior *meatus* they form a network so dense as to resemble a cavernous or erectile tissue[1] The *lymphatics* form a coarse meshwork in the deeper parts of the *tunica propria*. Injections of colouring matter into the sub-arachnoid space penetrate into the olfactory region by the sheaths surrounding the olfactory nerves and running through the *lamina cribrosa* of the ethmoid. Medullated nerve fibres, belonging to the 5th (*trigeminus*), are found in all parts of the nasal mucous membrane.

The *organ of Jacobson*, found well developed in herbivora, less so in carnivora, belongs to the olfactory region. Between the ciliated epithelial cells of its mucous membrane we find staff-like cells, connected with the ends of the olfactory filaments.

2. **Physical Causes of Smell.**—To excite smell it is supposed that substances must be present in the atmosphere in a state of fine subdivision, or existing as vapours or gases. The fineness of the particles is remarkable, because if the air convoying an odour is filtered through a tube packed with cotton wool and inserted into the nose, a smell is still discernible. This proceeding completely removes from the air organisms less than the $\frac{1}{1000000}$th of an inch in diameter, which are the causes of putrefaction and fermentation. A grain or two of musk will scent an apartment for years, and at the end of the time no appreciable loss of weight can be detected. Substances exciting smell are no doubt usually gases or vapours. The olfactory cells are not affected by a ·75 per cent. solution of common salt, but water quickly destroys them and smell is lost. The following gases have no smell :—Hydrogen, oxygen, nitrogen, water gas, marsh gas, olefiant gas, carbon monoxide, hydrochloric acid, formic acid, nitrous oxide, and ammonia. (It is necessary to distinguish between smell and the irritant action of such a gas as ammonia.) The gases exciting smell are chlorine, bromine, iodine, the compounds of the first two with oxygen and water, nitric peroxide, vapours of phosphorus and sulphur, arsenic, antimony, sulphurous acid, carbonic acid, almost all the volatile compounds of carbon except those already mentioned, some compounds of selenium and tellurium, the compounds of chlorine, bromine, and iodine, with the above named elements and some metals. Chlorine, bromine, iodine, sulphur, selenium, and tellurium, which are volatile, and give off vapour at ordinary temperatures, have each a characteristic smell.

Ramsay has advanced the theory that the sense of smell is excited by vibrations of a lower order than those which give rise to the sense of light or heat, and he points out a series of important facts in support of this view. He states that to produce the sensation of smell a substance must have a molecular weight at least fifteen times that of hydrogen. For instance, the specific gravity of marsh gas is eight (no smell); of ethane, fifteen (faint smell); of propane, twenty-two (distinct smell).

Haycraft, assuming the correctness of Ramsay's hypothesis, that smell depends on the vibratory motion of odorous particles, has endeavoured to show that the quality of the sensation depends on the kind of vibration producing it. He has also traced a correspondence between the character of the smell and the position of the body producing it in the groups in which Mendelejeff has arranged the elements to illustrate the periodic law.[1]

Smell may be excited by vibrations, and the period of vibration of the *lighter* molecules may be too rapid to affect the sense; at last a number of vibrations is reached capable of exciting the sense organ, and beyond an upper limit the sense is again lost. Graham pointed out that odorous substances are in general readily oxidized. Tyndall showed that many odorous vapours have a considerable power of absorbing heat.

Venturi, B. Prévost, and Liégeois have studied the well known movements of odoriferous particles, such as camphor, etc., when placed on the surface of water, and they have suggested that all odoriferous substances in a state of fine subdivision may move in a similar way on the moist surface of the olfactory membrane, and thus mechanically irritate the nerve endings. This explanation is too coarse; but it is well known that the odours of flowers are most distinctly perceived in the morning or after a shower, when the atmosphere contains a considerable amount of aqueous vapour. It would appear also that the odorous matters of animal effluvia are of a higher specific gravity than the air, and do not readily diffuse. Such smells are very persistent, and are difficult to remove from any surface to which they have become attached. Thus the smell of a *cadaver* may haunt a living person for days.

3. **Special Physiology of Smell.**—The air containing the odour must be driven against the membrane. Thus the nostrils may be filled with eau de Cologne, or with air impregnated with sulphuretted hydrogen, and still no odour is experienced if the person does not breathe. When a sniff is made, the air within the nasal passages is rarefied, and, as the air rushes in to equilibrate the pressure, it is forcibly propelled against the olfactory surface. The olfactory surface must be moist; if it is dry, or is covered with too thick a layer of mucus (as in catarrh), the sense is much weakened or lost. The first moment of contact is the most acute, and the sense quickly becomes blunted. The first scent of a flower is the strongest and sweetest; and after a few minutes' exposure the intensity of even a fœtid odour may not be perceived. The intensity of smell depends on (1) the area of olfactory surface affected, and (2) the degree of concentration of the odoriferous

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[1] J. Berry Haycraft, on the "Sense of Smell." *Proc. Roy. Soc., Edin.* 1887. See also Dr. Haycraft's speculations on "Taste," in *Proc. Roy. Soc., Edin.* 1886.

matter. Musk to the amount of the two-millionth of a milligramme, and 1 part of sulphuretted hydrogen in 1,000,000 parts of air may be perceived. If the two nostrils are filled with different odorous substances, there is no mixture of the sensations of odours, but we smell sometimes the one and sometimes the other.

The delicacy of the sense is much greater in many of the lower animals than in man. Odours may excite in the minds of many animals vivid impressions, and they have probably a memory of smells which the human being does not possess. Even in man the sense may be greatly improved by exercising it. A boy, James Mitchell, was born blind, deaf, and dumb, and chiefly depended on smell for keeping up a connection with the outer world. He readily observed the presence of a stranger in the room, and he formed his opinions of persons from their characteristic smells. The sense is occasionally congenitally absent. Subjective impressions of smells are occasionally, but rarely, observed in the insane. Finally, it may be observed that the sense of odour gives information as to the characters of food and drink, and as to the purity of the air. In the lower animals also, the sense is associated with the sexual functions. Althaus states that electrical stimulation causes a sensation of the smell of phosphorus.

C.—The Sense of Vision.

Chap. I.—STRUCTURE OF THE EYE.

The eye is a nearly spherical organ, formed of transparent parts situated one behind the other, and surrounded by membranous structures, of which the anterior part is transparent. The transparent parts in the interior of the eye are: (1) the *aqueous humour* in the anterior chamber; (2) the *crystalline lens*, formed by a transparent convex body, of which the anterior surface is less convex than the posterior; and (3) the *vitreous humour*, a semi-fluid substance, surrounded by a structureless membrane, the *hyaloid membrane*, in the posterior chamber. The *lens* is formed of a series of layers, which in turn are made up of fibres; and it increases in density from the circumference towards the centre. These transparent parts are surrounded by three layers of membrane, the one outside of the other—(1) an external layer, the posterior part of which is formed by the *sclerotic*, and the anterior part by the transparent *cornea*; (2) the *choroidal* or vascular membrane, composed of the choroid properly so called, which lines the internal surface of the sclerotic, and the anterior part of which forms the *ciliary processes* and the *iris*, a movable diaphragm, surrounding an aperture termed the *pupil*; and (3) the *retina*, which lines the posterior part of the eyeball, being placed between the choroid and the vitreous humour. The retina is the layer sensitive to light; but to reach it a luminous ray must pass from before backwards through the following transparent structures—cornea, aqueous humour, crystalline lens, and vitreous humour.

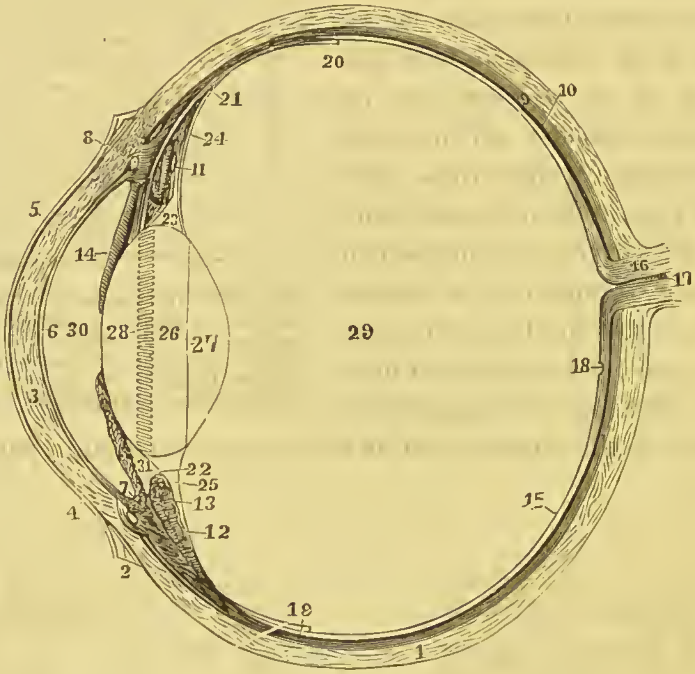

Fig. 298.—Diagrammatic section of the eyeball. 1, sclerotic; 2, junction of sclerotic and cornea; 3, cornea; 4, 5, anterior layer of epithelium (conjunctiva); 6, posterior elastic lamina; 7, junction of iris with choroid; 9, 10, choroid; 11, 12, 13, ciliary processes; 14, iris; 15, retina, lined by hyaloid membrane; 16, fibres of optic nerve; 17, arteria centralis retinæ; 18, yellow spot; 19, 20, anterior portion of retina; 21, 24, membrane passing behind lens; 22, 25, membrane passing in front of lens; 23, 25, canal of Petit; 26, 27, 28, lens; 29, vitreous humour; 30, anterior chamber, containing aqueous humour; 31, space between iris and anterior layer of capsule of lens; 8, canal of Schlemm.

1. The **Tunica Externa**, or outer coat, consists anteriorly of the transparent membrane, the *cornea*, and posteriorly of the fibrous structure, the *sclerotica*, or sclerotic.

(*a*) The *cornea* is formed of five strata in the following order from before backwards:—(1) the corneal epithelium; (2) the anterior elastic lamina; (3) the *substantia propria* of the cornea; (4) the posterior elastic lamina; and (5) the endothelium of the cornea (Fig. 299). The *epithelium* of the cornea is stratified pavement epithelium and consists, in its deepest part, of a layer of cylindrical sharply defined cells. Above these we find three or more layers of roundish cells, and towards the surface, the cells are flattened. The epithelial layer, constituting the ocular portion of the *conjunctiva*, is ·03 mm. thick in man. The *anterior elastic lamina*, or *Bowman's membrane*, is in man distinctly visible, homogeneous, and ·01 mm. in thickness. The upper surface shows fine spikes and ledges by which it is connected with the epithelium of the cornea, and its under surface shades off into the proper substance of the cornea. The *substantia propria*, forming the chief part of the cornea, is composed of delicate fibres, united by a cement substance into bundles, and these again are cemented together to form laminæ. The latter run parallel to the surface of the cornea; but as the cornea is curved, a perpendicular section may show them running obliquely, with fine curved bundles (*fibræ arcuatæ*) connecting adjacent laminæ. In the cement substance,

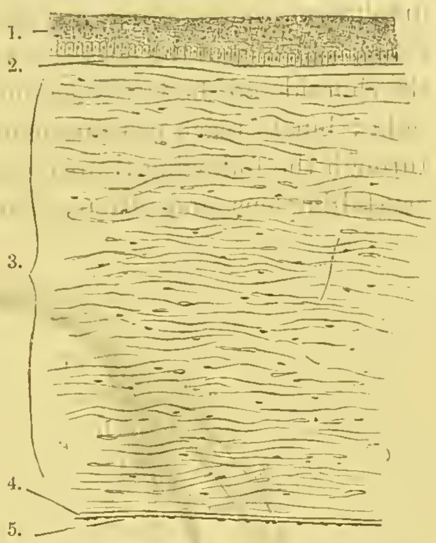

Fig. 299.—Vertical section through human cornea. × 100 d. 1, corneal epithelium, or conjunctiva; 2, anterior elastic lamina; 3, proper substance of cornea; 4, posterior elastic lamina; 5, corneal endothelium. (Method No. 99, Appendix.)

Fig. 300.—*A.* Small corneal canals (*k*) and lacunæ (*l*) of human cornea, seen from the surface. *n*, nuclei of corneal cells, acted on by silver. × 60 d. (Method No. 100 Appendix.) *B.* Two corneal lacunæ (*l*) of cornea of ox connected by small corneal canals (*k*), seen from surface. *Substantia propria* shows a dark granular appearance from action of silver nitrate. × 240 d. *C.* Small corneal canals (*k*) and corneal lacunæ (*l*) in human cornea, seen from surface. At *z*, in the lacunæ, observe the flat corneal cells. × 240 d. (Method No. 100, Appendix.)

we find in many animals, as, for example, in the frog, a system of ramified *canals* or fine tubes, which here and there widen out into *lacunæ*. These lacunæ lie between the lamellæ, while the canals run between the bundles and fibres. The canals and lacunæ contain a serous fluid, and in the lacunæ we also find (*a*) *corneal corpuscles*, which are flattened connective tissue cells, having a large nucleus, and adhering to one side of the lacunæ, and (*b*) leucocytes (Fig. 300). The *posterior elastic lamina*, or *membrane of Descemet*, is a clear, homogeneous, elastic structure, ·006 mm. in thickness, having minute nipple-like elevations on its posterior surface. It is lined on its posterior surface by a single layer of flat, nucleated, polygonal cells, the *endothelium* of the cornea.

(*b*) The *sclerotic* is formed of bundles of connective tissue, interwoven in all directions, and mixed with delicate elastic fibres, forming a network. Here and there connective tissue corpuscles lie in lacunæ. Between the choroid and sclerotic there is a loose connective tissue, containing numerous elastic fibres, and having branched pigment cells and non-pigmented flat cells (endothelial). This tissue, when the sclerotic is separated from the choroid, adheres to both. It is known as the *lamina supra-choroidea*, or *lamina fusca scleræ*. The sclerotic is thickest posteriorly, 1 mm., and it gradually diminishes anteriorly.

FIG. 301.—Pigmentary connective tissue corpuscles from choroid. (Method No. 101, Appendix.)

2. **The Tunica Media.**—The *choroid*, rich in vessels, is arranged in two layers. The *superficial layer*, next the *lamina supra-choroidea*, is termed the *stratum of the larger vessels*, and contains the ramifications of arteries and veins, embedded in a stroma or ground substance formed of fine elastic fibres, and numerous ramified pigment cells (Fig. 301). The *stroma* also contains fibrils of connective tissue, smooth muscular fibres, and flat unpigmented cells, which unite to form an *endothelial cuticle*. The *deeper* stratum, named the *membrana chorio-capillaris*, is formed of a narrow-meshed network of wide capillaries, in the meshes of which no formed elements exist. Between the *strata* we find a layer of fine elastic fibres, termed the *boundary stratum of the ground substance*. In ruminants and horses, this stratum contains numerous undulating bundles of connective tissue, giving a metallic lustre to the eye. This iridescent layer is the *tapetum fibrosum*. The tapetum of beasts and birds of prey is formed of several strata of flat cells, containing numerous small crystals. To the *membrana chorio-capillaris* is attached the *vitreous membrane*, a structureless lamella, about 2 μ thick, which shows on its

upper surface a delicate trellis-like marking, from coming into contact with the hexagonal retinal pigment. The choroid is continued forwards to form the *corpus ciliare*, which, in turn, is composed of the *processus ciliares* and of the *musculus ciliaris*, or ciliary muscle.

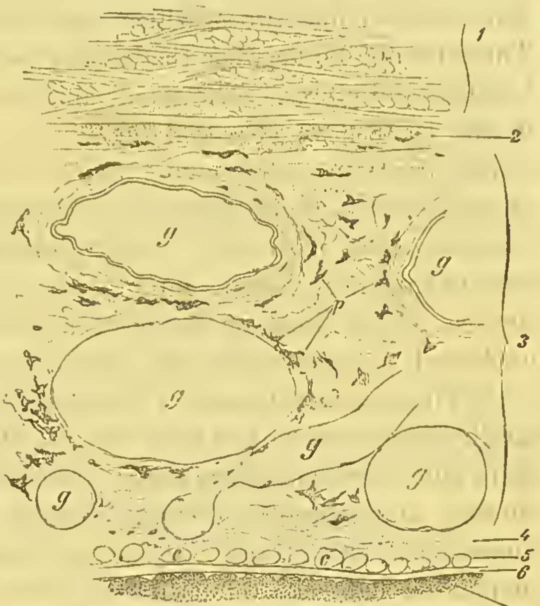

FIG. 302.—Vertical section through part of the sclerotic and through the entire choroid. × 100 d. *1*, bundles of sclera cut in different directions; *2*, *lamina supra-choroidea*; *3*, stratum of coarser vessels; *4*, boundary of ground substance; *5*, *membrana chorio-capillaris*; *6*, homogeneous membrane; *7*, pigment epithelium; *g*, larger vessels; *p*, pigment cells; *c*, transverse sections of capillaries. (Method No. 102, Appendix.)

The *processus ciliares* consist of from seventy to eighty meridionally-running folds, beginning at the *ora serrata*, and gradually rising to a height of 1 mm.; they terminate suddenly near the margin of the lens. Each process is formed of fibrillar connective tissue, and numerous blood-vessels, and it is lined by a continuation of the vitreous membrane, which is here thrown into folds. The *ciliary muscle* is a ring, 3 mm. broad, and ·8 mm. in thickness, which originates on the inner wall of *Schlemm's canal*. Its elements run in three directions: (1) *meridional* fibres (Fig. 304, 4), which are numerous bundles near the sclerotic, and

FIG. 303.—Teazed preparation of human choroid. × 240 d. *A*—*p*, pigment cells; *e*, elastic fibres; *k*, nucleus of flat cells, with no pigment—body of cell invisible. *B*, small portion of human *membrana chorio-capillaris* and of adhering vitreous membrane. × 240 d. *c*, wide capillaries, still containing (*b*) blood corpuscles; *e*, vitreous membrane, showing the trellis work. (Method No. 103, Appendix.)

extending to the choroid—they are termed the *tensor choroideæ;* (2) *radial* fibres, next the meridional, radiating in the direction of the centre of the eye, and curved at their posterior ends; and (3) *circular* or *equatorial* fibres, constituting the circular or sphincter *ciliary muscle of Müller.*

Fig. 304.—Meridional section through the ciliary region of human eye. × 30 d. *1*, epithelium; *2*, connective tissue of conjunctiva; *3*, sclerotic; *4*, *5*, *6*, *7*, and *8*, ciliary body—*4*, meridional, *5*, radiating, and, *6*, circular fibres of the ciliary muscle; *7*, processus ciliaris; *8*, *pars ciliaris retinæ;* *9*, *pars iridica retinæ*; *10*, stroma of iris; *11*, *12*, *13*, cornea—*11*, posterior elastic lamina; *12*, *substantia propria;* *13*, epithelium; *14*, Schlemm's canal; *15*, angle of iris. (Method No. 104, Appendix.)

The *iris* is formed of a stroma, divisible into three strata, covered in front by a continuation of the corneal endothelium, and behind by a modified layer of retina. There are thus five layers. (1) The *endothelium* on the anterior surface of the iris is formed of a single layer of flattened polygonal cells. (2) The *anterior* or *reticulated* stratum consists of four or five layers of networks, formed of star-shaped connective tissue cells, resembling the reticulum of adenoid tissue. (3) The *vascular* stratum, formed of loose connective tissue, in the meshes of which are numerous vessels radiating to the pupil. Each vessel and nerve in this region has a strong connective tissue sheath. Here also we find smooth muscular fibres arranged, so as to form (*a*) a ring round the margin of the pupil, the *sphincter pupillæ,* or circular fibres of iris, about 1 mm. in width, and (*b*) a few radiating fibres, the *dilator pupillæ.* In this layer we also find a few pigment cells, but these are absent in blue eyes. (4) The *posterior* stratum, a clear homogeneous membrane, is composed of condensed elastic substance. (5) The *pigmentary* stratum, or *pars iridica retinæ,* is formed of two layers, the anterior of which contains spindle-shaped pigment cells, and the posterior polygonal pigment cells. In albinos these cells contain no pigment. The posterior surface of this layer is covered with a fine cuticle, the *limitans iridis*, which is a continuation of the *limitans interna retinæ*, to be presently described.

FIG. 305.—Vertical section through the pupillary portion of the human iris. × 100 d. About one-fifth of the iris is shown. *g*, blood-vessels, with thick connective tissue sheath; *m*, *sphincter pupillæ*, cut transversely; *p*, pupillary vein of iris. (Method No. 105, Appendix.)

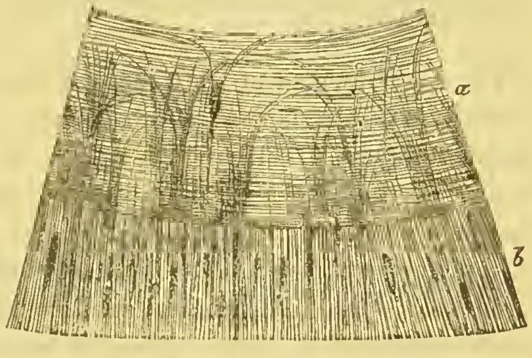

FIG. 306.—Surface view of human iris. *a*, sphincter; *b*, dilator of the pupil. (Iwanoff.)

The part of the eye where the sclerotic merges into the cornea requires special notice. Here the iris, cornea, and ciliary body impinge. The undulating fibres of the sclerotic merge into the bundles or laminæ of the cornea, and the canal systems of the two structures also freely communicate. The line of transition is not sharply indicated, but it is oblique in consequence of the external parts of the sclerotic becoming corneal sooner than the internal. The posterior end of the substantia propria of the cornea, the posterior elastic lamina, and the ciliary vein of the iris touch at a point known as the *angle of the iris* (Fig. 304, 15), and the iris here sends forward processes towards the posterior elastic lamina, which, as seen strongly developed in the eyes of the horse and ox, form the *ligamentum pectinatum iridis*. In man these are feebly developed. The posterior elastic lamina splits into fibres, which blend with the processes coming from the iris, and the angle of the iris is lined by a continuation of the endothelium on the posterior surface of the posterior elastic lamina.

The spaces, scarcely seen in man, that occur among the fibres of this region contain fluid. They communicate with the anterior chamber, and they are termed the *spaces of Fontana.*

3. The **Tunica Interna** consists of the *retina.* This structure, which is the terminal organ of vision, extends from the point of entrance of the optic nerve as far forward as the pupillary margin of the iris. It is divided into three zones: (1) the *pars optica retinæ*, in which the optic nerve fibres end, the only part sensitive to light, passing on to the ciliary body, and ending there in a sharp, indented line, the *ora serrata;* (2) the *pars ciliaris retinæ*, stretching from the *ora serrata* to the ciliary margin of the iris; and (3) the *pars iridica retinæ*, which covers the posterior surface of the iris from the ciliary margin to the edge of the pupil.

The *pars optica retinæ*, or *retina proper*, is divided, in the first instance, into (1) a *neuro-epithelial layer*, and (2) a *cerebral* layer. The neuro-epithelial layer has three layers, the cerebral layer has five, and if we add the layer of pigment, the retina shows nine layers which, proceeding from without inwards, are arranged in the following manner:—

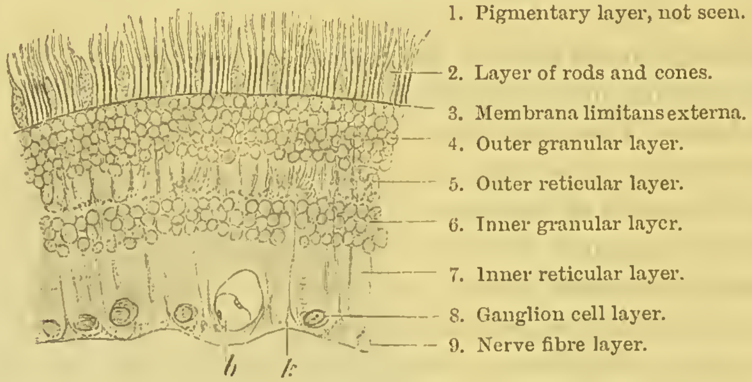

Fig. 307.—Vertical section of human retina. × 240 d. The stratum of nerve fibres is cut through transversely, and it is very thin, except at the back of the fundus of the eye. *b*, blood-vessels; *k*, radiate fibre cone. Some also reckon a *membrana limitans interna* as a 10th layer, but it is not an independent membrane. (Method No. 106, Appendix.)

The elements of the strata are partly of a nervous epithelial origin, and partly of a connective tissue origin, the latter forming the framework of the retina, or supporting structures. The most important of the supporting structures are the *radiate* or *Müllerian fibres*, which pass from the inner surface out to the layer of rods and cones. The inner ends of Müllerian fibres have cone-shaped feet (*k*), and these uniting give rise to a deceptive appearance of a membrane, the *membrana limitans interna* (Fig. 308, *l*). The fibres, becoming narrower, pass through the inner reticular layer, into the inner granular layer, and here they give off fine processes and show a nucleus (Fig. 315, *m*); the fibres then run on, giving off supporting processes through the outer reticular and the outer granular layer, up to the *membrana limitans externa*, with which they are connected. Minute fibres also spring from the upper surface of this membrane, which embrace the bases of the rods and cones, forming *fibre baskets* (Fig. 315, *f*). Finally, most of the reticular strata, and the small amount of cement in the stratum of ganglion cells, belong to the supporting structure.

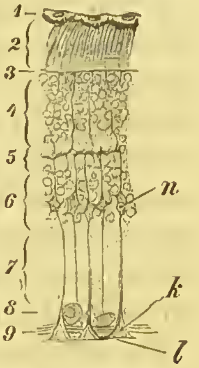

Fig. 308.—Perpendicular section of retina of rabbit. × 240 d. *1*, pigment epithelium (Fig. 150, p. 302, vol. I.); *2*, layer of rods and cones; *3*, *membrana limitans externa*; *4*, external granular layer; *5*, external reticular layer; *6*, internal granular layer; *7*, internal reticular layer; *8*, layer of ganglion cells; *9*, layer of nerve fibres; *k*, cone-shaped foot of Müllerian fibre; *n*, narrow part of fibre; *l*, *membrana limitans interna*. (Method No. 107, Appendix.)

(*α*) **The Cerebral Layers of the Retina.**—The layer of *nerve fibres* consists of naked axis cylinders, which form a kind of plexus. Found in greatest numbers at the point of entrance of the optic nerve, the fibres pass radially as far as the *ora serrata*, and as they pass on they bend backwards so as to end in the deeper (or more external) layers of the retina. The radiate arrangement is interfered with at the *macula lutea* (p. 589).

The layer of *ganglion cells* consists of a single layer of multipolar ganglion cells, which send a single nerve process (axis cylinder) towards the layer of nerve fibres, and one or more processes peripherally to the inner reticular layer. The *inner reticular layer* is formed of a fine network of supporting substance, probably the product of the cells of the inner granular layer, called *spongioblasts*, lying next it. . In this layer we also find protoplasmic filaments, which are derived from the ganglion cells, from the granules in the inner granular layer, and from the Müllerian fibres. The elements of the *inner granular layer* are of different kinds. The innermost consist of *spongioblasts*, which send one process into the inner reticular layer, and the rest of the layer is formed of minute bipolar ganglionic nerve cells. The central process from each may be traced into the inner reticular layer, and the peripheral process runs into the external reticular layer, and there dividing into two or more branches, it passes on to the surface. Here also we find the *nuclei* of the radiate or Müllerian fibres. The *outer reticular layer* is also a delicate network of supporting fibres, containing nuclei.

(*β*) **The Neuro-Epithelial Portion of the Retina.**—This consists of elements of two kinds: (1) *Rod and cone vision cells* (sometimes simply termed rods and cones), distinguished by having their nucleus in the inner half of the cells, while the outer half has no nucleus. This layer is sharply defined from the inner parts of the retina by a perforated membrane, the *membrana limitans externa.* (2) The layer of cells termed the outer granular layer. Strictly speaking, the cells in the outer granular layer and the rods and cones are the same structure, but the nucleus is in the part of the cell forming the outer granule, while it is absent from the rod or cone.

1. **The Rods.**—The *outer* half of each rod is an elongated cylinder, 60 μ long by 2 μ thick, which, in turn, is formed of a homogeneous external segment, and of a finely grained inner segment. The external segments alone contain vision-purple (Vol. I. p. 140), and the internal segment has, at its outer end, an ellipsoidal fibrous body. The *inner* half of the rod is called a *rod fibre*, and it consists of a delicate process or filament, having an enlargement containing a nucleus. This is the *rod granule.* The nucleus shows one to three bright transverse bands.

2. **The Cones.**—The outer half of each cone consists also of an external and an internal segment. The external segments are conical and they are shorter than those of the rods. The inner segments are thick and oval in form, and often show a longitudinal striation. The cone fibres are broad, they rest on the outer reticular layer, and they show a swelling containing a nucleus. This swelling is termed the *cone granule,* and it lies close to the *membrana limitans.*

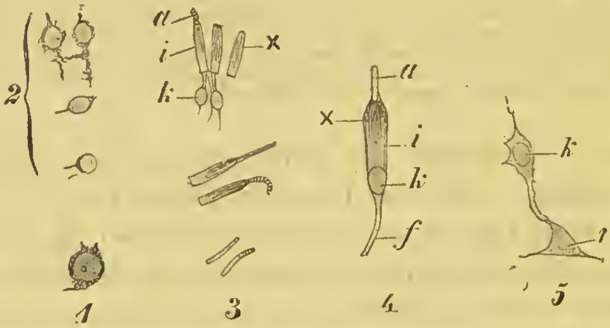

FIG. 309.—Elements of the retina of an ape, isolated. × 240 d. 1, ganglion cell; 2, from inner granular layer; 3, portions of rods. Immediately above figure 3 we see two external segments, one showing transverse striation, the beginning of resolution into small plates. Above, two small rods, showing the external segment of the lower one dividing transversely. At the top, more complete rods showing *a*, external segment; *i*, internal segment; *k*, rod granule; ×, fibrous structure. 4, cone, *a*, external segment; *i*, internal segment; *k*, cone granule; *f*, cone fibre; ×, fibrous appearance due to longitudinal striation. 5. Müllerian fibre; *k*, nucleus; *r*, conical foot. (Method No. 108, Appendix.)

The number of rods is greater than that of the cones. The latter occur at regular intervals, and three or four rods always lie between two cones (Fig. 313).

The *pigment epithelium* consists of a simple layer of hexagonal cells, which are free from pigment on their outer surface, turned to the choroid, while their inner surface shows numerous rod-shaped pigment granules, 1 to 5 μ in length. In albinos and on the tapetum the cells contain no pigment. (See Vol. I. p. 302, Figure 150.)

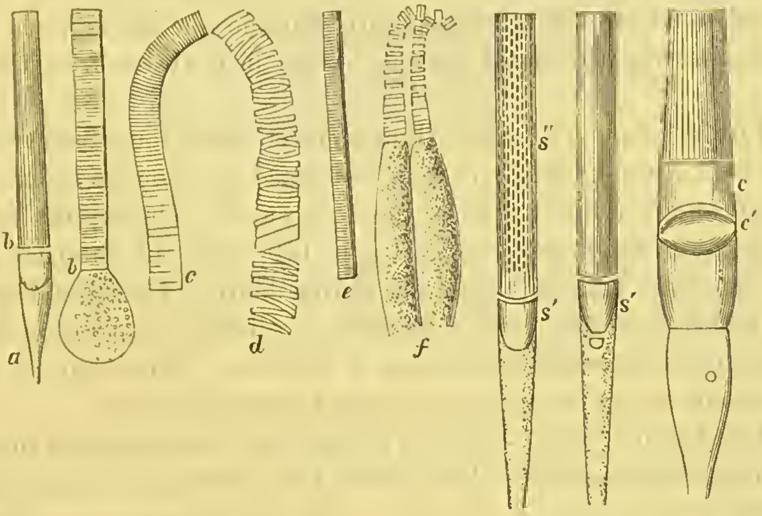

FIG. 310.—Various views of rods and cones. *a b c d*, rods from retina of frog. *a*, fresh rod, connected with inner segment, *a* ; *b*, a similar rod, showing tendency to transverse cleavage, in serum ; *c*, a similar rod, in a dilute solution of potash ; *d*, a rod cleaving into discs (1000 diameters) ; *e*, outer segment of rod from human retina in strong solution of perosmic acid, showing tendency to transverse cleavage (1000 diameters) ; *f*, twin cone from the retina of a perch ; *s' s''*, rods from retina of a falcon, showing highly refractile lenticular bodies in inner segment, *s' s'* ; the last figure to the right is a rod from the retina of a triton, showing a lenticular body, *c'*, in the internal segment. (Max Schultze.)

The structure of the retina, as above described, is modified in the *macula lutea*, or *yellow spot*, and *fovea centralis*, as well as in the *ora serrata.* In the *macula lutea* the delicate optic nerve fibres run from the point of entrance straight to the nearest mesial part of the *macula.* The thicker nerve fibres pass over and under these finer fibres, running in arches, and uniting in the lateral margin of the macula. The stratum of ganglion cells is thicker, so that instead of being in a single layer, they form as many as nine layers of superposed cells. The inner reticular, inner granular, and outer reticular layer show no obvious change, but the neuro-epithelial layer is formed solely of cone cells. At the margin of the *macula*, the rods diminish in number, and there are no rods in the *macula* itself. Only cones are found here, and the cone granules, being in great numbers, form several strata. The strata grow thinner towards the *fovea centralis*, the depression in the centre of the *macula lutea*, and in the *fovea*, they entirely cease. First the nerve fibre layer disappears, then the ganglion cells, then the inner reticular layer, then the inner granular layer, and finally the outer reticular layer, so that only the nerve epithelium is present in the centre of the *fovea—fundus foveæ*. A diffuse yellow pigment permeates only the brain stratum, but is absent in the neuro-epithelial stratum. Thus the *fundus foveæ* is colourless.

FIG. 311.—Right half of a vertical section through the *macula lutea* and *fovea centralis* of an adult man. × 70 d. On the right, the thickened strata of the *macula* are seen, which pass towards the left into the *fovea*. There are only traces of the optic fibres; none of the *membrana limitans externa* is to be seen with this magnifying power. The external segments of the cones are broken off. (Method No. 109, Appendix.)

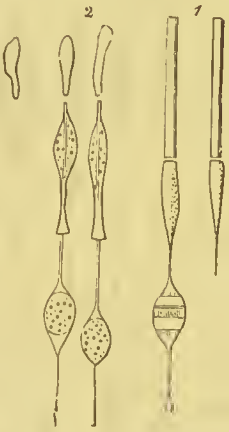

FIG. 312.—Rods of the retina. 1, from the guinea-pig; 2, from a monkey (*Macacus*). (Max Schultze.)

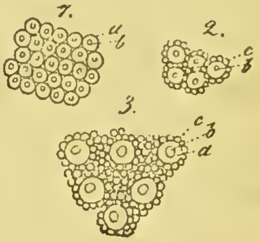

FIG. 313.—Ends of rods and cones. *a*, cones; *b*, centre of cones; *c*. rods. 1, from *macula lutea*; 2, border of same; 3, from middle of retina.

The layers of the retina also are deficient at the *ora serrata*; the nerve fibres and ganglion cells first disappear, then the rods vanish and only cones are present, and these are destitute of an external segment. The outer reticular layer then ceases, the outer and inner granular layers coalesce, and next the inner reticular layer is lost. The Müllerian fibres persist and are here strongly developed. The *ora serrata* is often the seat of senile changes. Thus gaps are seen, first in the outer granular layer, and extending into the other layers.

The *pars ciliaris retinæ* consists of a single layer of elongated cylindrical cells (Fig. 314, 11), which merge into one layer formed by the union of the outer and inner granular layers. These cells are covered by a cuticular membrane, a true *membrana limitans interna*, which is absent

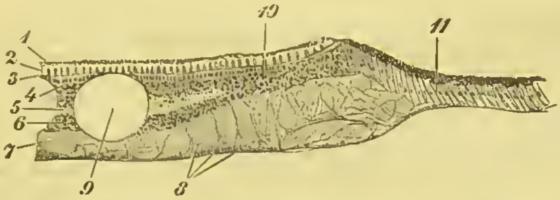

FIG. 314.—Meridional section of the *ora serrata* and of the parts bordering on it, the *pars ciliaris retinæ*, of a woman 78 years of age. × 70 d. 1, pigment epithelium; 2, cones lacking external segment; 3, *membrana limitans externa*; 4, outer granular layer; 5, outer reticular layer; 6, inner granular layer; 7, inner reticular layer; 8, Müller's fibres; 9, gap in the retina; and at 10, the outer and inner granular layers coalesce, and at 11 pass over into the cells of the *pars ciliaris retinæ*. (Method No. 110, Appendix.)

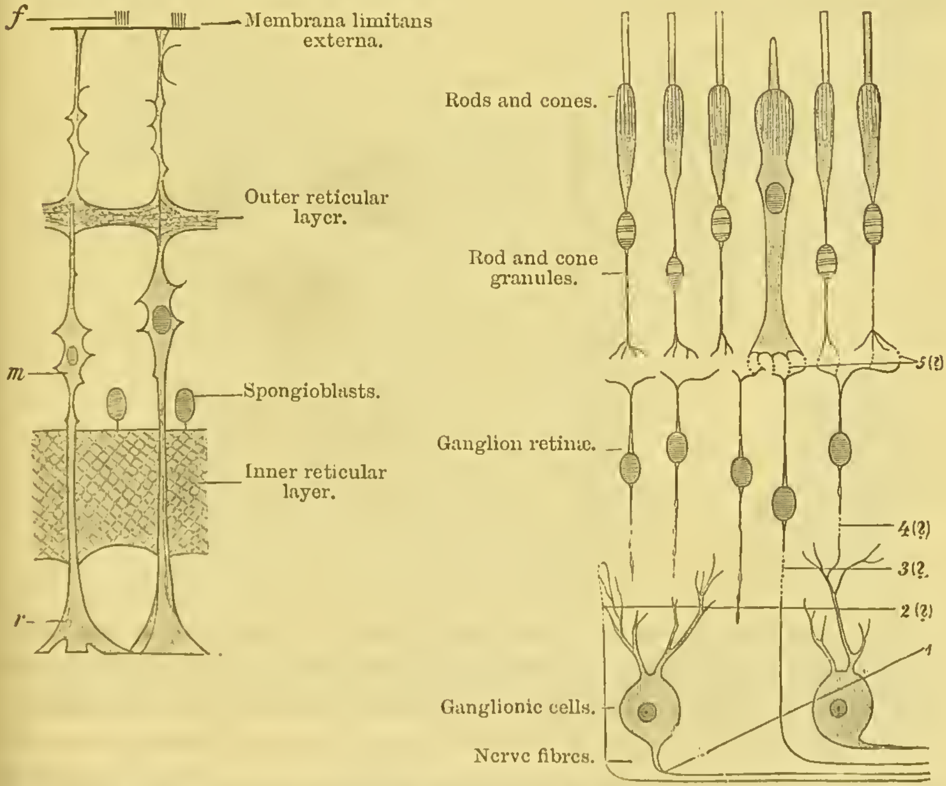

FIG. 315.—Diagram showing, on the left, the supporting elements and, on the right, the nervous elements of the retina. The figure on the left: *f*, the fibre baskets; *n*, nucleus of Müllerian fibres; *r*, base of the fibre. The figure on the right shows: 1, a nerve fibre passing to a ganglionic cell; 2, processes of ganglionic cell passing outwards; 3, nerve fibre passing direct to granule in ganglion retinæ; 4, process of ganglion cell passing to granule; and 5, fibre from granule in ganglion retinæ breaking up into fibrils which are connected with fibres of rods and cones.

from other parts of theretina. The outer surface of the cells is in contact with the pigment cells, which are continued from the pigment epithelium.

The *pars iridica retinæ* has already been described (page 584).

As to the connections of the elements of the retina, all that is certain is that the ganglion cells are united to the axis cylinders of fibres of the optic nerve, but as the number of these fibres is very much greater than that of the cells, they must have some other connections, such as with the other processes of the same ganglion cells. A direct connection of the rods and cones with the nerve fibres or with the processes of the ganglion cells has not been established with certainty. It is highly probable, however, that such a connection exists in the outer reticular layer. There is no doubt of the fact that the rods and cones are the parts of the retina sensitive to light.

3. **The Optic Nerve.**—This nerve, in its intra-orbital course, is enclosed in sheaths, which are continuations of the membranes of the brain. Externally, we find the dural sheath (Fig. 316, 1) consisting of compact longitudinal bundles of connective tissue. Within this there is a very delicate arachnoideal sheath (2) which sends numerous trabeculæ inwards to the sheath formed by the *pia mater*. Fine fibres also pass between the dural and arachnoideal sheaths. Lastly, we find

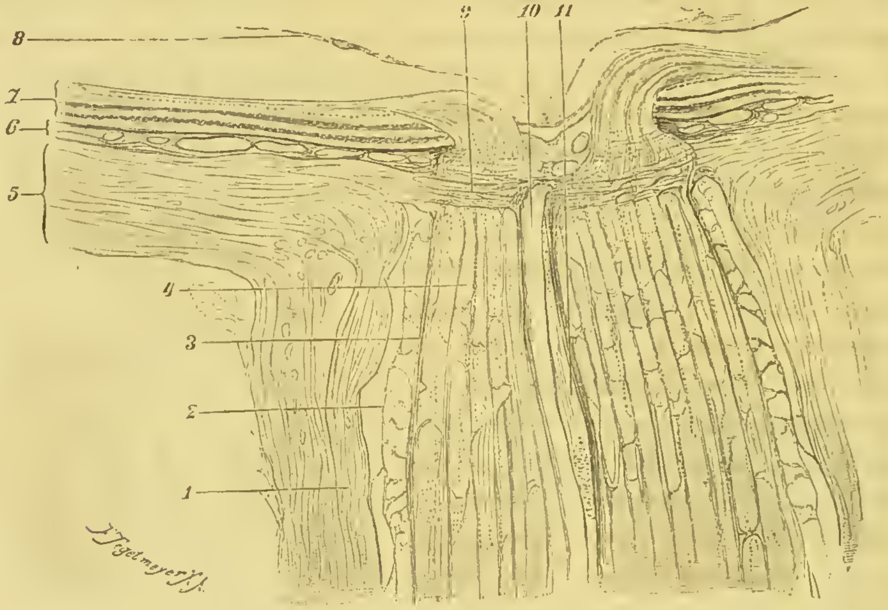

Fig. 316.—Longitudinal section of the entrance of the optic nerve of man. × 15 d. 1, dural sheath ; 2, arachnoideal sheath ; 3, pial sheath ; 4, bundles of fibres of optic nerve ; 5, sclerotic ; 6, choroid ; 7, retina ; 8, detached *membrana hyaloidea* ; 9, fibres of the *lamina cribrosa* ; above these is seen the narrowing of the optic nerve ; 10, artery ; 11, *vena centralis retinæ*, cut through longitudinally and higher up cut through tranversely. (Method No. 111, Appendix.)

innermost the pial sheath, closely surrounding the optic nerve, and sending laminæ of connective tissue into it. These unite so as to form a trellis work. The bundles of nerve fibres consist of fine medullated fibres, destitute, however, of Schwann's sheath. They are cemented together by neuroglia, rich in oval nuclei. At the point of entrance of the optic nerve, the dural sheath merges into the sclerotic, and the arachnoideal sheath ends in fibres, so that the sub-dural space situated externally to the arachnoideal sheath communicates with the sub-arachnoideal space, situated within the sheath. The pial sheath blends with the sclerotic, which is here perforated by numerous small holes for the passage of the fibres of the optic nerve, a part termed the *lamina cribrosa*, and in the formation of which the choroid coat also participates. The nerve fibres lose the medullary sheath at this point, and consequently the whole nerve becomes narrower. In the centre of the nerve, we find a small artery and the *vena centralis retinæ*, and the connective tissue sheath of these vessels is continued from the pial sheath and from the *lamina cribrosa*.

4. **The Lens.**—This consists of a proper substance (*substantia propria*), covered on its anterior surface with epithelium, and surrounded by a capsule. The *substantia propria* is composed of a softer cortical matter surrounding a nucleus, and it is formed of epithelial cells, which are drawn out to an enormous extent longitudinally, so as to form the *fibres of the lens*. These are hexagonal prismatic bands, thickened at their posterior extremity. The fibres of the cortex have smooth edges, and, near the equator, they show an oval nucleus; those of the central part of the lens have indented or serrated margins and they have no nuclei. Cement substance binds the fibres together, more especially at the anterior and posterior poles, where we find on maceration a beautiful star-like appearance. The fibres run in the lens in a meridional direction, beginning at the anterior star and ending at the posterior star, but no fibres pass the entire half of the lens, as the nearer a fibre starts from the anterior pole the further is it removed from the posterior pole at its termination. The

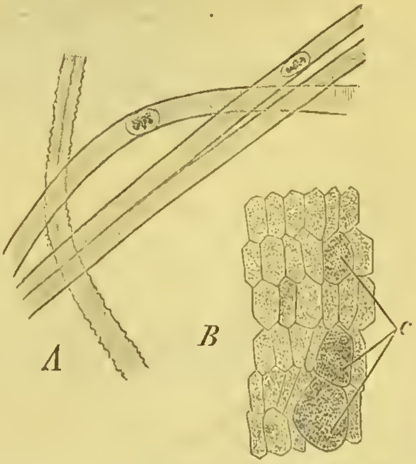

FIG. 317.—Lens fibres of a newly born child. A, isolated fibres, three having smooth margins, and those of the other indented. × 240 d. (Method No. 112, Appendix.) B, transverse section of lens fibres from man; c, divided portions of thickened end. × 560 d. (Method No. 113, Appendix.)

epithelium of the lens is a simple layer of cubical cells, which covers the anterior surface as far as the equator, where it merges into the fibres of the lens. The *capsule of the lens* is a homogeneous elastic membrane, 11 to 15 μ thick in front, and 5 to 7 μ behind. It is partly a cuticular formation formed by the epithelial cells, and partly a metamorphosed product of the embryonic connective tissue.

5. **The Vitreous Humour, or Vitreous Body,** is a fluid substance, the *humor vitreus*, interspersed with fibres passing through it in many directions. The outer surface is covered by a strong membrane, the *membrana hyaloidea.* The vitreous also contains round cells like leucocytes and stellate and spindle-shaped cells, sometimes showing vacuoles in their protoplasm.

6. **The Zonula Ciliaris.**—From the anterior margin of the *membrana hyaloidea*, and near the *ora serrata*, delicate fibres pass, in a meridional direction, towards the lens. They pass from the inner surfaces of the ciliary processes to the equator of the lens, where they are attached to the capsule. These fibres form a membrane, broken here and there by apertures, and known as the *zonula ciliaris* or *zonule of Zinn*, the triangular space between the fibres, passing to the anterior and the posterior surfaces of the lens, being called the *canal of Petit.* It is not a complete canal, but shows gaps in its anterior and posterior walls.

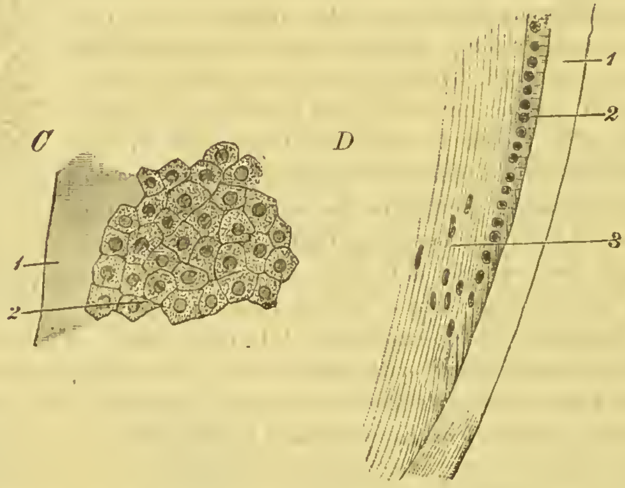

FIG. 318.—Lens capsule and lens epithelium from adult man. *C*, inner surface. (Method No. 114, Appendix.) *D*, seen from side in a meridional section through the equator of the lens. 1, capsule; 2, epithelium; 3, fibres of lens. (Method No. 115, Appendix.)

7. **The Blood-Vessels of the Eyeball.**—These are divided into two groups, which are closely related only at the point of entrance of the optic nerve.

(1) **The Vascular Region of the Vasa Centralia Retinæ.**—The *arteria centralis retinæ*, about 15 to 20 mm. behind the eyeball, is in the axis of the optic nerve, and it runs forwards in this position to the entrance of the nerve. It here divides into two chief branches, one going upwards and the other downwards, and these supply the entire *pars optica retinæ* as far as the *ora serrata*. The artery gives off numerous branches in the optic nerve itself, each enclosed in a sheath of *pia mater* and running between the nerve fibres. These anastomose with small vessels passing into the nerve, from the surrounding fatty tissue and also with twigs of the *arteriæ ciliares posticæ breves* (Fig. 320, *c*). In the retina the artery is resolved into capillaries, which extend to the outer reticular layer, and the veins arising from these run parallel with the arteries, and ultimately form a *vena centralis retinæ*, also in the axis of the optic nerve. Thus, it is only the cerebral layer of the retina that contains vessels, and there are none consequently in the *fundus foveæ centralis*. In the embryo, a branch of the *arteria centralis retinæ*, the *arteria hyaloidea*, passes through the vitreous body to the posterior surface of the lens. It soon atrophies, but the canal in which it ran may be seen in the eye of the adult, and is known as the *canal of Cloquet*, or *canalis hyaloideus*.

(2) **The Vascular Region of the Vasa Ciliaria.**—Here the veins run in quite a different way from the arteries. (A) *The arteries.* The *arteriæ ciliares posticæ breves* (*a*) supply the smooth part of the choroid, while the *arteriæ ciliares posticæ longæ* (*b*) (Fig. 320, Arabic numerals) and the *arteriæ ciliares anticæ* (*c*) (Fig. 320, Greek letters) are distributed to the ciliary region and the iris. The *arteriæ ciliares posticæ breves*, about twenty in number, perforate the sclerotic about the point of entrance of the optic nerve, and after giving off twigs (II) which supply the posterior half of the outer surface of the sclerotic, they are resolved into a narrow-meshed capillary network, the *membrana chorio-capillaris* (III) (Fig. 320). They anastomose at the entrance of the optic nerve with branches of the *arteria centralis retinæ* (Fig. 320, *c*), forming the *circulus arteriosus nervi optici*, and also in the *ora serrata* with twigs of the *arteriæ ciliares posticæ longæ* and of the *arteriæ ciliares anticæ*. Both the *arteriæ ciliares posticæ longæ* (1) perforate the sclerotic, near the entrance of the optic nerve. The one vessel passes to the nasal and the other to the temporal side of the eyeball, between the choroid and sclerotic, running as far forward as the ciliary region, where each vessel divides into two divergent branches, passing longitudinally to the ciliary margin of the iris. These branches anastomose with the branches of the other long ciliary artery to form a ring of vessels called the *circulus iridis major*. From this circle numerous twigs pass to the *processus ciliares* (3) and to the iris (4). Near the margin of the pupil the branches form an incomplete ring, the *circulus iridis minor*.

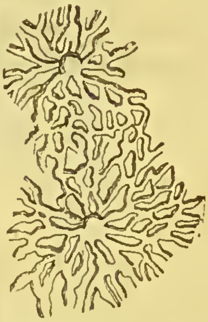
Fig. 319. — Arrangement of the capillaries of the *chorio-capillaris* of the cat.

The *arteriæ ciliares anticæ* come from the arteries supplying the *recti* muscles of the eyeball. They enter the sclerotic near the margin of the cornea, partly unite with the *circulus iridis major* (*β*), partly supply the ciliary muscle, and partly give branches which anastomose in the *membrana chorio-capillaris*. Before entering the sclerotic, they give off twigs posteriorly for the anterior half of the sclerotic, anteriorly for the conjunctiva of the sclerotic, and for the margin of the cornea. The cornea has no vessels, and we find only at its rim a looped network in the anterior lamellæ of the *substantia propria.*

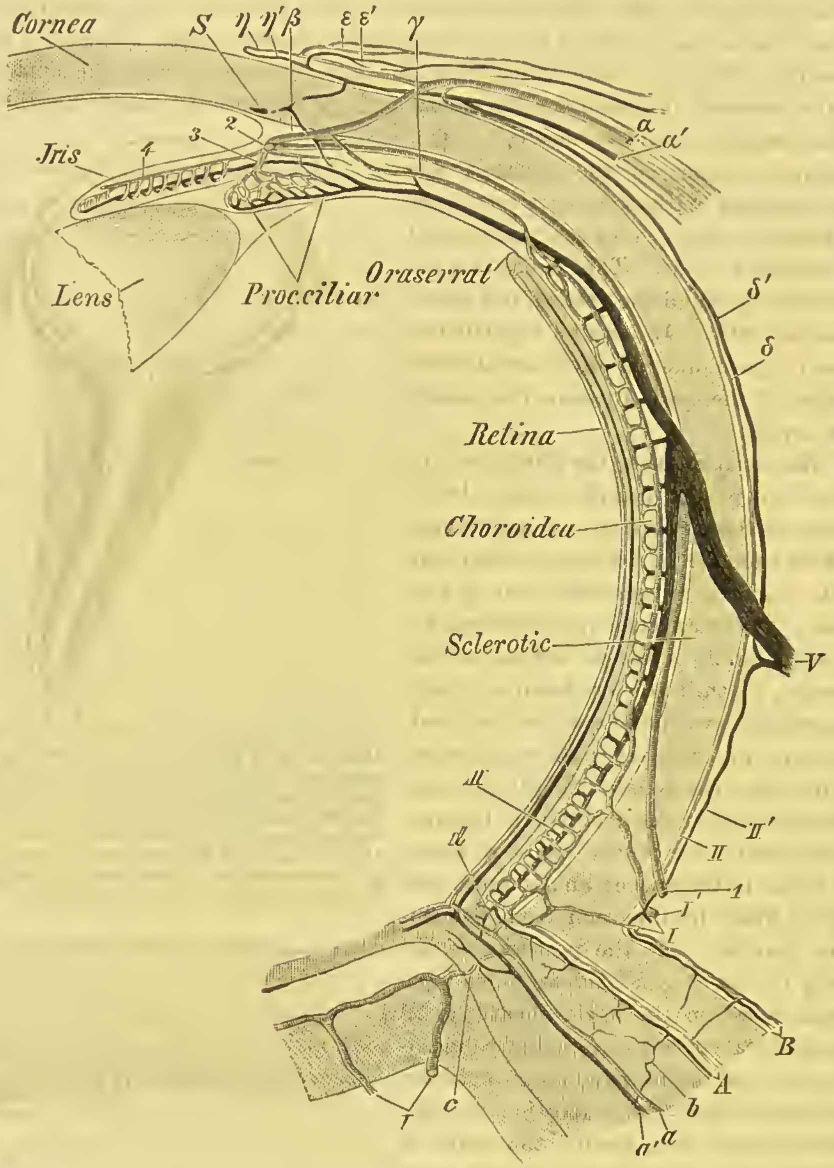

FIG. 320.—Diagram of the vessels of the eyeball. The *tunica externa* is finely dotted, the *tunica media* is white, and the *tunica interna* and optic nerve are marked by crossed lines. The arteries are clear and the veins black. *Region of the vasa centralia retinæ* (in small Roman letters). *a*, artery; *a′*, *vena centralis retinæ*; *b*, anastomosis with vessels of sheath; *c*, anastomosis with branches of the *arteriæ ciliares posticæ breves; d*, anastomosis with choroideal vessels. *Region of the vessels of the sheath* (in large Roman letters). *A*, inner; *B*, outer, sheath vessels. *Region of the vasa ciliaria postica brevia* (in Roman numerals). *I*, artery; *I′*, *venæ ciliares posticæ breves; II*, episclerotic arteries; *II′*, various episclerotic branches of *V*; *III*, capillaries of the *membrana chorio-capillaris. Region of the vasa ciliaria postica longa* (in Arabic numerals). 1, *arteria ciliaris postica longa;* 2, *circulus iridis major*, cut transversely; 3, branches to the ciliary region; 4, branches for the iris. Region of the *vasa ciliaria antica* (in Greek letters). α, artery; α′, *vena ciliaris antica*; β, connection with the *circulus iridis major;* γ, connection with *membrana chorio-capillaris*; δ, arterial, δ′, venous, episclerotic branches; ε, arterial, ε′, venous branches for the conjunctiva of the sclerotic; η, arterial, η′, venous branches to the corneal margin; *V*, *vena vorticosa; S*, section of Schlemm's canal.

The large *veins* run towards the equator, where they form four or five small trunks, the *venæ vorticosæ*, which perforate the sclerotic and open into one of the ophthalmic veins. The small *venæ ciliares posticæ breves* (I') run parallel to the *arteriæ ciliares posticæ breves* and to the *arteriæ ciliares anticæ*. The *venæ ciliares anticæ* (Fig. 320, a') obtain twigs from the ciliary muscle, from the episclerotic vascular network (δ), from the conjunctiva of the sclerotic (ϵ), and from the loops at the margin of the cornea (η'). The episclerotic veins, on the equator, are also connected with the *venæ vorticosæ*. The anterior ciliary veins are also related to *Schlemm's canal*. This canal is a fissure running round the cornea, but really in the sclerotic. It may be regarded as a lymph space opening into the anterior chamber of the eye. By some it is looked on as a vein.

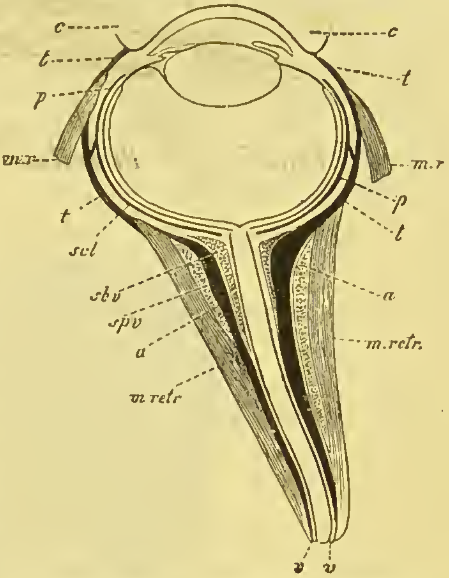

FIG. 321.—Posterior lymphatic circulation in the eye of a pig. *c*, conjunctiva; *m.r*, recti muscles; *m.retr.*, *retractor bulbi; a*, layer of fat; *v*, external sheath of optic nerve; *t*, Tenon's space opening behind into the supravaginal, *spv; sbv*, subvaginal space between the internal and external optic nerve sheaths; *p*, perichoroideal space communicating, by oblique passages, with Tenon's space.

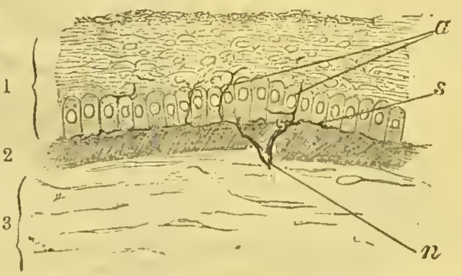

FIG. 322.—Vertical section through the human cornea. × 240 d. 1, corneal epithelium; 2, anterior elastic lamina; 3, a small part of the *substantia propria*; *n*, nerve dividing and perforating the anterior elastic lamina; *s*, subepithelial plexus, lying under the cylindrical cells; *a*, fibres belonging to the intra-epithelial plexus, running up between the epithelia cells. (Method No. 116, Appendix.)

8. **The Lymphatics of the Eyeball.**—The eye has no proper lymph vessels, but a number of fissure-like spaces, anastomosing with each other. There are two lymphatic regions, an anterior and a posterior. To the anterior region belong (1) the small canals of the cornea and of the sclerotic; (2) the anterior chamber, which communicates with Schlemm's canal, and, by means of capillary fissures between the iris and the lens, with (3) the posterior chamber of the eye, which, in turn, is connected with (4) the canal of Petit. The three latter spaces anastomose, and may be filled by injection from the anterior chamber. To the posterior region belong (1) the *canalis hyaloideus*, and the fissures between the optic sheaths; (2) the sub-dural space and the sub-arachnoideal space, and the narrow fissure between the choroid and the sclerotic; (3) the perichoroideal, and, finally, the space of Tenon, on the dural sheath of the optic nerve as far as the *foramen opticum*. These spaces are filled with injection from the sub-arachnoideal space of the brain. The spaces contain a fluid filtered from the blood-vessels, which also penetrates the vitreous humour. The amount of fluid in the posterior spaces is very small, but it facilitates the movements of the eyeball (Fig. 321).

9. **The Nerves of the Eyeball.**—These perforate the sclerotic in the region of the entrance of the optic nerve, and run between the sclerotic and choroid anteriorly.

During their course they give off branches, provided with ganglion cells, to the choroid, and, finally, they form a ring-like plexus in the ciliary region, termed the *orbiculus gangliosus ciliaris.* From this plexus branches pass to the ciliary muscle, the iris, and the cornea. The nerves for the cornea pass first into the sclerotic, and form a plexus round the margin of the cornea, the *plexus annularis*, from which branches run into the conjunctiva and the cornea. The fibres entering the substance of the cornea lose their white substance, and run on as naked axis cylinders. They form networks as follows: in the deepest layers of the cornea, a plexus of the stroma; then a sub-basal plexus under the anterior elastic lamina; and next a sub-epithelial plexus, close below the epithelium. From the latter plexus, delicate nerve fibres issue, which form again a very fine network, the intra-epithelial plexus, and they finally end as free fibres between the cells (Fig. 322)

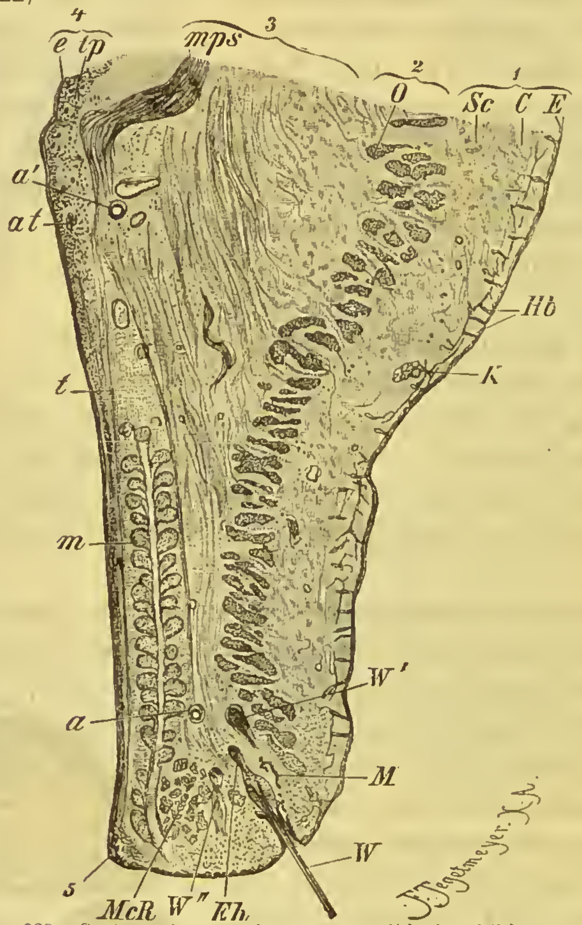

Fig. 323.—Section through the upper eyelid of a child. × 10 d. *1, skin portion—E*, epidermis; *C*, cutis; *Sc*, subcutaneous tissue; *Hb'*, hair follicles; *K*, sweat gland; *W*, eyelash, with rudiment of a reserve hair (*Eh*); *W' W″*, portions of follicles of eyelashes; *M*, a Mollian gland. *2, Region of the orbicularis palpebrarum muscle; O*, bundles cut transversely; *McR, musculus ciliaris Riolani. 3*, tendon of the *levator palpebrae superioris, mps. 4, conjunctival region—e*, conjunctival epithelium; *tp, tunica propria; at*, gland; *t*, tarsus; *m*, Meibomian gland; *a*, transverse section of the *arcus tarseus. 5, cornu of the lid.* (Method No. 117, Appendix.)

10. **The Eyelids.**—These are folds of the external skin, enclos-

ing muscles, connective tissue, and glands. The outer layer is like ordinary skin, and the inner, next the eyeball, is modified, and is termed the *conjunctiva palpebralis.* The outer layer covers the free margin of the lid. In a sagittal section, we see the following parts (Fig. 323): (1) The external skin. It shows very fine hairs, small sweat glands, and often pigmented connective tissue. The subcutaneous tissue is very loose, and contains many fine elastic fibres, but no fat cells, or very few. The *cutis vera* is more compact, and shows long papillæ pointing in the direction of the margin of the lids. Implanted on the margin we find two or three rows of large hairs, the eyelashes or cilia (*IV*), whose roots pass into the cutis. The eyelashes develop, reach maturity, and drop out, during a period of from 100 to 150 days. The hair follicles have the ducts of small sebaceous glands opening into them, and they also receive the ducts of the glands of Moll. These latter are modified sweat glands. (2) Below the subcutaneous tissue we find transverse bundles of the *orbicularis palpebrarum* muscle, and the part of this muscle immediately behind the eyelashes is termed the *musculus ciliaris Riolani.*

(3) Behind the orbicularis muscle we find the tendon of the *levator palpebræ superioris.* Some of its fibres end in connective tissue, forming the *fascia palpebralis*, and others, enclosing smooth muscular fibres, pass on to the upper margin of the tarsus. The smooth fibres constitute *Müller's muscle*, or *palpebralis superior.* Similar smooth fibres occur in the lower eyelid, forming a *palpebralis inferior.*

(4) The *tarsus* is a compact plate of connective tissue which gives support to the eyelid. It lies in front of the palpebral conjunctiva, and it occupies the lower two-thirds of the eyelid. The Meibomian glands exist in the tarsus (Fig. 324). They are elongated bodies, consisting of a wide duct, into which short stalked vesicles open. The duct opens at the corner of the lid. The gland is a modified sebaceous gland. Along the upper end of the tarsus, we find small racemose glands, somewhat tubular in structure, and hence called *acino-tubular glands.* They occur especially in the nasal half of the eyelid, and they are modified lachrymal structures.

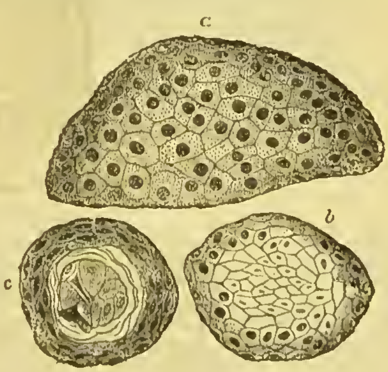

FIG. 324.—Meibomian gland. *a*, acinus; *b*, small acinus; *c*, duct.

Behind the tarsus lies the conjunctiva, consisting of an epithelium and a *tunica propria.* The epithelium is stratified cylindrical epithelium, with roundish cells in the deeper parts, and small cylindrical cells on the upper surface. On the surface we find a narrow cuticular border. Goblet cells also occur. The lower part of the conjunctiva is smooth, but in the upper region we may find depressions which are sometimes so deep as to look like glands. The *tunica propria* consists of connective tissue. Lymph cells occur in it, and in some animals, as in ruminants, they may form small lymphoid glands. Leucocytes wander through the epithelium to the surface. The palpebral conjunctiva merges into that covering the front of the eyeball. At the bend, the underlying tissue is loose and contains small mucous glands. The conjunctiva on the sclerotic shows stratified pavement epithelium, which is continuous with that of the cornea.

The rudimentary third eyelid (*plica semilunaris*) consists of connective tissue and of stratified pavement epithelium. The *caruncula lacrymalis* resembles in its finer structure the skin, but the *stratum corneum* is absent. They contain very fine hairs and sebaceous and sweat glands.

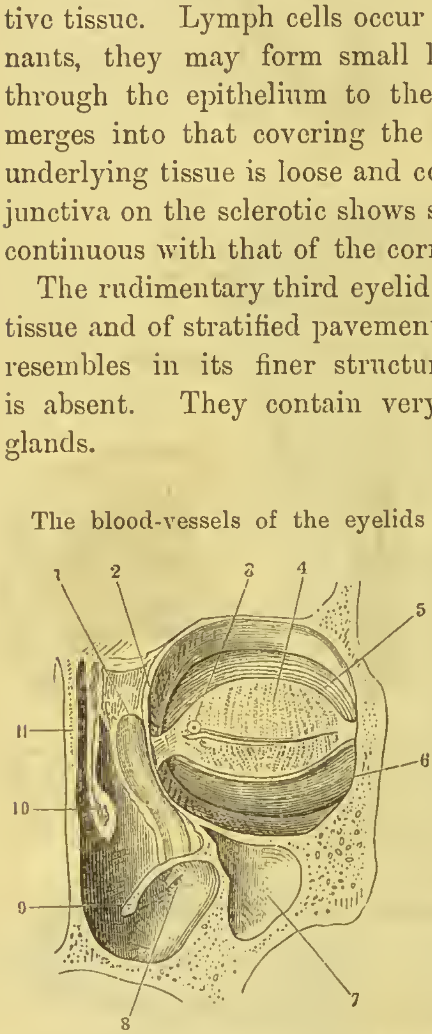

FIG. 325.—View of the right naso-lachrymal duct, two-thirds natural size. 1, upper end of lachrymal sac; 2, *ligamentum palpebrale mediale*; 3, orifice of tear duct; 4, Meibomian glands in upper eyelid; 5, *stratum orbitale* of *orbicularis palpebrarum*; 6, muscular stratum in lower eyelid; 7, right *sinus maxillaris*; 8, opening of the *ductus naso-lacrymalis*; 9, inferior meatus of nose; 10, middle meatus; 11, *septum narium.* (Krause.)

The blood-vessels of the eyelids come from vessels which, running from the outer and inner angle of the eye, form an arch on the margin of the lid, *arcus tarseus*, and another arch along the upper border of the tarsus, the *arcus tarseus externus.* They supply the tissues of the eyelid by minute twigs. Some of these, supplying the conjunctiva, anastomose with the *arteria cilaris antica.*

The lymphatics form a dense network in the tarsal conjunctiva. Those in the conjunctiva in front of the sclerotic and around the margin of the cornea probably unite with the small canals of the latter.

The nerves form a rich plexus on the margin of the lid, and in the conjunctiva of the cornea they terminate in end knobs, found below the epithelium.

11. The Lachrymal Organs.—The lachrymal gland is a racemose structure having several ducts. The ducts (Fig. 326, *B*) are clothed with cylindrical epithelium, and they end in intercalary portions, clad with pavement epithelium. These pass into *acini*, showing the characters of a serous gland.

The small lachrymal canals are lined by stratified pavement epithelium, resting on a *tunica propria,* which is rich in elastic fibres. Longitudinal muscular fibres are also present. The lachrymal sinus and the nasal tear duct consist of a *tunica propria,* containing adenoid tissue, and separated from the periosteum underneath by a dense plexus of veins. There is also a stratified layer of cylindrical epithelium.

FIG. 326.—Transverse section of lachrymal gland of man. × 240 d. *A*, body of gland; *a*, acinus; *a'*, group of acini; *s*, intercalary portion; *s'*, intercalary portion, in transverse section, showing cylindrical cells; *b*, connective tissue; *B*, transverse section of duct; *e*, two stratified layers of cylindrical epithelium; *b*, connective tissue. (Method No. 118, Appendix.)

The structure described in the foregoing pages is an example of the most complex form of a simple eye. It is interesting to contrast it with the optical apparatus termed a compound eye, as this is found in crustacea and insects (Fig. 327). The typical compound eye consists of a number of corneal lenses (*c*) developed from the cuticle. Below these we find crystalline cones, one to each lens, and still deeper, nervous structures termed *retinulæ* (*r*). Each of these again consists of an axial rod, or *rhabdom,* with cells surrounding it.

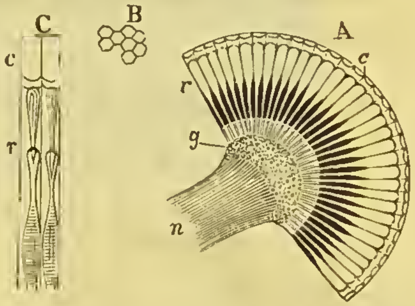

FIG. 327.—Diagrammatic view of a compound arthropod eye. *A*, section through the eye; *B*, corneal facets; *C*, two segments of eye; *c*, corneal lenses; *r*, retinulæ with rhabdoms; *n*, optic nerve; *g*, ganglionic swelling of optic nerve. (Gegenbaur.)

CHAP. II.—THE OPTICAL CONSTRUCTION OF THE EYE.

A *luminous sensation* may be caused by irritation of the retina or of the optic nerve. Pressure, cutting, or electrical shocks act as stimuli, but the normal stimulus is the action of light on the retina. Physically, light is a vibration occurring in the ether which pervades all space. When the vibrations of light act on the retina with sufficient intensity, molecular changes occur in that structure, which in turn excite the fibres of the optic nerve; then a stimulus is conveyed to the brain, and the result is a sensation of light. Thus, light is regarded by the physicist as a mode of movement, or a condition of *matter*; whilst the physiologist studies the effect of these movements on the *sentient organism.* Such movements, acting on retina, optic nerve, and brain, result in *consciousness* of a particular kind, which we call a *luminous sensation.* Outside of the body, these movements have been studied with a great degree of accuracy and precision; but within the organism, as we have to deal with more complex conditions, it is impossible to follow them in the same way. We are conscious only of the result, say of red or of violet light; but the physicist states that, in the first instance, the sensation of red, at the lower end of the spectrum, is produced by 435,000,000,000,000 (billions)'of impulses per second, and that the sensation of violet, at the upper end, corresponds to 764 billions of impulses per second. Below the low red, and above the high violet, vibrations still occur, but they do not cause luminous sensations. The rays below the low red are thermal rays, whilst those beyond the extreme violet are distinguished by their chemical activity. Thus, we have thermal, luminous, and actinic rays, the intensities of which are represented graphically in Fig. 328.

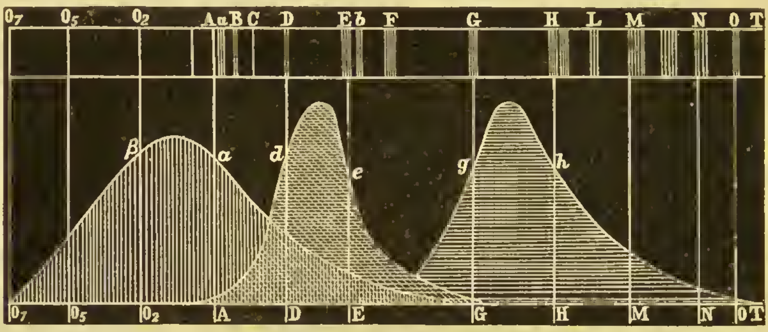

FIG. 328.—Curves of the intensity of thermal, luminous, and actinic rays in the different regions of the solar spectrum. The *luminous* spectrum ranges from A to G; the *ultra violet,* from G to T; and the *ultra red,* from O_7 to A.

The number of vibrations of the extreme violet is not double that of the low red, so that the sensibility of the eye to vibrations of light does not range through an octave. The ultra-violet rays may act on the retina in certain conditions, as when they are reflected by a solution of sulphate of quinine, constituting the phenomenon of *fluorescence.* White light, when passed through a prism, is decomposed or dispersed so as to produce a spectrum.

We shall now consider some of the phenomena of light on which visual sensations depend. A luminous body generates that rhythmical disturbance of the surrounding ether, which, when it reaches the retina of the eye, gives rise to the sensation of light. This disturbance is propagated from the luminous body in all directions, with a velocity of about 300,000 kilometres per second, which for most purposes may be regarded as instantaneous propagation.

When a screen, with a small hole through it, intercepts all the light emanating from a luminous point, excepting a small beam, this beam is observed to proceed in a straight line, which passes through the luminous point and the hole in the screen. This experiment illustrates the *rectilinear propagation of light;* every beam may be supposed to consist of an infinite number of rays, each of which continues in a straight line, unless when reflected, refracted, or otherwise intercepted. In the Newtonian emission-theory, each ray was supposed to be the path of one light corpuscle.

Reflexion.—When light falls on a smooth surface, the whole or part of each ray suffers a change by reflexion, in which case the reflected ray proceeds along a straight line, lying in that plane, perpendicular to the reflecting surface, which contains the original line of the ray; and the new and old lines of the ray make equal angles with the reflecting surface (Fig. 329).

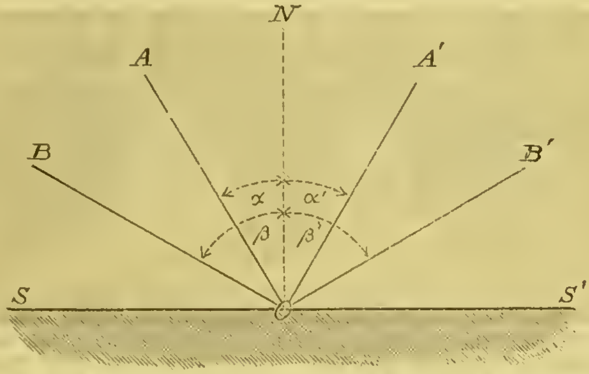

FIG. 329.—To illustrate law of reflexion of light. $S S'$, reflecting surface; $N O$, line perpendicular to $S S'$; $B O$, ray reflected in direction $O B'$; $A O$, ray reflected in direction $O A'$; α, angle of incidence of ray, $A O$; α', angle of reflection of $O A'$; β, angle of incidence of ray $B O$; β', angle of reflection of $O B'$.

Refraction.—When the media on both sides of the surface are transparent, as, for example, glass and air, a part of the ray may undergo refraction, *i.e.*, it becomes bent at the surface at the point where it enters the second medium, in such a way that the refracted ray lies in the same plane which contains the original and reflected rays, and in such a direction as to satisfy the equation—

$$\mu_1 \sin \alpha_1 = \mu_2 \sin \alpha_2 ;$$

μ_1 and μ_2 being the *indices* of *refraction* of the first and second media respectively, and α_1 α_2 the angles made with the normal to the surface by the original and refracted rays respectively.

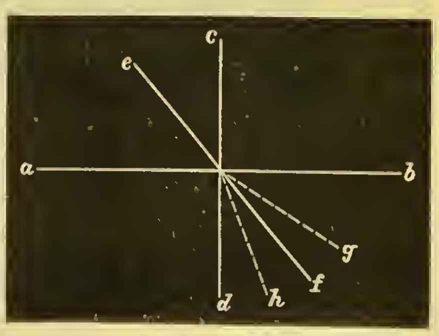

FIG. 330.—Diagram illustrating the refraction of light.

For example, in Fig. 330, suppose the line, a b, to represent a surface separating two media of different refractive power, and e f the direction of a ray which meets the surface obliquely. If the refractive powers of the two media had been equal, the ray would have proceeded with its direction unaltered; if the second medium has the higher index of refraction, the ray will be bent towards h; if, on the contrary, the first medium have the higher index of refraction, the ray will go towards g, *i.e.*, away from the normal, $c\ d$.

A normal ray, as $c\ d$, has its direction unaltered in every case.

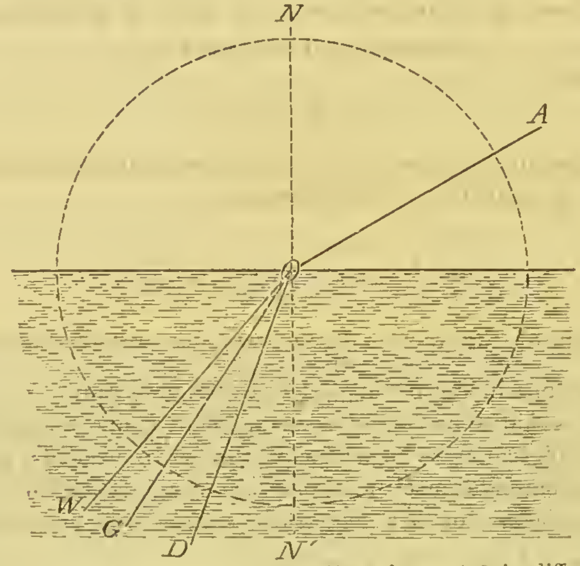

Fig. 331.—Diagram showing refraction of ray, *A O*, in different media. *O W*, water; *O G*, crown glass; *O D*, diamond.

The value of μ is constant for each medium, whatever be the angle of incidence, and is usually greater for a medium whose density is greater. Thus, when a ray passes from a rarer to a denser medium, its course is brought nearer to the normal to the separating surface (Fig. 331).

The value of μ for a vacuum is taken as unity, and that for air is very slightly greater. For water it is about $\frac{4}{3}$ and for some kinds of glass $\frac{3}{2}$.

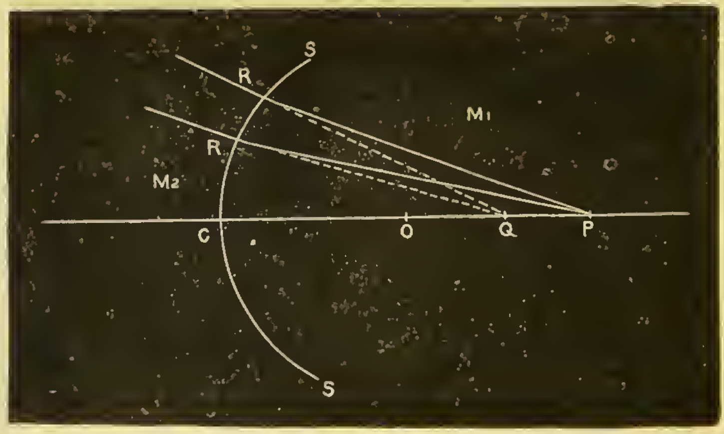

Fig. 332.—Formation of image by refraction at a spherical surface.

Formation of an Image by Refraction at a Spherical Surface.—Let P be a luminous point in a medium whose refractive index is μ_1, and let SS be the surface of separation between this medium and one whose refractive index is μ_2. The ray, POC, which passes through the centre, O, of the spherical surface and meets the surface at right angles, is called the axis. All rays which do not diverge far from the axis are so refracted that their lines of direction after refraction pass, if produced backwards, very nearly through a certain point, Q, which is called the *image* of P. The property of this point is that the rays from P proceed after refraction as if they had come from Q. The position of the point Q is determined as follows—

Let $CO=r$, $CP=u$, and $CQ=v$.

Then the equation

$$\frac{\mu_2}{v}-\frac{\mu_1}{u}=\frac{\mu_2-\mu_1}{r}$$

enables us to determine v, since r and u as well as μ_1 and μ_2 are known.

This equation is equivalent to the following—

$$\frac{\frac{\mu_2}{\mu_1}}{v}-\frac{1}{u}=\frac{\frac{\mu_2}{\mu_1}-1}{r}, \quad \text{or} \quad \frac{\mu}{v}-\frac{1}{u}=\frac{\mu-1}{r},$$

where μ is written for the fraction $\frac{\mu_2}{\mu_1}$, and would represent the index of refraction of the second medium if that of the first were taken as unity.

The image, Q, is said to be *virtual* when, as in the above instance, the lines of the rays after refraction require to be produced in order to meet in a point (the image). When the rays themselves meet in a point, the image is said to be *real*.

The formula for refraction at a *plane* surface may be deduced from the above by making r infinite or $\frac{1}{r}$ zero. We have then

$$\frac{\mu_2}{v}-\frac{\mu_1}{u}=o \quad \text{or} \quad v=\frac{\mu_2}{\mu_1}u.$$

Formation of Images by Reflection.—With the same notation as above, the position of the image after reflection is given by the equation

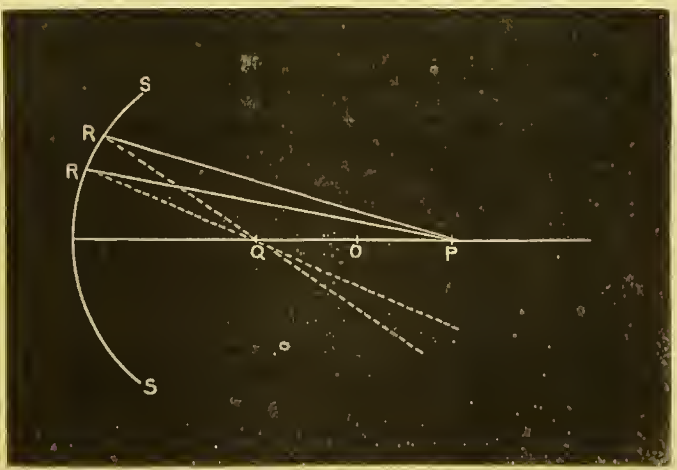

FIG. 333.—Formation of image by reflection at a spherical surface.

$$\frac{1}{v}+\frac{1}{u}=\frac{2}{r},$$

which may be derived from the formula for refraction by putting $\mu_2=-\mu_1$.

In the cases shown in Figs. 332 and 333, where the concave side of the surface faces the incident light, the image is virtual in the case of refraction, and real or virtual in the case of reflection. Were the concavity turned the other way, we should require to consider r as negative in the equations, and the image would be virtual in the case of reflection, real or virtual in the case of refraction.

From these results we can deduce the course of a ray and the image of a point for any system of plane or spherical reflecting or refracting surfaces by finding the image of the point for the first surface, then the image of that image for the second surface, and so on till we get the final image.

Lens.—A simple case of the combination of refracting surfaces is that of a lens, which is a refracting body bounded by two spherical surfaces, or a spherical and a plane surface. The effect of a double convex lens in forming the image of an object is shown in Fig. 334. It will be observed that to every point in the object, DE, there corresponds a point in its image, *de*. Thus *d* corresponds to D, and every ray proceeding from D and passing through the lens passes through the point *d*, the rays afterwards proceeding *as if they emanated from d.*

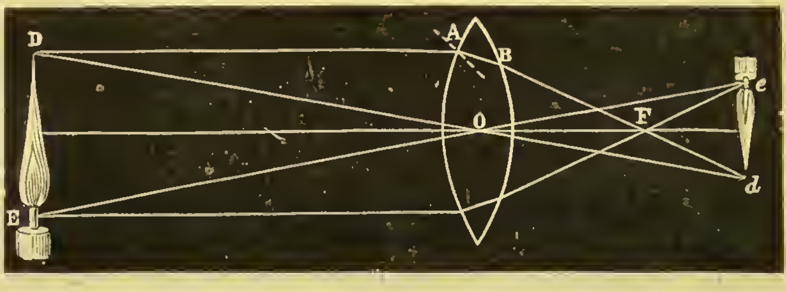

FIG. 334.—Inversion of an image by a biconvex lens.

The calculation of the position of the image of a point, in the case when the medium on both sides of the lens is the same, depends on a single constant—the focal distance, p, which again depends on the refractive index of the material of the lens, and the radii of curvature of its surface. If these be denoted by μ, r_1, and r_2 respectively, we have

$$\frac{\mu-1}{r_1}+\frac{\mu-1}{r_2}=\frac{1}{p}.$$

If a and α represent the distances from the lens of an object and of its image, we have

$$\frac{1}{p}=\frac{1}{a}+\frac{1}{\alpha} \text{ or } \alpha=\frac{ap}{a-p}.$$

It is evident from this equation that the image of an infinitely distant point by refraction through the lens is at a distance, p, from it. In the foregoing it has been assumed that the thickness of the lens is small. When the thickness is considerable, a correction has to be introduced into the formulæ.

In the case of any centred system of refracting surfaces, it has been shown by Gauss and Listing that the course of the ray after refraction may be determined when we know six points called the **Cardinal Points** of the system. These are as follows :—(1) The **First and Second Principal Points**, which have the property that each point in the one principal plane (the plane perpendicular to the axis through a principal point) has its image after refraction at a point in the other principal plane, which is at the same distance from the axis and on the same side of it. Thus any figure in the one principal plane has its image in the other, and equal and similarly situated to itself. (2) **The First and Second Focal Points**, which are such that every ray from the first focal point becomes, after passing through the refracting system, parallel to the axis, and that every ray which before refraction is parallel to the axis, passes, after refraction, through the second focal point, that is to say, the images of the two focal points are at an infinite distance. The same is true for all points in the planes through the focal points perpendicular to the axis. (3) **The First and Second Nodal Points** have the property that every ray, whose line of direction before refraction passes through the first or anterior nodal point, proceeds after refraction in a line parallel to that direction and passing through the second or posterior focal point.

The term *anterior principal focal length* is given to the distance between the first or anterior focal point and the first principal point ; and the term *posterior principal focal length* to the distance from the posterior focal point to the second principal point. These principal focal lengths are proportional to the refractive indices of the media on their respective sides of the refracting system.

The distance between the first nodal point and the first principal point is the same as that between the second nodal and principal points, and also the same as the difference between the anterior and posterior principal focal lengths. It follows that the first and second principal points have the same distance from one another as the first and second nodal points, as may be seen by inspecting the next diagram. From these properties of the cardinal points we may construct geometrically, or calculate, the course of any ray through a centred system, such as the eye.

Fig. 335.—*x*, *x*, axis ; F_1, F_2, first and second focal points ; H_1, H_2, first and second principal points ; K_1, K_2, first and second nodal points.

To Trace the Course of a Ray.—Let Q R be the line of any ray, supposed to come from the right towards the left in the figure, Q and R being the points in which it cuts the first focal plane and the first principal plane respectively. Draw R S parallel to the axis, and S q parallel to Q K_1, then S q is the line of the ray after refraction ; for since the ray passes through R, therefore by the property of the principal planes, it will pass, after refraction, through S which is in the second principal plane and at the same distance from the axis as R. Again, since all rays from Q, which is in the focal plane, are parallel after refraction, they must be parallel to Q K_1, which, by the property of nodal points, is a ray whose direction is unaltered by refraction (Fig. 335).

To Construct the Position of the Image of a Point.—For this it is sufficient to construct two rays proceeding from the point according to the rule just given. It is convenient to choose one of the rays parallel to the axis, and the other passing through the first focal point. Thus let P be the point. Join P K_1 and draw K_2 p parallel to P K_1; draw P R S parallel to the axis, and join S F_2; S F_2 produced will meet K_2 p in the point, p, which is the image of the point, P (Fig. 336).

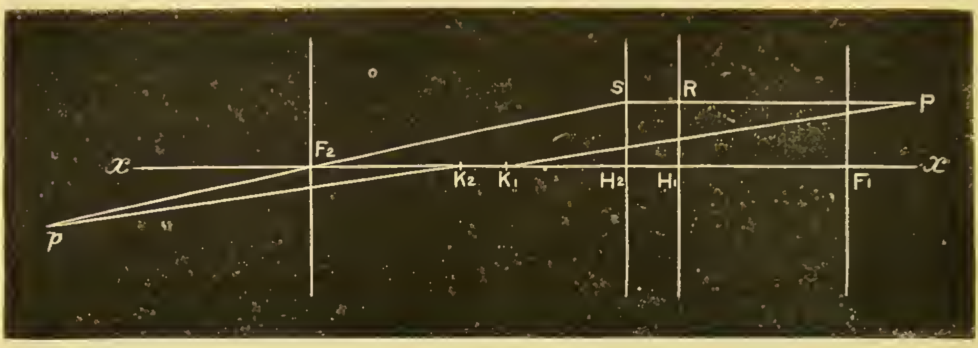

FIG. 336.—Image of a point.

The Eye as a Dioptric System.

The refracting surfaces of the eye are four in number, viz., the anterior and posterior surfaces of the cornea, and the anterior and posterior surfaces of the crystalline lens. But since the two surfaces of the cornea are nearly parallel to one another, and since the index of refraction of the cornea differs very little from that of the aqueous humour, we may neglect the effect of the posterior surface of the cornea without sensible error. On the other hand, the density of the crystalline lens is not the same throughout, but increases towards the middle parts, so that the lens is not a simple one. Thus the eye may be practically considered as a dioptric system, consisting of a spherical refracting surface (that of the cornea) together with a lens which, though of a complex character, is equivalent to a simple double-convex lens.

Formation of an Image on the Retina.—An inverted image of an object placed before the eye falls on the retina, the rays from each point of the object being caused by refraction through the transparent media of the eye, to converge to the corresponding point on the retina. As a matter of fact, the refracting surfaces are not exactly spherical, nor do their centres lie in the same straight line, nor are the media quite homogeneous; but the main features of the normal eye as a dioptric system may be elucidated by assuming it to be a centred system. Apart from these irregularities in its structure, the eye, considered as an optical instrument, has two defects which arise from its constitution. These are called respectively *Chromatic Aberration* and *Spherical Aberration.*

Chromatic Aberration is due to the fact that the rays of light of different colours have slightly different refrangibilities. This causes the separation of white light into its component colours when a beam is made to pass through a prism. The red rays which are at one extremity of the spectrum are less refrangible than the violet rays which are at the other end. From this cause, the rays of any one colour emanating from an illuminated point are brought to a focus by the refracting system of the eye at a point different from that to which the rays of any other colour are brought to focus. In fact, the image of every object is composed of a great number of images of different colours, nearly, but not quite, coinciding with one another. Again, if the red rays from a point be brought to a focus on the surface of the retina, the violet and intermediate rays will be brought to focus slightly in front of it, and will have again diverged, forming a small pencil of rays, before they fall on the retina. In other words, when the eye is perfectly accommodated for distinct vision for one colour, it is not perfectly accommodated for other colours.

In ordinary vision, the effect of chromatic aberration cannot be noticed, but various experimental arrangements have been devised for making it apparent. Thus, if we look at a small violet light, which contains rays chiefly from the two extremes of the spectrum, a red speck with a small blue halo, or a blue speck with a small red halo is seen, according as the eye is accommodated for the blue rays or the red. Again, short-sighted persons find that they can see red objects clearly at a greater distance than blue, because the red rays are less refrangible.

Spherical Aberration.—When the rays from a point are refracted by a system of spherical surfaces bounding homogeneous media, they do not all come to a focus at a point, those falling on the refracting surface at points farther from the axis being brought together at a less distance, so that, when the rays near the axis come to a focus on the retina, those farther from the axis have diverged again somewhat, and fall within a small circle, called a circle of diffusion. This circle is greater, in proportion to the opening of the pupil, so that when the pupil is dilated, vision is less distinct.

Astigmatism.—But the refracting surfaces of the eye are not symmetrical, so that, instead of *circles of diffusion*, there are really irregular shaped figures, which may be observed by looking at a bright star, or small distant light, at night. Astigmatism has been distinguished as *regular* or *irregular*. By regular astigmatism is meant the state of eyes, in which the horizontal meridian of the cornea has a different curvature from the vertical one, so that, when the eye is accommodated to bring rays in the same vertical meridian to a focus, it is not accommodated for rays in a horizontal meridian. This may be tested by looking at a figure composed of a number of horizontal lines, ruled close to one another, and a number of vertical lines, at equal distances. When the eye is accommodated for vertical meridians, the former will be seen distinctly, and when for horizontal meridians, the latter; if the eye has regular astigmatism, the horizontally and vertically ruled lines cannot both be seen distinctly at once. As a rule, the vertical meridians are most curved. This defect may be neutralized by the use of spectacles with plano-cylindrical glasses. In these, the curved or refracting surface, instead of being a portion of a sphere, is a portion of a cylinder. Such a lens, if placed in front of an astigmatic eye, with the axis of the lens vertical, increases the total refraction of the rays in the horizontal meridian, until their focus coincides with that of the rays that have been strongly refracted in the vertical meridian.

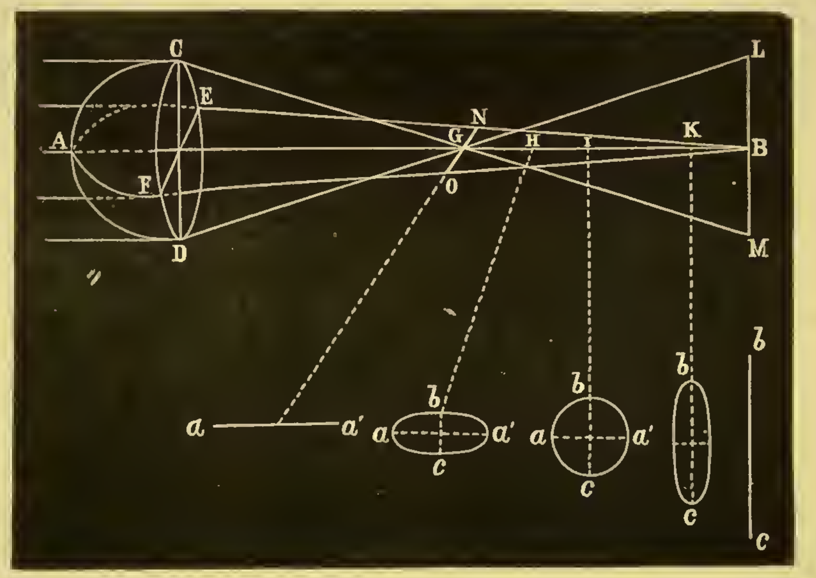

FIG. 337—Diagram illustrating astigmatism.

Irregular astigmatism cannot be thus corrected, as it consists in an irregular variation of curvature in different meridians. Regular astigmatism depends chiefly on the form of the corneal surface. Irregular astigmatism is usually caused by the crystalline lens.

The Schematic Eye.—The dimensions of different eyes are found to present great variety, and it is found that some of the dimensions of an individual eye vary according to the distance of the objects it views. It is therefore impossible to give measurements which shall apply to all eyes, or to the same eye in different states, but the following numbers have been given by Listing as an approximation to the measurements of an average normal human eye, when adjusted for distant vision.

Taking the index of refraction of air as $n=1$:—

Index of refraction of the *aqueous humour* and *vitreous body*, $n' = 1{\cdot}3365$.

Index of refraction of the *crystalline lens*, $n'' = 1{\cdot}14371$.

Radius of curvature of *cornea*, $r = 7{\cdot}829$ mm.

Radius of curvature of *anterior surface of lens*, $r' = 10$ mm.

Radius of curvature of *posterior surface of lens*, $r''=6$ mm.

Distance between anterior surfaces of *cornea* and of *lens*, 4 mm.

Thickness of *lens*, $\epsilon = 3{\cdot}6$ mm.

Distance from anterior surface of *cornea* to *anterior* surface of crystalline *lens*, $aa' = 3{\cdot}6$ mm.

Distance from anterior surface of *cornea* to *posterior* surface of crystalline *lens*, $aa'' = 7{\cdot}2$ mm.

The foci are as follows :–

Surface of cornea—

$$\text{First focal distance, } fo' = \frac{r}{n'-1} = \frac{7{\cdot}829}{1{\cdot}3365-1} = 23{\cdot}266 \text{ mm.}$$

$$\text{Second focal distance, } fo'' = \frac{n'r}{n'-1} = \frac{1{\cdot}3365 \times 7{\cdot}829}{1{\cdot}3365-1} = 31{\cdot}095 \text{ mm.}$$

Anterior surface of crystalline lens—

$$\text{First focal distance, } f^{1'} = \frac{n'r'}{n''-n'} = \frac{1{\cdot}3365 \times 10}{1{\cdot}4371 - 1{\cdot}3365} = 132{\cdot}853 \text{ mm.}$$

$$\text{Second focal distance, } f^{1''} = \frac{n''r'}{n''-n'} = \frac{1{\cdot}4371 \times 10}{1{\cdot}4371 - 1{\cdot}3365} = 142{\cdot}853 \text{ mm.}$$

Posterior surface of crystalline lens—

$$\text{First focal distance, } f^{2'} = \frac{n''r''}{n'-n''} = \frac{1{\cdot}4371 \times 6}{1{\cdot}3365 - 1{\cdot}4371} = 85{\cdot}7117 \text{ mm.}$$

$$\text{Second focal distance, } f^{2''} = \frac{n'r''}{n'-n''} = \frac{1{\cdot}3365 \times 6}{1{\cdot}3365 - 1{\cdot}4371} = 79{\cdot}7113 \text{ mm.}$$

The *principal points* of the cornea coincide with its summit, and the *principal plane* with its anterior surface. The focal distances of the *crystalline* are equal. Call these ψ, and the thickness of the lens (3·6 mm.) ϵ. Then,

$$\psi = \frac{f^{1'}f^{2'}}{f^{1''} + f^{2'} - \epsilon} = \frac{132{\cdot}853 \times 85{\cdot}7117}{142{\cdot}853 + 85{\cdot}7117 - 3{\cdot}6} = 50{\cdot}6168 \text{ mm.}$$

The *first principal point* of the eye is 1·7532 mm. behind anterior surface of cornea.

The *second principal point* is 2·1101 mm. behind anterior surface of cornea.

The two principal points are therefore in the anterior chamber in front of the lens, and the distance between them is $2{\cdot}1101 - 1{\cdot}7532 = 0{\cdot}3569$ mm.

The *first principal focus* of the eye is $\phi\text{H}' - \text{AH}' = 15{\cdot}4983 - 1{\cdot}7532 = 13{\cdot}7451$ mm. in front of cornea.

The *second principal focus* of the eye is $\text{AH}'' + \text{H}''\phi = 2{\cdot}1101 + 20{\cdot}7136 = 22{\cdot}8237$ mm. behind the cornea.

The *first nodal point* is 6·9865 mm. behind summit of cornea, and it is situated in the lens, ·2315 mm. in front of its posterior surface. The *second nodal point* is

7·3254 mm. behind vertex of cornea, that is, ·1254 mm. *behind* the posterior surface of the lens.[1]

An ideal eye having the above dimensions was called by Listing *the schematic eye.* For many purposes, however, a simpler scheme is quite sufficient, and such a scheme also has been given by Listing under the name of *the reduced eye.* This is got from the schematic eye by supposing the two nodal points to coincide with one another, which implies that the principal points with their planes also coincide.

The dimensions in this case would be :—From anterior surface of cornea to the principal point, 2·3448 mm. ; from the nodal point to the posterior surface of the lens, ·4764 mm. The positions of the focal points remain unaltered.

The *radius of curvature* of the refracting surface = 5·1248 mm. The *first focal distance* is 15·036 mm., the second focal distance is 20·113 mm. The index of refraction is $\frac{103}{77}$ = the index of refraction of the vitreous body. The second focal distance is about the length of the emmetropic reduced eye. Luminous rays given off from the first focal point are parallel in the interior of this eye.

According to Von Helmholtz, Listing's reduced eye may be simplified by comparing it to a plane sphere of 10 mm. diameter whose vertex lies 1·9 mm. behind the cornea and whose centre is ·5 mm. in front of the posterior surface of the lens, that is 7 mm. behind the anterior plane of the cornea.

In the horse, the radius of curvature of the cornea is 19·8 mm., of the anterior surface of the lens 12·3 mm., and of the posterior surface 11·3 mm. The distance from the vertex of the cornea to the anterior surface of the lens is 7 mm., to the posterior surface of the lens 20·2 mm., and to the retina 44·1 mm. From nodal point to the retina is 27 mm.

The construction for the course of a ray in the reduced eye would be as follows :—

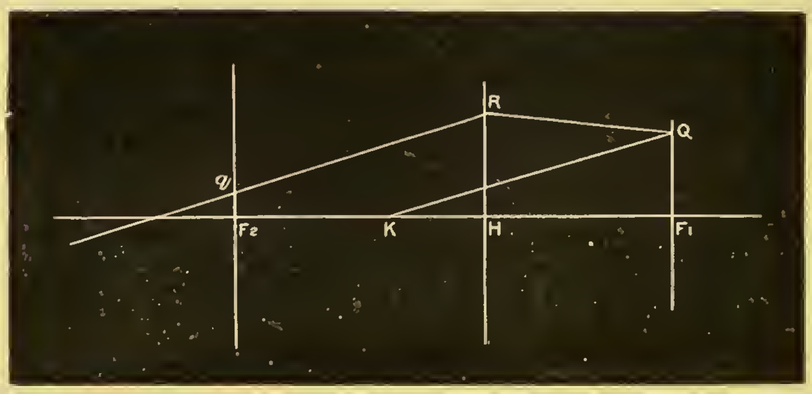

Fig. 338.—Course of ray in reduced eye.

Let Q R be the line of a ray coming from the right, meeting the principal plane in R (Fig. 338). Draw R q parallel to Q K, which will give the line of the ray after

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[1] Stammeshaus, *Dioptrik des normalen menschlichen Auges*, p. 129; see also Landolt, *The Refraction and Accommodation of the Eye*, p. 79. For the researches of Von Helmholtz, see *Optique Physiologique ;* of Donders, *Anomalies of Accommodation and Refraction ;* of Listing, in Wagner's *Handwörterbuch der Physiologie*, iv. See also M. Woinow, *Ophthalmometrie.*

refraction. To construct the image of a point, P (Fig. 339), draw P R parallel to the axis meeting the principal plane in R, join R F_2, then P K produced to meet R F_2 produced gives the image of P at their intersection p. It will be seen that the course of the rays in the reduced eye is the same as in the case of refraction at a spherical surface at H, whose centre is K and foci, F_1 and F_2.

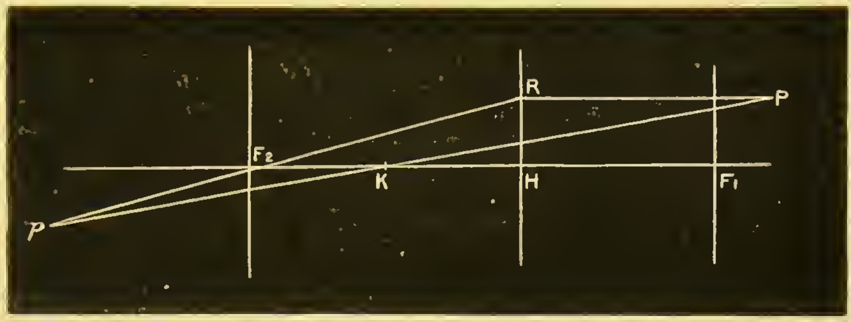

FIG. 339.—Image of a point with reduced eye.

Visual Axis.—The optical axis of the eye we have defined to be the straight line which contains the centres of the refracting surfaces. It has been shown by Von Helmholtz, by means of an instrument invented by him, termed the *ophthalmometer*, that this does not coincide with the *visual axis*, which is the straight line joining the second nodal point with the *fovea centralis*. The latter axis is found to leave the eye in a direction inwards from, and usually somewhat above, the former, the angle between them being often about 5° and occasionally attaining the size of about 14°.

Circles of Diffusion, Sighting Lines.—For distinct vision the image of the object should fall on the retina. Now, when the eye is adjusted so that a certain point is distinctly seen, the rays from a more distant point will be brought to a focus before they reach the retina, and will have diverged into a cone of rays which will be cut by the surface of the retina in a small circle called a *circle of diffusion*. Again, the rays from a point nearer to the eye will be intercepted before they come to a focus, again forming a circle of diffusion on the retina. In 'sighting' two points, *i.e.*, bringing them into apparent coincidence in the field of vision, either one or both must give rise to diffusion circles on the retina. When the centres of these coincide, the sighting is effected. The *line of sighting* is the common axis of the two conical pencils of rays from the two points, each of which is bounded by the edge of the iris.

The following terms should be distinguished :—

1. The **Direction of Vision** of any point is given by the line joining any point in the field of vision with the first nodal point, or by joining its image on the retina with the second nodal point.

2. The **Visual Axis, or Line of Vision**, is the line which gives the direction of vision when the point is *directly* viewed, *i.e.*, when its image is at the *fovea centralis*.

3. **Lines of Sighting** pass through the centre of the corneal image of the iris, or, in other words, from the point of fixation through the centre of the pupil.

4. The **Line of Regard, or Line of Fixation**, is the line joining the centre of rotation of the eye with a point which is seen *directly*. The line of regard thus

differs slightly from the line of vision, since the centre of rotation of the eye probably lies near the optical axis while the nodal point does not in general lie on this axis.

In order to determine the cardinal points of an eye it is necessary to measure the dimensions of its refracting media as well as the indices of refraction. This has been the subject of many experimental investigations. These may be classed under two heads: those performed with dissected eyes, and those in which observations were made upon the living eye. Among the former were Brewster's determinations of the refractive indices of the media. He took a microscope and fitted a piece of glass with plane faces close to the objective, so that when the intervening space was filled with the medium under investigation it formed a plano-concave lens, which altered the focal length of the objective. This required the object viewed to be moved further from the objective to get distinct vision, and this change of position was measured. Water was then substituted for the optic medium, and the change of position required again measured. The refractive index of the medium could then be compared with that of water, which is known. Later investigators adopted a similar arrangement, with this difference, that the change in the size of the image of an object was measured by means of a micrometer, instead of the change of position as in Brewster's investigations. Von Helmholtz used his ophthalmometer for measuring the size of the image. Another investigation of the dissected eye was the measurement by Von Helmholtz of the focal length of the crystalline lens. He laid one, freshly dissected, upon a brass plate with a circular hole countersunk through it, surrounding it with vitreous humour to prevent it from shrinking, and by means of the ophthalmometer he measured the image of the opening through the plate formed by refraction through the lens. This determination, along with the measurements of the thickness of the lens and of the curvature of its surfaces (by means of reflected images) enabled him to calculate the optical constants of the lens.

Chap. III.—SPECIAL FUNCTIONS OF THE EYE.

The *inversion* of the image will be understood with the aid of Figs. 334 and 340. Suppose *c*, *d*, *e*, to be luminous objects, the rays proceeding from their surface above the optic axis cross in the eye so as to be brought to a focus below the axis, and *vice versâ*. Thus an inverted image is formed on the retina at *a b*. The angle, *x*, is termed the *visual angle*, and its size will depend on the size of the object and the distance of the object from the eye. Thus, objects of different sizes, *c*, *d*, and *e*, may be included in the same visual angle, as they are at different

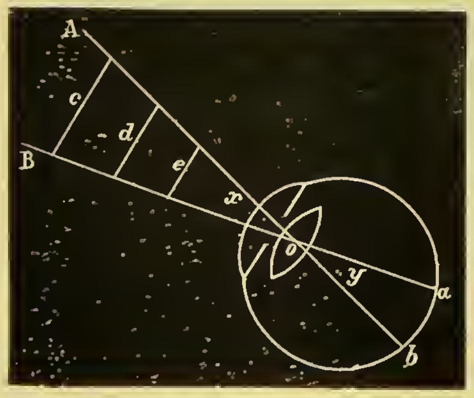

Fig. 340.—Diagram showing the visual angle.

distances from the eye. The *size* of the image on the retina may be calculated if we know the size of the object, its distance from the nodal point, *o*, and the distance of the nodal point from the retina. In a normal eye, the nodal point is 7 mm. behind the centre of the cornea, and 16 mm. in front of the retina. Let A be the size of the object, B its distance from the centre of the cornea, *b* the distance of the centre of the cornea from the nodal point (7 mm.), and *c* the distance of *o*, the nodal point, from the retina (16 mm.): then the size of the retinal image is $x = \frac{A \times c}{B + b}$, or, $\frac{A \times 16}{B + 7}$. Suppose a rod, 2 metres high, to be placed at a distance of 10 metres from the eye, the retinal image would be $\frac{2{,}000 \times 16}{10{,}000 + 7} = 2{\cdot}97$ mm. Taking the distance of the moon from the earth at 24,000 miles, and the diameter at 2,144 miles, the breadth of the retinal image of the full moon is about $\frac{1}{17}$th of an inch, or 1·47 mm. The area of the retinal image to that of the object is as the square of the distance from the nodal point to the retina to the square of the distance of the object from the nodal point. The smallest visual angle in which two distinct points may be observed is 60 seconds; below this, the two sensations fuse into one, and the size of the retinal image corresponding to this angle is ·004 mm. The diameter of the end of a single retinal rod or cone is about ·0032 mm., so that the image falling within the smallest visual angle is ·0008 mm. larger than the breadth of the end of a rod or cone. If the images of two points are so close together as to fall on *one* rod or cone, then only one point will be seen. Thus, two objects (included in a visual angle of less than 60 seconds) appear as one point.

A small visual angle is in most eyes a condition of sharpness of definition. With a large angle objects appear less sharply marked. A minute image, if thrown on a single retinal element, is sufficient to excite it. Thus, it is possible to see a brilliant point at a distance of 25 mm. in an angle even so small as ·25 of a sec., and a sharp eye can see a body the $\frac{1}{50}$th of a line in diameter—that is, about the $\frac{1}{600}$th part of an inch, or ·04 ($\frac{1}{600}$ inch $= \frac{25}{600}$ mm. $= \frac{1}{24} = {\cdot}04$) mm. This at 25 mm. distance would give a retinal image of about ·002 mm.

The *acuteness* of vision, v, may be tested by Snellen's types. It has been determined that square letters, which have limbs and parts equal in breadth to ·2 of the height of the letters, are distinctly legible to a normal eye under an angle of five minutes. These letters are numbered, the numbers expressing in metres, or parts of a metre, the distance at which the letter can be seen under an angle of five minutes

(D). The eye is tested with smaller and smaller letters at the same distance from the eye, say 6 metres (*d*). Suppose No. 6 type is thus seen, $\text{V} = \frac{d}{\text{D}}$, or $\frac{6}{6} = 1 =$ the acuteness of vision of a normal eye. If number 8 is seen at 6 metres then the acuteness of vision is $\frac{6}{8}$ths or $\frac{3}{4}$ths that of the normal. An eye which can read No. 60 has $\text{V} = \frac{6}{60}$, or $\frac{1}{10}$th of the normal.

(*c*) **Optical Defects of the Eye.**—As an optical instrument the eye is defective; but from habit and want of attention its defects are not appreciated, and consequently they have little or no influence on our sensations. They are chiefly of two kinds: (1) those due to the curvature of the refractive surfaces; and (2) those due to the dispersion of light by the refractive media.

(1) *Aberration of Sphericity.*—This has already been explained (p. 609). In the eye this defect is to a large extent corrected by the following arrangements: (1) the iris cuts off the outer and more strongly refracted rays; (2) the curvature of the cornea is more ellipsoidal than spherical, and consequently the rays farthest from the axis are least deviated; (3) the anterior and posterior curvatures of the lens are such that the one corrects, to a certain extent, the action of the other; and (4) the structure of the lens is such that its power of refraction diminishes from the centre to the circumference, and consequently the rays farthest from the axis are less refracted.

Another defect of the eye is due to different meridians having different degrees of curvature. This defect is known as *astigmatism.* The optical cause has already been explained (p. 609). The condition was first detected in his own eyes by Thomas Young in 1793, and it was rediscovered by George Airy in 1827. The name astigmatism was first given to it by Whewell, and it was elaborately investigated by Donders in 1862. In the cornea, the vertical meridian has a shorter radius of curvature, and is consequently more refractive than the horizontal. The meridians of the lens may also vary; but, as a rule, the asymmetry of the cornea is greater than that of the lens. A distant light appears like a rayed star to an astigmatic eye. The eye of the rabbit is slightly astigmatic, whilst the eye of the cat and of the calf shows the defect to a very marked degree. Astigmatism of the lens is pronounced in the larger mammalia.

(2) *Aberration of Refrangibility.*—This has been described (p. 609).

(3) *Defects due to Opacities, etc., in the Transparent Media.*—When small opaque particles exist in the transparent media, they may cast their shadow on the retina, so as to give rise to images which are projected outwards by the mind into space, and thus appear to exist outside of

the body. Such phenomena are termed *entoptic*, and they may be of two kinds: (1) *extra-retinal*, that is, due to opaque or semi-transparent bodies in any of the refractive structures anterior to the retina, and presenting the appearance of drops, striæ, lines, twisted bodies, forms of grotesque shape, or minute black dots dancing before the eye; and (2) *intra-retinal*, due to opacities, etc., in the layers of the retina in front of Jacob's membrane. The intra-retinal phenomena may be produced, in a normal eye, in various ways: (1) Throw a strong beam of light on the edge of the sclerotic on the outer part of the eye, and a curious branched figure will be seen, which is an image of the retinal vessels (*Purkinje's figures*, Fig. 342); (2) Look at a strong light through a minute aperture, in front of which a rapid to-and-fro movement is made, and an image of the vessels will also be seen; and (3) Look at a very brilliant light passing through a long tube, moving the head to and fro, and numerous round and faintly-marked bodies, the blood corpuscles, may be detected. Thus, by such arrangements, an observer may see the circulation in his own eye. Such experiments also prove that the sensitive part of the retina is its

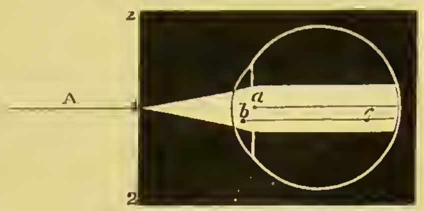

Fig. 341.—Diagram illustrating entoptic phenomena. 2 2, a screen, admitting light from A, by a minute aperture, 1. Observe the form of the pencil of rays. *a*, *b*, minute bodies (extra-retinal) casting a shadow on retina; *c*, body (intra-retinal) casting a shadow on the layer of rods and cones (Jacob's membrane).

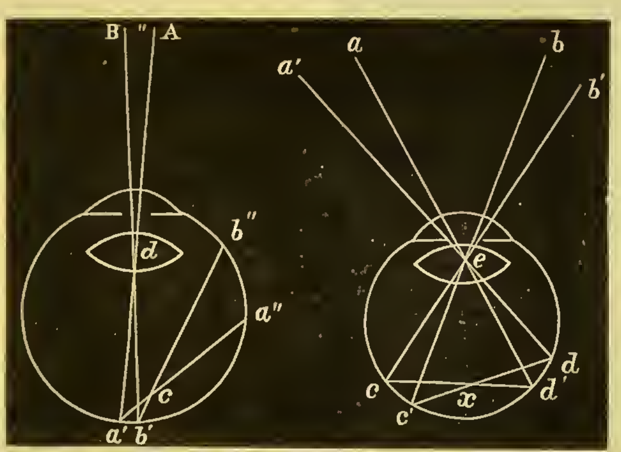

Fig. 342.—Diagram to illustrate the formation of Purkinje's figures. In figure to the left the rays passing through sclerotic at *b''* in direction *b''c* will throw a shadow of a vessel at *c* on retina at *b'*, and this will appear as a dark line at B. If light move from *b''* to *a''* the retinal shadow will move from *b'* to *a'*, and the line in field of vision will move from B to A. The distance *c b'* is equal to the distance of the vessel from the layer of rods and cones. In figure to the right, if *a* be moved to *a'*, *d'* will move to *d*, the shadow on the retina from *c* to *c'*, and image *b'* to *b*.

deepest and most external layer (the layer of rods and cones—Jacob's membrane). Müller calculated from the apparent size of the shadow-like figure and the movements of the source of light that the sensitive part of the retina must be ·2 to ·3 mm. behind the vessels. This agrees with the histological fact that the layer of rods and cones is ·25 mm. behind the layer in which the vessels lie.

(*d*) **Accommodation or the Mechanism of Adjustment for different distances.**—When a camera is placed in front of an object, it is necessary to focus accurately in order to obtain a clear and distinct image on the sensitive plate. This may be done by moving either the lens or the sensitive plate backwards or forwards so as to have the posterior focal point of the lens on the sensitive plate. In the eye we also find a mechanism of accommodation. We may regard the different refractive media as forming one convex lens of a definite focal length, and it is evident that this focal length may correspond with or be different from the length of the antero-posterior axis of the eyeball. If the length of the antero-posterior axis is such that the chief focal point of the refractive media falls on the retina, parallel rays, such as proceed from objects at an infinite distance, will be focussed on the retina. Such an eye is *emmetropic*, that is, *in measure*. On the other hand, the axis of the eye may be longer or shorter than the focal length of the refractive media, and it is out of measure, or *ametropic*, of which there are two varieties: (1) one, the *myopic* or *hypometropic*, or *short-sighted* eye, in which the axis is too long, and (2) the other, the *hypermetropic*, or *far-sighted* eye, in which the axis is too short (Fig. 343). The ordinary length of the axis of an emmetropic or normal eye is 24·5 mm., the shortest hypermetropic eye that has been measured had an axis of 16 mm., and the longest myopic eye had an axis of 34 mm. The term *hypermetropia* means strictly that the focal length is too great, but the focal length is really the same as in the normal eye, but the axis is too short. The term *myopia* has been given to the short-sighted form of

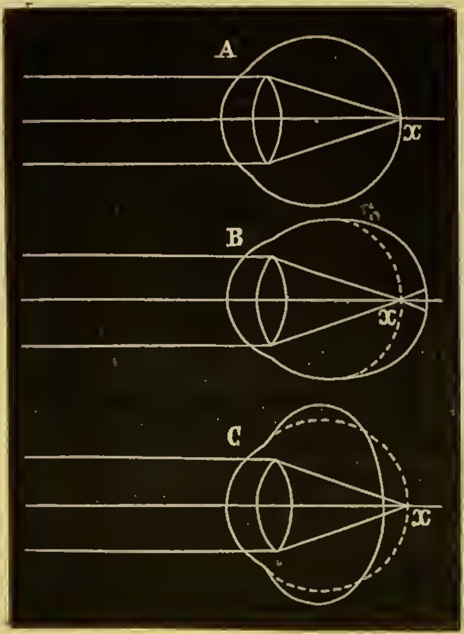

FIG. 343.—A, emmetropic or normal eye; B, myopic or short sighted eye.; C, hypermetropic or long sighted eye.

eye, because short sighted persons "diminish the circles of light-diffusion by partial closing or nipping together of the lids" (Brudenell Carter), and the term *brachymetropia*, suggested by Donders, more accurately indicates the condition.

If the refractive powers of the two eyes are the same, the eyes are *isometropic*, and if they are unlike, they are said to be *anisometropic*. It is clear that if we place a convex lens, which converges parallel rays of light, before a hypermetropic eye, we can move the focal point forwards so as to bring it on the retina, and that a concave lens, which diverges parallel rays, before a myopic eye, will move the focal point backwards till it falls on the retina. This restores distinct vision in both cases, and the number of the lens required to produce the effect measures the ametropia of the eye concerned. To determine this, oculists now use a metrical scale of test lenses in which the unit (1 of the series) is a lens of one metre focal distance, termed a *dioptric*. No. 2 is a lens of double the power of the dioptric, or $\frac{1}{2}$ the focal length, that is, it is 2 dioptrics and its focal length is $\frac{1}{2}$ metre; No. 3 is 3 dioptrics and its focal length is $\frac{1}{3}$ metre, and so on—each whole number of the lens expressing the number of dioptrics to which it is equal. The dioptric value of any lens is measured by an instrument invented by Snellen, termed the *phakometer*.[1] Having ascertained that an eye is ametropic by the use of Snellen's types, accommodation is paralysed by atropin, and a concave or convex glass of one dioptric is placed before the eye. If the vision is improved by the convex glass, the eye is hypermetropic, if by the concave glass, it is myopic. The degree of hypermetropia and of myopia is then ascertained by finding the lens that gives distinct vision. Thus, if a hypermetropic eye requires a convex lens of 4 dioptrics, the degree of hypermetropia is 4, and if a myopic eye requires a concave lens of 3 dioptrics, the degree of myopia is 3.

From any point 65 metres distant, rays may be regarded as almost parallel, and the point will be seen without any effort of accommodation. This point, either at this distance or in infinity, is called the *punctum remotum*, or the most distant point seen without accommodation. In the myopic eye it is much nearer, and for the hypermetropic, there is really no such point, and accommodation is always necessary.

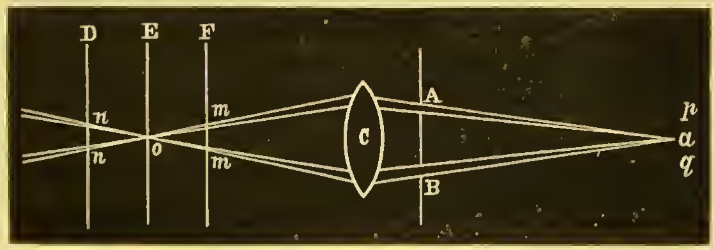

FIG. 344.—Experiment of Scheiner.

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[1] R. Brudenell Carter, "Defects of vision." For a description of the phakometer, see p. 19.

In the normal eye, as already stated, parallel rays coming from infinity are brought to a focus on the retina. When the rays are not brought accurately to a focus on the retina the image is indistinct, and *circles of diffusion* are formed. These may be readily studied by the following experiment, known as the *Experiment of Scheiner.*

Let C be a lens, and D E F be screens placed behind it; hold in front of the lens a card perforated by two holes A and B, and allow rays from a luminous point *a* to pass through these holes; the point *o* on the screen E will be the exact focus of the rays emanating from *a*; if *a* were removed farther from the lens, the focus would be on F, and if it were brought nearer to C, the focus would then be on D. The screens F and D show two images of the point *a*. If then we close the upper opening in A B, the *upper* image *m* on F and the *lower* image *n* on the screen D, disappear. Suppose then that the retina be substituted for the screens D and F, the same will take place along with reversal of the retinal image. If the retina be placed at *o*, only one image will be seen, but if it be placed either in the plane of F or D, then two images will be seen as at *m m* or *n n*, consequently in either of these planes there will be circles of diffusion and indistinctness, and only in the plane E will there be sharp definition of the image.

It is evident that if an object be brought too close to the eye for the refractive media to focus it on the retina, circles of diffusion will be formed, with the result of causing indistinctness of vision, unless the eye possess some power of adapting itself to different distances. That the eye has some such power of accommodation is proved by the fact that if we look through the meshes of a net at a distant object, we cannot see both the meshes and the object with equal distinctness at the same time. Again, if we look for some time at very near objects, the eye becomes fatigued. Beyond a distance of 65 metres, accommodation is not necessary, but within it, the condition of the eye must be adapted to the diminished distance until we reach a point near the eye, which may be regarded as the limit of visibility for near objects. This point, called the *punctum proximum*, is usually 20 centimetres ($\frac{1}{5}$th of a metre) from the eye. The range of accommodation is thus from the punctum remotum to the punctum proximum.

Accommodation is effected by a change in the curvature of the anterior surface of the crystalline lens. If we hold a lighted candle in front, and a little to the side, of an eye to be examined, three reflections may be seen in the eye, usually termed the *Sanson-Purkinje reflections.* The middle of these images, on the anterior surface of the cornea, was first observed by Sanson; the posterior was detected by Purkinje, and the change in the relative positions of the three reflections during accommodation was first described by Cramer. This experiment may be done with considerable facility by using an instrument devised by Von Helmholtz, and termed a *Phakoscope*, shown in Fig. 345.

It consists of a triangular box having the three angles squared off as seen in the figure. To the right of the figure two prisms are seen, by which light from a candle is concentrated on the eye under examination. This eye is placed before an aperture on the side of the box opposite to *c*, and the eye of the observer is placed at *a*.

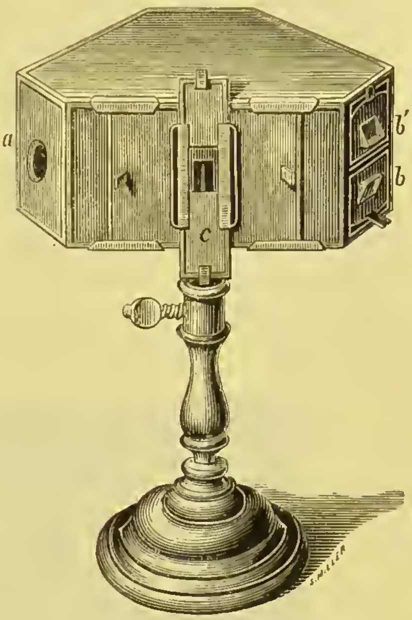

Fig. 345.—Phakoscope of Helmholtz. For description, see text.

The three images thus seen are shown in Fig. 346. The first, on the left (in each figure *A* and *B*), is erect, large and bright, from the anterior surface of the cornea; the second, also erect, but dim, from the anterior surface of the crystalline lens; and the third, on the right (in each figure *A* and *B*), inverted, and very dim, from the posterior surface of the lens, or perhaps the concave surface of the vitreous humour to which the convex surface of the lens is adapted. Suppose the individual gazes at a distant object through the window *c*, and the relative position of the images be noted, if he then be directed to fix his eye on a needle point, suddenly pushed up by the shutter *c*, the observer at *a* will see the middle image (in Fig. 346) advance towards the front image, that is the anterior surface of the lens becomes more convex. The change in convexity is shown in Fig. 347. The changes occurring during accommodation are: (1) the curvature of the anterior surface of the crystalline lens increases, and the length of the radius may pass from 10 to 6 mm.; (2) the pupil contracts, although accommodation may occur without this; and (3) the intra-ocular pressure increases in the posterior part of the eye.

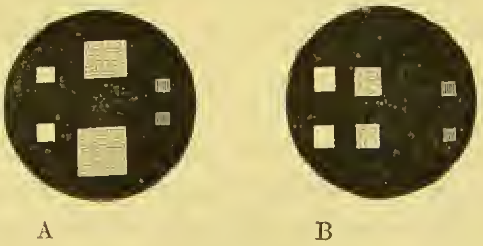

Fig. 346.—Reflected images in the eye. A for distant, and B for near vision.

Von Helmholtz gives the following measurements made with the ophthalmometer:—

	For an infinite distance in mm.	For near objects. in mm.
Radius of curvature of cornea, - - - - -	8	8
Radius of anterior surface of lens, - - - -	10	6
Radius of posterior surface of lens, - - - -	6	5·5
Distance of vertex of cornea to anterior surface of lens,	3·7	3·3
Distance to posterior surface of lens, - - - -	7·5	7·6
Thickness of lens, - - - - - - -	3·8	4·3

An explanation of the increased curvature of the anterior surface of the lens during accommodation has been thus given by Von Helmholtz. In the normal condition, that is for the emmetropic eye, the crystalline lens is flattened anteriorly by the pressure of the anterior layer of the capsule; during accommodation, the radiating fibres of the ciliary muscle (sometimes termed the *tensor choroideæ* or *Brücke's muscle*) draw forward the ciliary processes and the retina, releasing the tension of the zonule of Zinn. When this occurs, the lens at once bulges forward, and becomes thicker, by its elasticity. In the living eye, during rest, a certain amount of tension exists in the zonule, so that the edge of the lens is drawn backwards and is thus flattened. When the fibres of the ciliary muscle act, they pull towards their fixed point at the edge of the cornea, draw the *ora serrata* towards the edge of the cornea, and thus diminish the radial tension of the zonule. The pulling forwards of the choroid has actually been seen in the eye of the dog, cat, and monkey. The ciliary muscle receives motor nerves from the ciliary ganglion, and these are derived from the 3rd nerve, so that on paralysis of this nerve the power of accommodation is lost.

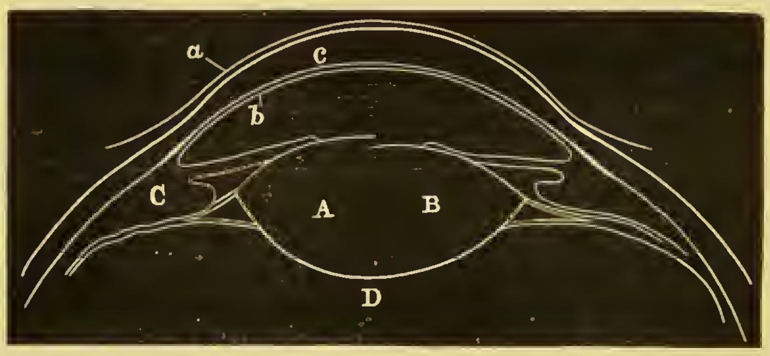

Fig. 347.—Mechanism of accommodation. A, the lens during accommodation showing its anterior surface advanced; B, the lens as in distant vision; C, position of the ciliary muscle; D, the vitreous; *a*, anterior elastic lamina of cornea; *c*, corneal substance proper; *b*, posterior elastic lamina, or membrane of Descemet.

The change of shape occurs chiefly in the anterior surface, but the posterior surface also becomes slightly more convex. At the same time, the pupil contracts and the tissue of the iris becomes tense. As pointed out by Brudenell Carter, the effect is the same as if a convex lens of a certain dioptric value had been placed in front of the eye. Thus, suppose an emmetropic eye has its far point at an infinite distance, and that it then sees an object distinctly at a distance of 20 centimetres, the effort of accommodation produces the same effect as if we placed before the eye a convex lens of the same focal length as the distance of the eye from the near point, that is $\frac{1}{5}$th of a metre, or a lens of 5 dioptrics. The accommodating power diminishes as age advances. At the age of 10, the accommodating power is equal to 13·5 d., in other words, the near point is $\frac{1}{13}$th of a metre distant; at 13 years, 12 d.; at 17, 10·5 d.; at 21, 9 d.; at 26, 7·5 d.; at 32, 6 d.; at 40, 4·5 d.; at 50, 3 d.; at 60, 1·5 d.; and at 75, accommodation is lost. By dividing 1000 mm. by the figures giving the number of dioptrics, the distance of the near point at the above ages is given. Thus at 10, we have it 74·7 mm.; at 21, 111 mm.; at 50, 333 mm.; and at 60, 666 mm. In old age, the eye may now be hypermetropic and require a weak convex lens for infinitely distant objects, and the acquired hypermetropia may begin so soon as the forty-fifth year. The term *presbyopia* indicates the alteration of vision caused by the removal of the near point farther and farther from the eye by the power of accommodation becoming weaker, and technically it begins when the near point (with binocular vision) has receded to a distance of 8 inches, that is about 20 centimetres. The condition is remedied by the use of convex glasses of sufficient dioptric power to bring the near point to about 20 centimetres. Thus, at the age of 78, a presbyopic eye would require a lens of 4·5 dioptrics to place the near point at 8 inches, but if the eye of a person at this age had acquired hypermetropia, a lens of 7 d. is necessary to produce the same result. As a rule, it is not necessary to use lenses of such strength, and a near point of 25 to 32 centimetres is more convenient. (The effect of the binocular convergence of the eyes as a factor in clear vision will be considered later (p. 640).

CHAP. IV.—THE ABSORPTION AND REFLECTION OF LUMINOUS RAYS FROM THE EYE.

When light enters the eye it is partly absorbed by the black pigment of the choroid and partly reflected. The reflected rays are returned through the pupil, following not only the same direction as that of the rays entering the eye, but uniting to form an image at the same point in space as the luminous object. The pupil of an eye appears black to an observer, because the eye of the observer does not receive any of these reflected rays. If, however, we strongly illuminate the retina, and hold a lens in front of the eye to be observed, so as to bring these reflected rays to a focus on the retina of the observing eye, then an image of the retina will be seen. Such is the principle of the *ophthalmoscope*, invented by Von Helmholtz in 1851.

In Fig. 348 is shown the fundamental experiment of Von Helmholtz on which the principle of the ophthalmoscope depends. Let S be a glass plate held obliquely between the eyes, B and C. Rays from the flame, A, are reflected into the eye, C; they then return from the eye, C, and passing through the glass, S, form an image of A in the eye, B, as if it were at a; or, in other words, the eye, B, sees the illuminated retina of the eye, C. In the experiment just described it is necessary that the eye, B, be either myopic or hypermetropic to the same degree as the eye, C. To get rid of this difficulty an artificial dioptric is placed in front of C to see the retina distinctly. This arrangement is shown in the next figure (Fig. 349). Suppose rays emanating from the eye, A, passed out without encountering the lens, B, they would be brought to a focus at b. If a plano-concave lens, B, be interposed between the eye, A, and the eye of the observer, the rays coming from a would be refracted so as to be focussed at p; or, in other words, an image of a is formed on the retina of the observer's eye. This image would be inverted. In using the ophthalmoscope, it is important to be able to see the image of the retina as it actually exists, and the method adopted is shown in Fig. 350. A large field of the retina is illuminated by reflecting into the eye light from a lamp caught on a mirror having a small hole in the centre (first proposed by Reuter), and held in front of the eye of the observer (Fig. 351). If a biconvex lens, B, is held in front of the eye, A, most of this light is conveyed into the eye, C, as shown by the dotted lines. At the same time, an image of the point, a, is brought to a focus at d, and will be seen by the eye, C, as if it were at d. The same applies to all points of the arrow, a, in A, and consequently an inverted or real image of a is seen at d, when d is at the near point of distinct vision of c. If the plane in

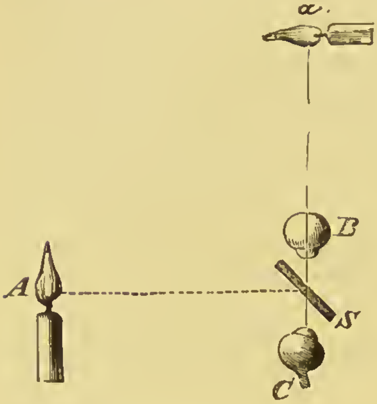

FIG. 348.

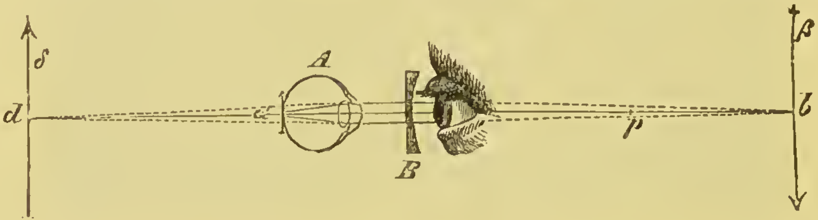

FIG. 349.

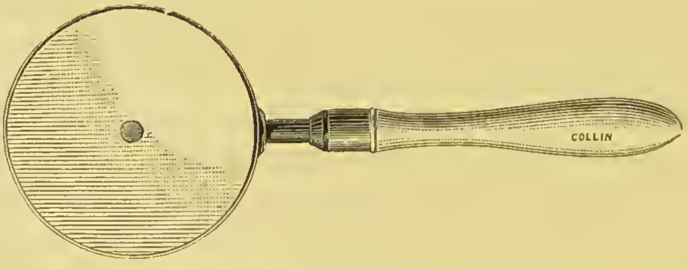

FIG. 350.—Reflecting ophthalmoscopic mirror.

which *d* is seen distinctly is farther off than the near point of distinct vision, then in front of *C* we place a collecting lens which forms from the real image at *d* a

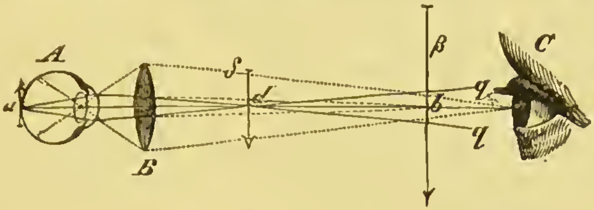

Fig. 351.

virtual image at the near distance of distinct vision. The ophthalmoscope shows a reddish disk, the retina, and in it a small circular white spot, somewhat raised—the papilla of the optic nerve. From the latter, vessels may be seen passing out which break into a number of branches, radiating irregularly over the retina. A distinction may be observed between the bright red arterial branches and a broader and darker venous branch. We also notice a small light spot, the yellow spot, *macula lutea*. It is remarkable that few vessels are seen in the retina of the horse, and only in an area of 3 to 6 mm. round the optic papilla. The retina of many animals shows no vessels.

Eyes deficient in pigment, as in albinos, appear luminous, reflecting light of a red or pink colour; but if we place in front of such an eye a card perforated by a round hole of the diameter of the pupil, the hole will appear quite dark, like the pupil of the ordinary eye. In many animals (hyæna, fox, cat) a portion of the fundus of the eyeball has no pigment, and presents an iridescent appearance. This is called a *tapetum*, and probably renders the eye more sensitive to light of feeble intensity. The tapetum is always above the point of entrance of the optic nerve, and it is usually triangular in shape. In solidungula and ruminants it is of a bluish-green or azure-blue colour. The colour is not due to pigment, but is iridescence, caused by interference of waves of light. The yellow tapetum of carnivora is caused by several layers of polygonal cells, blue by reflected and yellow by transmitted light. The light penetrates these layers and then is reflected from a finely striated surface.

The image on the retinal surface is not on a flat surface, but on a segment of a hollow sphere. In this respect the eye has an advantage over a *camera obscura* in which the field is flat, so that if the external object placed before it be of sufficient size the lateral parts may be less distinct than the central parts, because they are somewhat out of focus. For the same reason, the lateral parts of the image on the flat plate of the camera may not be in straight lines, but more or less curved and distorted. The concave form of the retina, however, allows the rays from all points of an object in the field of sight to be sharply focussed, and the image is consequently distinct and not out of shape.

CHAP. V.—THE FUNCTIONS OF THE IRIS.

The iris constitutes a diaphragm which regulates the amount of light entering the eyeball. The aperture in the centre, the *pupil*, may be dilated by contraction of a system of radiating fibres of involuntary muscle, or contracted by the action of another system of fibres forming a sphincter at the margin of the pupil. The radiating fibres are controlled by the sympathetic, while those of the circular set are excited by the 3rd cranial nerve. The variations in diameter of the pupil are determined by the greater or less intensity of the light acting on the retina. A strong light causes contraction of the pupil; with light of less intensity the pupil will dilate. In the human being a strong light acting on one eye will often cause contraction of the pupil not only in the eye affected but in the other eye. These facts indicate that the phenomenon is of the nature of a reflex action, in which the fibres of the optic nerve act as sensory conductors to a centre in the encephalon, whence influences emanate which act on the pupil. It has been ascertained that if the fibres of the optic nerve are stimulated in any way, contraction of the pupil follows. The centre is probably in the anterior pair of the *corpora quadrigemina*, as destruction of these bodies causes immobility of the pupil. On the other hand, the dilating fibres are derived from the sympathetic; and it has been shown that they come from the lower part of the cervical, and upper part of the dorsal, region of the cord. But the iris seems to be directly susceptible to the action of light. Thus, as was first pointed out by Brown-Séquard, the pupil of the eye of a dead animal will contract if exposed to light for several hours, whereas, if the eye on the opposite side be covered, its pupil will remain widely dilated, as at the moment of death. This phenomenon is seen with most marked effect in the eyes of cats.

The pupil *contracts* under the influence (1) of an increased intensity of light, (2) of the effort of accommodation for near objects, (3) of a strong convergence of the two eyes, and (4) of such active substances as nicotin, morphia, and physostigmin; and it *dilates* under the influence (1) of a diminished intensity of light, (2) of vision of distant objects, (3) of a strong excitation of any sensory nerve, (4) of dyspnœa, and (5) of such substances as atropin and hyoscyamin. The chief function of the iris is so to regulate the amount of light entering the eye as to secure sharpness of definition of the retinal image. This it accomplishes by (1) diminishing the amount of light reflected from near objects by cutting off the more divergent rays and admitting only those approaching in a parallel direction, which, in a normal eye, are focussed on the retina; and (2) preventing the error of spherical aberration by cutting off divergent rays which would otherwise impinge near the margin of the lens, and would thus be brought to a focus in front of the retina.

Chap. VI.—THE NORMAL EXCITATION OF THE RETINA.

The retina is the terminal organ of vision, and all the parts in front of it are optical arrangements for securing that an image will be focussed upon it. The natural stimulus of the retina is light. It is often said that it may be excited by mechanical and electrical stimuli, but such an observation applies to the stimulation of the fibres of the optic nerve. It is well known that such stimuli applied to the optic nerve behind the eye produce a luminous impression, but there is no proof that the retina, strictly speaking, is similarly affected. Pressure or electrical currents may act on the eyeball, but in doing so they not only affect the retina, consisting of its various layers and of Jacob's membrane, but also the fibres of the optic nerve. It is probable that the retina, by which the author means all the layers except those on its surface formed by the fibres of the optic nerve, is affected only by its *specific* kind of stimulus—light. This stimulus so affects the terminal apparatus as to set up actions which in turn stimulate the optic fibres. The next question naturally is, What is the specific action of light on the retina? Holmgren individually, and Dewar and the author conjointly, have shown that when light falls on the retina it excites a variation of the natural electrical current, obtained from the eye by placing it on the

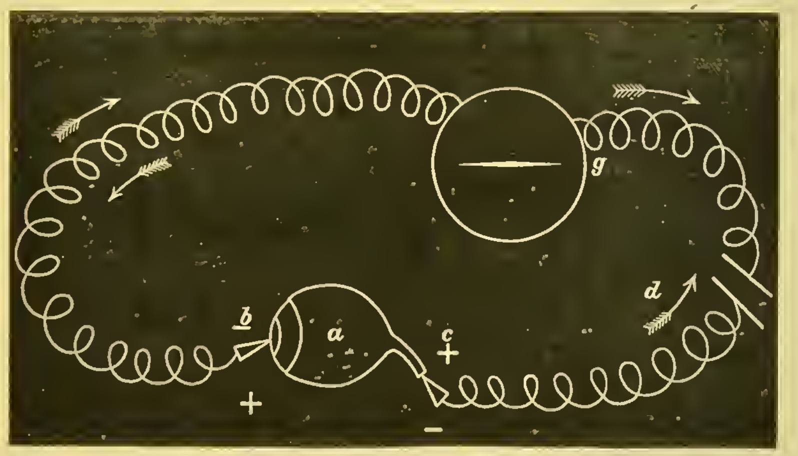

Fig. 352.—Diagram to illustrate the phenomena of the retina current:—*a*, eye; *b*, clay pad on corneal surface; *c*, clay pad on transverse section of optic nerve; *g*, galvanometer; *d*, key. Arrows represent direction of current—those outside when cornea is positive and those inside when it is negative to the transverse section.

cushions of a sensitive galvanometer (Fig. 352). The eye is placed on the clay pads of the troughs, the one pad touching the cornea and the other the posterior part of the eyeball. When the key is opened there is a swing of the needle of the galvanometer, and the spot of reflected light, after taking up a position and remaining tolerably steady, may be brought to the centre of the surface of a revolving cylinder, and in the dark it would follow the dotted line, *a h*, seen in Fig. 353. If light is thrown on the eye at *a*, the needle of the galvanometer swings to the right, as indicated by the curve, *a b c*, indicating *an increase in the natural current.* During the action of light, the current falls below the normal amount, as shown by the curve, *c d e*; and on the removal of light, as at *e*, there is often a second increase of the current, as shown by the curve, *e f g*; afterwards the amount of current falls below the normal. These results were ascertained by experiments on the eyes of many different animals, and they show that light produces a variation of the natural electrical current obtained from the living eye. It was also ascertained in this research that the amount of electrical variation produced by light of various intensities corresponded pretty closely to the results expressed in Fechner's law, as stated on page 567. If so, then this law applies to the phenomena happening in the terminal organ, and not, as generally supposed, *only* to those occurring in the brain. Such electrical phenomena must result either from thermal or chemical changes in the retina. Recent researches of Boll (1876) and Kühne have shown that light produces chemical changes in the retina. If an animal is killed in the dark, and its retina is exposed only to *yellow* rays, the retina has a peculiar purple colour, which is at once destroyed if exposed to ordinary light. (As to the nature and properties of this colouring matter, see Vol. I. p. 140.) The purple matter is decomposed by light. Kühne has also shown that an image or optogram may be *fixed* on the retina by plunging it

FIG. 353.—Curve of the variation in the natural electrical current of the eye produced by the action of light.

nto a 4 per cent. solution of alum immediately after death (Fig. 354). Visual purple occurs in the rods only. It has been found in the rods of all vertebrates examined, from the amphioxus to man, except in bats, pigeons, and hens. It has also been found in the rods of the eye of the fœtus removed from the uterus. It abounds in the eye of nocturnal birds, such as owls. It is never present in cones. Thus it would appear that light affects the purple matter of the retina, and the result of this chemical change is to stimulate the optic filaments; if the action be arrested we may have a picture on the retina, but if it be not arrested the picture is evanescent—the purple matter is used up and new matter of the same kind is formed from the pigment epithelium to take its place. If the retina of a frog's eye is peeled off the choroid, it soon becomes pale, from the visual purple being consumed, but if it is then laid back on the choroid, the purple colour returns. The retinal epithelium, in its turn, no doubt secretes the purple matter from the blood plasma oozing from the vessels near it. The retina might, therefore, be compared to a sensitive plate having the sensitive matter quickly removed and replaced by chemical changes, and it is probable that the electrical expression of these changes is what has been above described. At the same time, as we see most distinctly with the cones in which there is no visual purple, it is evident that visual purple is not necessary for vision. The probability is that colourless matters, having a similar photo-chemical sensitiveness, exist in the retina.

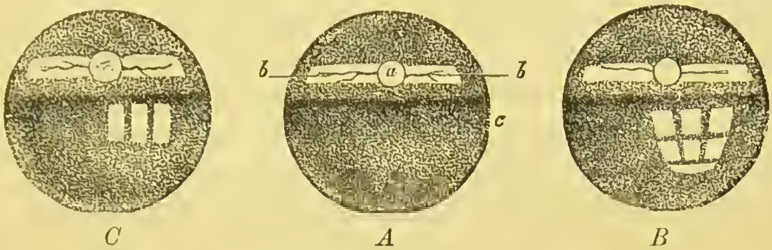

FIG. 354.—*A*, retina of rabbit killed in the dark—*a*, yellow spot; *b*, white streak of nerve fibres. *B*, optogram of a window, and *C*, of a skylight four metres distant.

Various observers, Angelucci, Boll, and Van Genderen Stort, have described peculiar movements of the pigmentary cells of the retina under the influence of light. While the eye is resting in the dark, the pigment is massed near the external part of the rods, in the vicinity of the junction between the inner and outer segments, but after exposure to daylight for an hour or so, the pigment is diffused over the rod nearly as far inwards as the *membrana limitans.* This phenomenon has been observed in the retinæ of the frog, triton, perch, pig, pigeon, and in man. Stort has also shown that light causes a slight elongation of the rods.[1]

Luminous impressions may also be produced by pressure on the eyeball. Such impressions, termed *phosgenes*, usually appear as a luminous centre, surrounded by coloured or dark rings. Sometimes they seem to be small, bright scintillations of various forms. Similar appearances may be observed at the moment of opening or of closing a strong electrical current transmitted through the eyeball. Thus, when a current is caused to pass from the retina along the optic nerve a light violet disk, or a dark spot surrounded by a yellow zone, may be seen. When the margins of the retina are irritated, a peculiar violet glimmer may be seen, especially if the current passes from the nerve to the retina. On opening and shutting the current, sensations of bright flashes occur. The law is that if we see a certain colour in passing the current down the nerve, the complementary colour is observed when the current passes up the nerve.

The visual field, even when the eyelids are closed in a dark room, is not absolutely dark. There is a sensation of faint luminosity, which may at one moment be brighter than at another. This is termed *the specific light of the retina*, and it indicates a condition of molecular activity, even in darkness.

(*a*) **The Excitability of the Retina.**—The retina is not equally excitable in all its parts. At the entrance of the optic nerve, as was shown by Mariotte in 1668, there is no sensibility to light; hence this part of the retina is called the *blind spot.* If we shut the left eye, fix the right eye on the cross seen in Fig. 355, and move the book towards and from the eye, a position will be found when the round spot dis-

FIG. 355.

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[1] A. G. H. Van Genderen Stort, Bewegingen van de Elemente der Retinæ onder den invloed van het Licht. Onderzoekingen gedaan in het Physiologisch Laboratorium der Utrichtsche Hoogeschool. 1887.

appears, that is, when its image falls on the entrance of the optic nerve. There is also complete insensibility to colours at that spot. The diameter of the optic papilla is about 1·8 mm.; this gives an angle of six degrees; this angle determines the apparent size of the blind spot in the visual field, and it is sufficiently large to cause a human figure to disappear at a distance of two metres.

The *yellow spot* in the centre of the retina is the most sensitive to light; and it is chiefly employed in direct vision. Thus, if we fix the eye on a word in the centre of this line, it is distinctly and sharply seen, but the words towards each end of the line are vague. If we wish to see each word distinctly, we "run the eye" along the line—that is, we bring each successive word on the yellow spot. This spot has a horizontal diameter of 2 mm., and a vertical diameter of ·8 mm.; and it corresponds in the visual field to an angle of from 2 to 4 degrees. It is believed that the fossa (*fovea centralis*) in the spot, where there are almost no retinal elements except Jacob's membrane, consisting here entirely of cones (2,000 in number), is the area of most acute sensibility. This fossa has a diameter of only ·2 mm., which makes the angle ten times smaller. Thus the field of distinct vision is extremely limited; and, at the same moment, we see only a very small portion of the visual field. Images of external objects are brought successively on this minute sensitive area, and the different sensations seem to be fused together, so that we are conscious of the object as a whole.

Towards the anterior margin of the retina, sensitiveness to light becomes diminished; but the diminution is not uniform, and it varies in different persons.

(*b*) **Duration and Persistence of Retinal Impressions.**—To excite the retina, a feeble stimulus must act for a certain time; but, if the stimulus be strong, it may be of very short duration. When the retina is excited, the impression lasts after the cessation of the stimulus.

Thus, the duration of an electrical spark is extremely short ($\frac{1}{1000000}$th of a second), but the impression on the retina is so powerful, and remains so long, as to make the spark visible. If we rotate a disc having white and black sectors, we see continuous dark bands. Even if we paint on the face of the disc a single large, round, red *spot*, and rotate it rapidly, a continuous red *band* may be observed. Here the impressions of red on the same area of retina succeed each other so rapidly that before one disappears another is superadded, the result being a fusion of the successive impressions into one continuous sensation. This phenomenon is called the *persistence of retinal impressions.* It has been ascertained that an impression lasts on the retina from the $\frac{1}{50}$th to $\frac{1}{30}$th of a second. If we look steadily at a bright light for a few seconds, and then quickly close the eyes or gaze into a dark room, a luminous image of the light will be visible for a short time. Such an appearance is called a *positive accidental image*, or a consecutive image. It may also be observed in this experiment that the intensity of the retinal excitation is not uniform. It increases quickly at its commencement, and, after it has reached a maximum, it slowly declines; indeed, its progress might be represented graphically by the muscle curve. Many familiar toys, such as the *thaumatrope*, or *wheel of life*, *stroboscopic discs*, and the *phénakistoscope*, produce curious effects due to persistence of retinal impressions. In these instruments, series of pictures representing different phases of a periodical process or occurrence, such as dancing, jumping, flying, etc., are shown to the eye so quickly that the after image of the one phase exists while the retina is affected by the phase next following, and the result is, one appears to see the figures in actual motion.

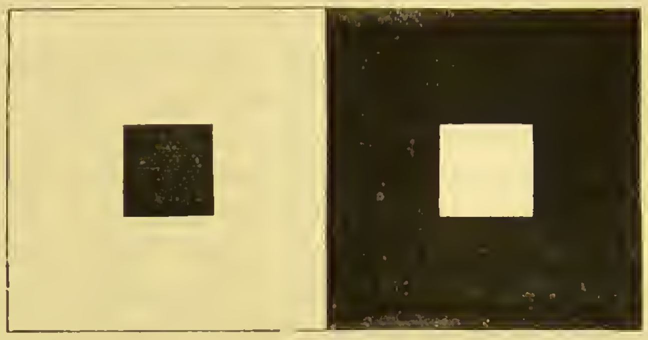

Fig. 356.—Illustration of Irradiation.

If we look at Fig. 356, the white square in the black field appears to be larger than the black square in the white field, though both are of precisely the same size. This is due to *irradiation*, a phenomenon explained by Von Helmholtz by stating that the borders of the clear surfaces advance in the visual field, and encroach on obscure surfaces. It is probable that even with the most exact accommodation, a penumbra or shadow of diffusion images forms around the edge of a white surface, so as to cause it to appear larger than it really is.

(*c*) **Intensity of Light required to Excite the Retina.**—To excite the retina, light must have a certain intensity. It is impossible to fix the minimum intensity necessary, as the effect will depend not only on the intensity of the stimulus, but on the degree of retinal excitability at the time. Thus, after the retina has been for some time in the dark, its excitability is increased; on the other hand, it is much diminished by fatigue. The sensibility of the eye to light is measured by instruments termed *photometers;* the principle of which is that the intensities of two lights are inversely proportional to the squares of their distance from a screen.

(*d*) **Consecutive Retinal Images.**—Images which persist on the retina are either positive or negative. They are termed *positive* when the bright and obscure parts of the image are the same as the bright and obscure parts of the object; *negative* when the bright parts of the object are dark in the image, and *vice versâ.* Positive images are strong

FIG. 357.—Figure to illustrate the formation of a consecutive image.

and sharply marked when an intense light has acted for not less than one-third of a second. If the excitation be continued longer, a negative, and not a positive image, will be seen. If, when the positive image is still visible, we look on a brilliantly illuminated surface, a negative image appears. Negative images are seen with greatest intensity after a strong light has acted for a considerable time. These phenomena may be best studied when the retina is excitable, as in the morning, after a sound sleep. On awaking, if we look steadily *for an instant* at the window, and then close the eyes, a *positive* image of the window will appear; if we then gaze fixedly at the window for one or two minutes, then close the eyes two or three times, and then look at a dark part of the room, a *negative* image will be seen floating before us. The positive image is due to excitation of the retina, and the negative to fatigue. If we fatigue a small area of the retina with white light, and then allow a less intense light to fall on it, the fatigued area responds feebly, and consequently the object, such as a window pane, appears to be dark. Many curious experiments may be made to illustrate the laws of consecutive images.

Thus, if we stand near a gaslight and look fixedly, without winking, at the little black dot under the chin of the figure seen in Fig. 357, for one minute, and then, after closing the eyelids two or three times, if we gaze into a dark part of the room, a white spectre will be seen floating in the air before us. A similar figure, white on a black ground, will produce a black spectre, a green figure a red, and a red a green, the reproduced colour being always complementary to that of the figure. Many spectral illusions, accepted as real by the superstitious, have been thus produced.

CHAP. VII.—SENSATIONS OF COLOUR.

Colour is a sensation excited by the action on the retina of rays of light of a certain wave-length, or, in other words, it depends on the number of waves striking the retina in a unit of time. Thus we have a sensation of red with a certain number of waves, and with about twice that number in the same time, the sensation will not be of red but of violet. When we examine a spectrum, we see a series of colours merging the one into the other, thus: red, orange, yellow, green, blue, indigo, and violet. These are termed *simple* colours. If two or more coloured rays of the spectrum act simultaneously on the same spot of the retina, they give rise to sensations of *mixed* colours. These mixed colours are of two kinds: (1) those which do not correspond to any colour in the spectrum, such as purple and white, and (2) those which do exist in the spectrum. White is produced by a mixture of two simple colours, then said to be *complementary.* Thus red and greenish blue, orange and cyanic blue, yellow and indigo-blue, and greenish yellow and violet, all produce white. Purple is produced by a mixture of red and violet or red and bluish violet. When white light falls on a surface, the surface may absorb all the rays except the red. If the red rays are alone reflected, then the object will be red; if the green rays are reflected, then the object will be green. Again, if we look through a red glass, all the rays are absorbed except red, and consequently external objects appear red, and so with regard to other transparent coloured media. The phenomena of colour may be studied by various methods; one of the simplest is that of Lambert, illustrated by Fig. 358. Place a red wafer on *d* and a blue wafer on *b*, and so angle the glass plate, *a*, as to throw a reflection of the object on *d in the same line* as the object on *b*. The sensation will then be purple. By substituting wafers of different colours, many experiments may be performed.

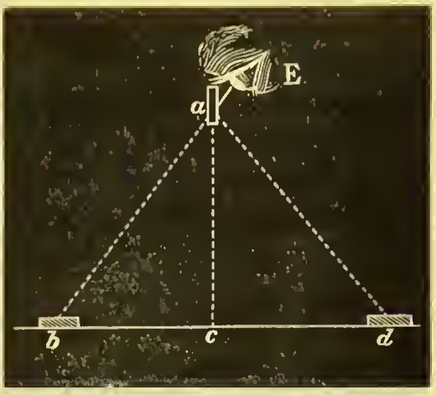

FIG. 358.—Lambert's method of studying combinations of colours.

Another method is to use a rotating disc, on the surface of which coloured sectors are painted, as represented in Fig. 359. With sectors of the size seen in the figure, *white* will be produced on rotating the disc rapidly. The *colour top* of Clerk-Maxwell is a top on the flat surface of which discs of various colours may be placed. Dancer has added to it a method by which, while the top is rotating rapidly, and the sensation of a mixed colour is perceived, the eye may be able to see the *simple* colours of which it is composed. This is done by placing on the handle of the top, a short distance above the coloured surfaces, a thin black disc, perforated by holes of various size and pattern, and weighted a little on one side. This disc vibrates to and fro rapidly, breaks the continuity of the colour impres-

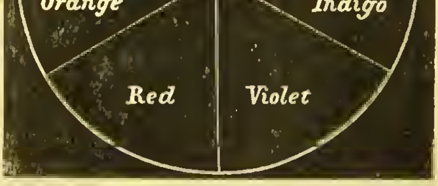

FIG. 359.—Rotating disc of Sir Isaac Newton for mixing colours.

sions, and thus the constituent colours are readily seen. Brücke held that all the ultra-violet rays are absorbed by the media of the eye and never reach the retina, but Von Helmholtz succeeded in stopping all the rays of the spectrum and still he saw a peculiar grey glimmer above the violet end of the spectrum, due, he supposed, to ultra-violet rays having an intensity 1,200 times less than that of the violet light at the upper ordinary limit of visibility. These rays are made visible by passing them through a solution of sulphate of quinine (fluorescence).

All colours have three characters : (1) *tone*, depending on the number of vibrations per second; (2) *intensity*, on the amplitude of the vibrations, passing from sombre to brilliant shades, and (3) *saturation*, on the amount of *white* the colour contains—a colour is saturated, when there is no white, as in the pure colours of the spectrum. There may be an infinite number of degrees of saturation from a pure colour to white. All colours, with light of feeble intensity, acquire *colour tones*, thus a feebly illuminated white seems grey, a weak yellow, brown, a weak red also brownish-red, a weak green, that of olive green.

(*a*) Theories of Colour Perception.

1. A theory which has met with much favour was first proposed by Thomas Young. and afterwards revived by Von Helmholtz. It is based on the assumption that three kinds of nerve fibres exist in the retina, the excitation of which give respectively sensations of red, green, and violet. It is further assumed that each cone is related to three such nervous filaments. Red, green, and violet are regarded as *fundamental* sensations. Homogeneous light excites all three, but with different intensities according to the length of the wave. Thus long waves excite most strongly fibres sensitive to red, medium waves those sensitive to green, and short waves those sensitive to violet. Fig. 360 shows graphically the irritability of the three sets of fibres. Von Helmholtz thus applies the theory :—

> "1. Red excites strongly the fibres sensitive to red, and feebly the other two—sensation, *red*.
> 2. Yellow excites moderately the fibres sensitive to red and green, feebly the violet—sensation, *yellow*.
> 3. Green excites strongly the green, feebly the other two—sensation, *green*.
> 4. Blue excites moderately the fibres sensitive to green and violet, and feebly the red—sensation, *blue*.
> 5. Violet excites strongly the fibres sensitive to violet, and feebly the other two—sensation, *violet*.
> 6. When the excitation is nearly equal for the three kinds of fibres, then the sensation is *white*."

This theory explains some of the phenomena of what is called *colour blindness* or *Daltonism.* All individuals have some kind of colour sensation; in some, however, there may be no sensation for particular colours. The most common defect is insensibility to *red* (Daltonism). The spectrum to such an eye is deficient in red, and the sensation corresponding to compound colours containing red, is that of the complementary colour only. Thus white is bluish-green, and intense red appears green, so that red poppies in a green corn field do not appear of a very different hue from the green by which they are surrounded. If we suppose in such cases an absence or paralysis of the red fibres, the phenomena are accounted for. True Daltonism occurs in about 3 per cent. of human beings, and it is about ten times more common in man than in woman. Blindness to green and violet is rare.

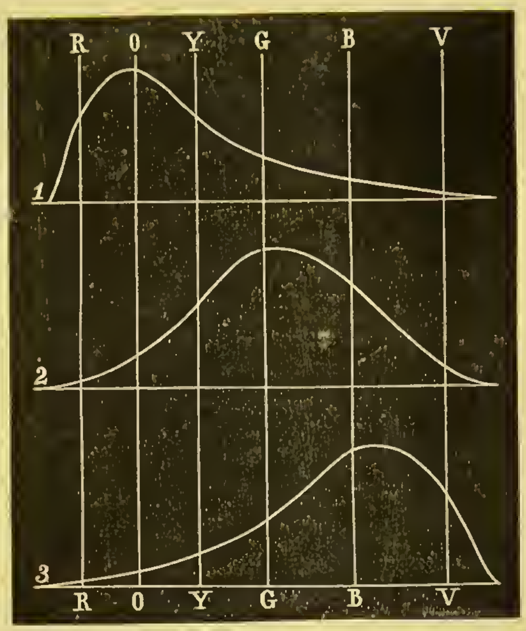

FIG. 360.—Diagram showing the irritability of the three kinds of retinal elements. 1, red; 2, green; 3, violet. R O Y G B V, initial letters of colours. Thus, to produce orange, *red* fibres are excited most, *green* less, *violet* least.

Young's theory explains the appearance of the consecutive coloured images. Suppose that we look at a red object for a considerable time, the retinal elements sensitive to red become fatigued. Then (1) if the eye be kept in *darkness,* the fibres affected by red being fatigued, do not act so as to give a sensation of red; those of green and of violet have been less excited, and this excitation is sufficient to give the sensation of pale greenish blue; (2) if the eye is fixed on a *white* surface, the red fibres, being fatigued, are not excited by the red rays contained in the white light; on the contrary, the green and violet fibres are strongly excited, and the consequence is that we have an intense complementary image; (3) if we look at a *bluish green* surface, the complementary of red, the effect will be to excite still more strongly the green and violet fibres, and consequently to have a still more intense complementary image; (4) if we regard a *red* surface, the primitive colour, the red fibres are little affected, in consequence of being fatigued, the green and violet fibres will be only feebly excited, and therefore only a very feeble complementary image will be seen ; and (5) if we look at a surface of a *different* colour altogether, this colour may combine with that of the consecutive image, and produce a mixed colour, thus on a *yellow* surface we will see an image of an orange colour. The retinal elements sensitive to red are wanting near the outermost edge of the retina. The image of a rod of red sealing wax appears to be black when allowed to fall on this part of the retina. Violet and green are well recognized even to the anterior margin of the retina.

2. Another theory of colour sensation has been proposed by Hering. He supposes that sensations of colour depend on different kinds of molecular processes occurring in the retina. Thus, he regards black, green, and blue as due to anabolic or constructive changes, and white, red, and yellow to katabolic or destructive changes, of a hypothetical visual substance. The three pairs of colour tones are thus not complementary but antagonistic. It is not easy to see why rays of the wave-length of green light should have an entirely different action from the slightly longer waves corresponding to red light.

3. Wundt has expounded a third theory, in which he asserts that in every excitation of the retina two different processes occur—one a chromatic process, a function of the wave-length of light, giving rise to colour tones, and the other, an achromatic, also dependent on wave-lengths, but varying in intensity while it remains the same in character. The achromatic stimulus reaches a maximum in yellow and shades off to each end of the spectrum, and the chromatic changes continuously with the wave-lengths. While the extreme differences at the two ends of the spectrum produce much the same results, the effects of intervening wave-lengths are such "that opposed phases of one and the same movement equalize each other perfectly."

On the whole, although no colour theory at present offered is free from imperfections, that of Young and Von Helmholtz, as it assumes the existence of three retinal components, instead of a series of merely qualitative changes, appears to be the most satisfactory. No doubt the adjustment of the three components occurs in the cerebral centre and not in the retina, but most of the phenomena of colour can be explained by assuming three pairs or series of components (retinal or cerebral)—one for red and green, one for yellow and blue, and one for white and black.

(*b*) The Contrast of Colours.

If we look at a small white, grey, or black object on a coloured ground, the object appears to have the colour complementary to the ground. Thus, a circle of grey paper on a red ground appears to be of a greenish-blue colour, whilst on a blue ground it will appear pink. This effect is heightened, if we place over the paper a thin sheet of tissue paper; but it disappears at once if we place a black ring or border round the grey paper. Again, if we place two complementary colours side by side, both appear to be increased in intensity. Various theories have been advanced to explain these facts. Von Helmholtz is of opinion that the phenomena consist more in modifications in judgment than in modifications of sensation. Plateau explained them by the formation of consecutive images.

CHAP. VIII.—THE MOVEMENTS OF THE EYE, BINOCULAR VISION, AND VISUAL IMPRESSIONS.

The globe of the eye has a *centre of rotation* which is not exactly in the centre of the optic axis, but a little behind it. According to Donders, it is 13·6 mm. from the vertex of the cornea, that is 2·2 mm. beyond the centre of the eye. On this centre it may move round *axes of rotation*, of which there are three: an antero-posterior, a vertical, and a transverse. In normal vision, the two eyes are always placed so as to be fixed on one point, called the *fixed point*, or the *point of regard*, or *visual point*. A line passing from the centre of rotation to the point of regard is called the *visual line*. The two visual lines form an angle at the visual point, and the base is formed by a line passing from the one centre of rotation to the other. A plane passing through both lines of regard is called the *visual plane*. The movements of the eyeball are of three kinds: (1) *First Position.*—The head is erect, and the *visual line* is directed towards the distant horizon. (2) *Second Position.*—This includes all the movements round the transverse and vertical axes. When the eye rotates round the first, the visual line is displaced above or below, and makes, with a line indicating its former position, an angle, termed the angle of *vertical displacement*, or the *ascensional angle*; and when it rotates round the vertical axis, the visual line is displaced from side to side, forming, with the median plane of the eye, an angle called the angle of *lateral displacement*. (3) *Third order of Positions.*—This includes all those which the globe may assume in performing a rotatory movement, along with lateral or vertical displacements. This movement of rotation is measured by the angle which the visual plane makes with the transverse plane, the *angle of rotation* or of *torsion*. Listing has formulated the following law regarding the rotations of the eyeball: When the visual line passes from its first position to any other position, the angle of torsion in this second position is the same as if the eye had come into this position in turning around a fixed axis perpendicular to the first and to the second position of the visual line. The result of this is that the axis of rotation of the eye is always in the frontal plane or equator of the eye. The eye never rotates round its antero-posterior axis.

The two eyes move together as a system, so that we direct the two lines of regard to the same point in space. The action of the muscles has already been described (p. 548).

The *visual field* is the area intercepted by the extreme visual lines which pass through the centre of the pupil, the amount of dilatation of which determines its size. It follows the movements of the eye, and is displaced with it. Each point in the visual field has a corresponding point on the retina; but the portion which secures our attention is that falling on the yellow spot.

Binocular Vision.—In normal vision when we look at an object with both eyes, its image falls upon the two yellow spots, and it is seen as one object. If, however, we displace one eyeball by pressing it with the finger, then the image in the displaced eye does not fall on the yellow spot, and we see *two* objects, one less distinctly than the other. It is not necessary, however, in order to see a single object with two eyes, that the two images fall on the two yellow spots; an object is single if its image fall on *corresponding points* in the two eyes. Thus, in the experiment above described, after having seen two images by displacing one eyeball, we may be able again to see only one image by pressing on the other eyeball. There are then corresponding points in the two retinæ, so that if they were superposed, the two yellow spots would coincide; the upper and lower parts of the left retina would touch the upper and lower parts of the right retina; the nasal side of the left retina would correspond to the temporal side of the right retina, and the reverse would also hold good. Thus, in Fig. 361, an object at a'' or at b'' or at c'' will be seen singly by the two eyes, A and B, as the images fall on corresponding points in the retinæ, namely, $a\ a'$, $b\ b'$, and $c\ c'$. It will be observed that if the eye, B, were displaced, the images would not fall on corresponding points, and consequently two would be seen. The name *horopter* has been given to a line connecting those points in the visual field which form their image on corresponding points of the retina. The older physiologists first gave this name to a straight line or plane passing through the point of convergence of the axes of the eyes, or the point to which the eyes are directed, but Vieth and Müller showed that it cannot be a straight line or plane, but must have a circular form.

Thus, if the points, $a\ b\ c$, in Fig. 361, correspond to the points, $a'\ b'\ c'$, the angles 4 and 1 in the one eye must correspond to the angles 4 and 1 in the other. Then $a\ b$ being equal to $a'\ b'$, and the angle 1 in eye A equal to angle 1 in eye B, the angles

$1'$ and $1'$ will be equal. Since the angles 2 and 2 are equal, the angles 3 and 3 must also be equal. In the same way the angle 5 is equal to angle 3. For $b\,c = b'\,c'$, and angle 4 = angle 4. Thus the angles 3, 3, and 5 are equal, and $a''\,b''\,c''$ cannot lie in a straight line, for it is the property of a circle only that triangles erected on the same chord, and reaching the periphery, have at the periphery equal angles.[1] A line joining $a''\,b''\,c''$ is therefore the horopter, and its form is illustrated by Fig. 362.

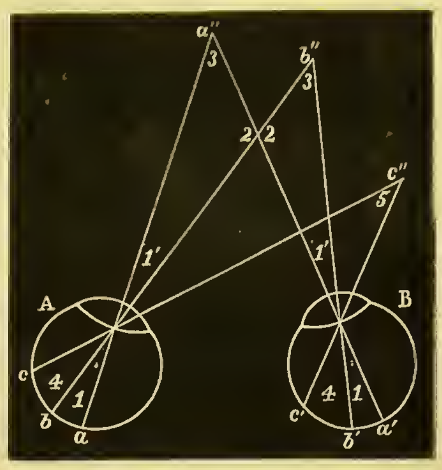

Fig. 361.—Diagram to illustrate theory of corresponding retinal points.

It is a circle, of which the chord is formed by the distance between the points of decussation of the rays of light in the eye. Its size is determined by the position of the two eyes, and the point towards which their axes converge. Thus, if A in Fig. 362 were nearer the eyes, the horopter would be the chord of a smaller circle. The form of the horopter in tertiary positions is extremely complicated.

All objects not found in the horopter, or which do not form an image on corresponding points of the retinæ, are seen double. When the eyeballs are so acted upon by their muscles as to secure images on non-corresponding points, and consequently double vision, the condition is termed *strabismus*, or squinting.

The accommodating mechanism of the eye is correlated to the movements of convergence necessary for single vision. Thus, when we see a single object, we not only converge the eyeballs so as to bring the pictures on the yellow spots, but we accommodate at the same time. An association of functions exists between the *rectus internus* and *rectus externus* which determines the angle of convergence and the mechanism of accommodation. When the axes of the eyes are parallel, as in looking at an object placed at an infinite distance, accommodation is at rest; but when the axes are turned

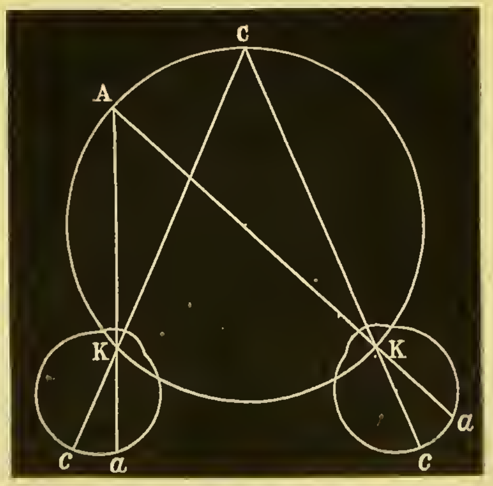

Fig. 362.—Diagram to illustrate the horopter.

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[1] Müller's *Physiology*, vol. ii. p. 1195.

inwards, the pupils contract, and the ciliary muscles also contract. Further, the two eyes can only be raised or depressed at the same time, so that both lines of vision must lie in the same plane. Nor can the axes be made divergent. Thus there is a correlation between the *rectus internus* of the one side and the *rectus externus* of the other.

In the fusion of double images, however, we must assume not only that there are corresponding points in the retinæ, but also that there are corresponding points in the brain, at the central ends of the optic fibres. One can imagine that the cerebral effect (except as regards consciousness) will be the same when a single object is placed before the two eyes, in the proper position, whether the individual is conscious or not. On the other hand, as we are habitually conscious of a single image, there is a psychical tendency to fuse double images when they are not too dissimilar.

Binocular vision of colour may be illustrated by the following experiment:— Take two No. 3 eye-pieces of a Hartnack's microscope, place one in front of each eye, direct them to a clear window, in daylight, and two luminous fields will be seen, one corresponding to each eye. Then converge the two eye-pieces until the two luminous circles cross, and the central part, like a biconvex lens, will appear clear and bright, while the outer segments will be much less intense, and may appear even of a dim grey colour. Here, evidently, the sensation is due to a fusion of impressions in the brain. With a similar arrangement, blue light may be admitted by the one eye-piece and red by the other, and on the convergence of the two, a resultant colour, purple, will be observed.

Theories of Binocular Vision.—We not only see a single object with two eyes, but the object, say a cube or a book lying on the table, is seen in relief, that is, we take cognizance of the third dimension occupied by the body in space, although the two retinal pictures are on a plane. Further, it can readily be demonstrated that the two retinal pictures are dissimilar, and yet the two images are fused into one and give the impression of a single object occupying three dimensions. To explain these phenomena, Wheatstone suggested that the mind fused the dissimilar pictures into one, and that whenever there occurs mental fusion of images dissimilar, and incapable of mathematical coincidence, the result is a perception of depth of space or solidity, or relief. The objection to this theory is that complete fusion does not take place. It is possible by close analysis of visual perceptions to distinguish between the two retinal pictures. Further, if the fusion is mental, it is an example of unconscious cerebration. Another explanation has been suggested by Brücke, which may be thus stated.

When we look at objects near at hand, the optic axes are converged strongly, and they become less and less converged as we gaze at objects farther and farther away. There is thus a series of adjustments, the muscular movements giving rise to sensations, by which we estimate the relative distance of objects in the field of view. A man with one eye cannot judge by this method. We habitually depend upon binocular vision in all movements requiring an exact estimate of the respective proximity of two or more objects. An illustrative experiment is to suspend a curtain ring so as to present its edge at the distance of four or five feet from the eye, and then to try to push sideways through its hoop the curved handle of a walking stick held by the lower end. This can be readily accomplished with binocular vision, but it is difficult when one eye is closed, until a succession of trials has enabled the experimenter to measure the distance of the ring by the muscular movements of his arm.[1] According to Brücke, the two eyes are in a state of motion, and their position of convergence, now greater, now less, passes from one side to the other, so that the observer combines successively the different parts of the two pictures, thus giving rise to sensations of depth of space and of relief. Brücke's theory, in short, is that our perception of depth depends on the fusion of nervous impressions coming from the muscles of the eyeballs. It was, however, pointed out by Dove that the sensation of relief, solidity, or perspective, is perfect even when natural objects or stereoscopic pictures are seen momentarily by an electric flash lasting only $\frac{1}{24000}$th of a second, during which time it is inconceivable that there can be any change in the degree of convergence of the optic axes. This experiment is fatal to Brücke's theory, and Wheatstone was right in asserting that the sensation of relief is instantaneous.[2] No doubt, there are behind the phenomena referred to the retina, nervous operations unconsciously performed, which fuse together the results of the retinal impressions. Corresponding points are points which furnish images habitually combined or fused. We also get into the habit of fusing the images of two not perfectly corresponding points which, under certain circumstances, we should perceive as double. When the mind unites images which do not fall upon corresponding points, the conception is added that the corresponding points in the object occupy the situation for which the

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[1] W. B. Carpenter, *Edinburgh Review.* 1858.

[2] For an account of a theory by J. Le Conte, see *American Journal of Science and Arts*, vol. ii. 1871. See also article "Stereoscope," by Author, in *Encyclopædia Britannica*, 9th ed.

eye would have to be arranged in order that the images should coincide.[1]

CHAP. IX.—PSYCHICAL RELATIONS OF VISION.

(a) Characters of Visual Perceptions.

All visual perceptions, if they last for a sufficient length of time, appear to be external to ourselves, erect, localised in a position in space, and more or less continuous.

(1) *Visual Sensations are referred to the Exterior.*—This is due to habit. Those who have been born blind, on obtaining eyesight by an operation, have imagined objects to be in close proximity to the eye, and they have not had the sense of exteriority which most individuals possess. Slowly, and by a process of education, in which the sense of touch played an important part, they gained the knowledge of the external relations of objects. Again, phosgenes, when first produced, appear to be in the eye; but, when conscious of them, by an *imaginative* effort, we may transport them into space; yet they never appear very far off.

(2) *Visual Sensations are referred to Erect Objects.*—Although the images of objects are *inverted* on the retina, we see them erect. The explanation of the effect is, that we are conscious not of the image on the retina, but of the luminous object from which the rays proceed, and we refer the sensation in the *direction* of these rays. Again, in running the eye over an object, say a tall pole, from base to apex, we are not conscious of the different images on the retina, but of the muscular movements necessary to bring the parts successively on the yellow spot.

(3) *Visual Sensations are referred to a Position in Space.*—The localization of a luminous point in space can only be determined by observing its relations to other luminous points with a given position of the head and of the eye. For example, in a perfectly dark room, if we look at a single luminous point, we cannot fix its exact position in space, but we may get some information, of a vague character, by moving the head or the eye. If, however, a second luminous point appear in the darkness, we can tell whether it is nearer or farther distant, above or below, the first. So with regard to other luminous points: we observe their reciprocal relations, and thus we localise a number of visual impressions.

(4) *Visual Sensations are Continuous.*—Suppose the image of a luminous line falls on the retina, it will appear as a line although it is placed on

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[1] Hermann's *Physiology*, translated by Gamgee, p. 430.

perhaps 200 cones or rods, each of which may be separately excited, so as to cause a *distinct* sensation. Again, on the same principle, the impression of a superficial surface may be regarded as a kind of *mosaic*, made up of individual portions corresponding to the rods or cones on which the image of the surface falls. But in both cases the sensation is continuous, so that we see a line or a surface. The individual images are fused together.

Each part of the retina is in relation with a certain part of the visual area in the cortex of the brain, and with every visual perception we have, as it were, a mental image of that spot of light on the retina. But experience has taught us, especially by the sense of touch, that when we have a sensation of light, it is caused by an object outside the eye. The mind, therefore, concludes that when a sensation of light is felt, it is caused by something external to the eye, and it is localised in the periphery. From each point of the retina, which has its corresponding point in the brain, the mind projects the image outwards in the direction of the rays that form the image on the retina. Thus objects are seen to be upright although the image is reversed on the retina, the rays crossing at the nodal point. In a similar way, entoptic phenomena are referred to the field of sight, and if irritation occurs in the cortical cerebral area, causing hallucinations of sight in the form of phantasms, they are referred to the outer world in the direction in which they would have been produced had they been true sensations corresponding to real external objects.

(b) Notions derived from Visual Perceptions.

(1) *Apparent Size.*—This, so far as regards a comparatively small object, depends on the size of the retinal image, as determined by the visual angle. With a very large object, there is an appreciation of size from the muscular sensations derived from the movements of the eyeball, as we "range" the eye over it. It is difficult to appreciate the distance separating two points between which there are other points, as contrasted with an apparently similar distance without intermediate points. For example, the distance, A to B, appears to be greater than from B to C in Fig. 363, although the two distances are equal.

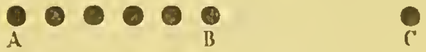

FIG. 363.—Illusions of size.

(2) *Direction.*—As the retina is a curved surface, a long straight line, especially seen from a distance, appears curved. In Fig. 364, an illusion of direction, first shown by Zoellner, is depicted. If these lines be

looked at somewhat obliquely, say from one corner, they will appear to converge or diverge, and the oblique lines, on each side of the vertical lines, will appear not to be exactly opposite each other. But the vertical lines are parallel, and the oblique lines are continuous across them. The effect is evidently due to an error of judgment, as it may be controlled by an intense effort, when the lines will be seen as they really are.

FIG. 364.—Zoellner's Figure, showing an illusion of direction.

(3) *Apparent Distance.*—We judge of distance, as regards large objects at a great distance from the eye, (1) from their apparent size, which depends on the dimensions of the visual angle; and (2) from the interposition of other objects between the eye and the distant object. Thus, at sea, we cannot form, without great experience, an accurate estimate of how many miles we are off the coast, and all know how difficult it is to estimate accurately the width of a river. But if objects are interposed between the eye and the distant object, say a few vessels, at different distances, at sea, or a boat on the river, then we have certain materials on which to form a judgment, the accuracy of which, however, even with these aids, will depend on experience. When we look at a near object, we judge of its distance chiefly by the sense of effort put forth in bringing the two lines of regard to converge upon it.

(4) *The Movement of a Body.*—If the eye is fixed, we judge of movement by successive portions of the retina being affected. When

the eye moves so as to "follow" the object, there is a sense of muscular effort, which is increased when, in addition, we require to move the head, and still more when we require to move the body.

(5) *The Apparent Solidity of an Object.*—If we look at an object, say a cube, first with the right eye and then with the left, it will be found that the two images of the object are somewhat different, as in Fig. 365.

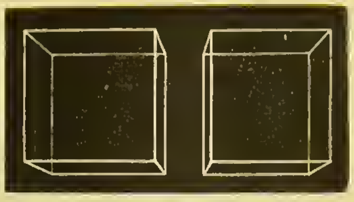

FIG. 365.—Illustrating stereoscopic vision.

If, then, by means of a stereoscope, or by holding a card between the two eyes and causing a slight convergence of the eyes, the two images are brought upon corresponding points of the two retinæ, the image will be at once seen in relief[1] (p. 642).

D.—THE SENSE OF TOUCH.

The sense of touch is located in the skin. The following structures constitute the terminal organs:—

CHAP. I.—STRUCTURE OF TACTILE ORGANS.

1. **Free Nerve Terminations.**—In some situations, nerve fibres, after losing the medullary sheath, divide and subdivide into fine fibrils, which end in fine pointed filaments. Such terminations occur in stratified epithelium, as in the cornea (Fig. 366). They also occur in the mucous membrane of the mouth, and in the deeper layers of the epidermis (Fig. 367, *n*). In the latter situation we also meet with cells having long branched processes, the *cells of Langerhans*, which are probably nerve endings (Fig. 367, *l*).

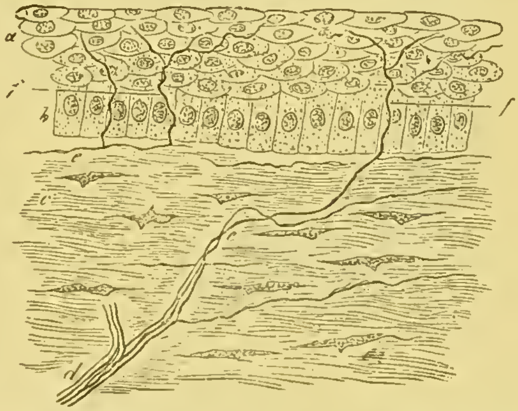

FIG. 366.—Vertical section of cornea of a rabbit, treated with chloride of gold. *a*, older, *b*, younger, epithelial cells of conjunctiva; *c*, corneal tissue; *d*, nerve fibre; *e*, fine nerve fibril; *f*, splitting up and termination of *e* in epithelium.

2. **Nerve Terminations in Corpuscles.**—These may consist of one cell, but usually they are formed of a number of cells, on

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[1] See article "Stereoscope" by Author, in *Encyclopædia Britannica*, 9th ed.

which the ends of the nerve fibrils rest. Thus we find (*a*) simple tactile cells; (*b*) groups of tactile cells; (*c*) touch corpuscles; and (*d*) end bulbs, including the complicated form called a Pacinian corpuscle.

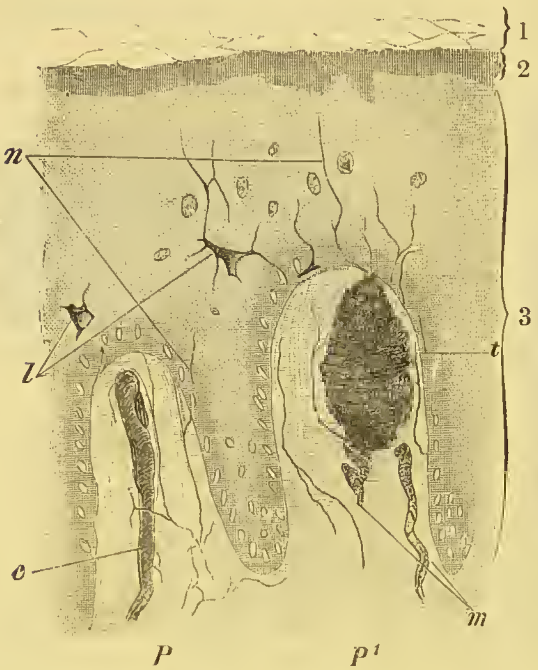

FIG. 367.—Vertical section through skin of great toe of man twenty-five years of age. × 240 d. The nuclei of the cells in the *stratum mucosum*, seen only in the deepest layer. *l*, Langerhans' cells; *n*, inter-epithelial nerve fibres; *P*, *P*¹, two papillæ of *cutis vera*; *P*, contains a plexus of capillaries, *c*, of which only one loop is seen; *P*¹, contains a touch corpuscle of Wagner, *t*, on which two medullated nerve fibres, *m*, are seen. Non-medullated nerve fibres are also seen in the papilla. 1, upper layer, 2, mid-layer, and 3, deep layer of epidermis. (Method No. 119, Appendix.)

(*a*) **Simple Tactile Cells** are oval, nucleated cells, 6 to 12 μ in diameter (Fig. 369, *tz*), situated either in the deepest layers of the epidermis, or in the true skin quite close to the epidermis. Non-medullated fibres sometimes end in disc-shaped bodies, a *touch meniscus* (Fig. 368, *tm*) on the under surface of the tactile cell.

(*b*) **Simple Tactile Corpuscles.**—These, sometimes called the corpuscles of Grandry, or the corpuscles of Merkel, consist of two or more flattened cells, each larger than a simple tactile cell, and about 15 μ in length and 50 μ in breadth. Each cell contains a nucleus. A medullated nerve fibre (Fig. 370, *n*), on approaching the corpuscle, loses its white substance, and the axis cylinder ends in a flat disc (Fig .369, *ts*), the *tactile disc*, lying between two touch cells. The white substance ends, as already mentioned, before the axis cylinder joins the tactile disc, but the sheath of Henle is continued into the connective tissue covering of the tactile corpuscle. Structures consisting of two tactile cells are called *twin tactile cells* (Fig. 369, *B*, 2), and those formed of several tactile cells

FIG. 368.—Vertical section through skin of great toe of man, twenty-five years of age. × 240 d. The outlines of the cells and nuclei of epidermis are indistinct. *tm*, touch meniscus, seen from the side, on the under surface of a touch cell, the nucleus of which is invisible. The connection with the nerve has been divided. A touch meniscus is seen connected with the nerve fibre, *n*; *p*, connective tissue layer; ×, touch cells in the corium, connected with delicate nerve endings. Method No. 120, Appendix.)

(Fig. 369, *B*, 1) are termed *simple tactile corpuscles.* The latter have as yet only been found in the skin of the bills and in the tongues of birds, especially of aquatic birds, and they are situated almost exclusively in the uppermost layers of the corium.

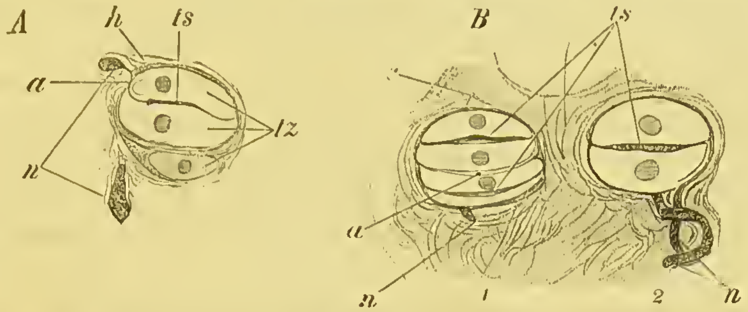

Fig. 369.—Vertical section through the skin covering the attached end of the upper mandible of a goose. × 240 d. *A*, simple tactile corpuscle, divided parallel to the plane of entrance of the nerve. *n*, medullated nerve, divided by the section; *a*, axis cylinder; *ts*, tactile disc, divided perpendicularly; *h*, connective tissue covering; *tz*, tactile cells, the lowermost only divided. *B*, two touch cells divided transversely to the plane of entrance of the nerves. 1, tactile corpuscle, consisting of four tactile cells; 2, twin tactile cells, *ts*; tactile disc, *a*; *n*, to the left, transverse section of axis cylinder; *n*, to the right, medullated nerve fibre; *c*, corium. (Method No. 121, Appendix.)

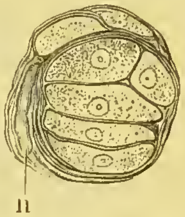

Fig. 370.—Corpuscle of Grandry; *n*, nerve.

(*c*) **Compound Tactile Corpuscles.**—These, sometimes termed the corpuscles of Wagner, or the corpuscles of Meissner, are oval bodies, 40 to 200 μ in length, and 30 to 60 μ in breadth, showing a striated appearance on the surface. They are found in the papillæ of the cutis vera, especially in the palm of the hand and sole of the foot. Each tactile corpuscle has one or two medullated nerve fibres twisted spirally round it. The spirals are chiefly near the lower pole of the corpuscle, and towards the upper pole the nerve fibres lose the white substance, and the axis cylinders end in flat excrescences on the surface of the corpuscle. The corpuscle itself consists of flattened cells, the boundaries of which cause the striated appearance above mentioned. Comparing them with the tactile bodies found in the bills of birds, it is evident that they are built up of a greater number of tactile discs and of tactile cells. Thus they may be termed compound tactile corpuscles. The perineurium of the nerve is continued into the connective tissue layers of the corpuscles (Fig. 371).

Fig. 371.—Tactile corpuscle from a vertical section of the great toe of a man, twenty-five years of age. × 50 d. *n*, medullated nerve fibres; *e*, nerve endings, with flat excrescences; *h*, connective tissue. (Method No. 122, Appendix.)

The globular *end knobs* of Krause are bodies allied in structure and function to the tactile corpuscles. They consist of a number of cells, between which are found delicate nerve fibres, and the whole is surrounded by a covering of connective tissue. They are found in the conjunctiva, in the mucous membrane of the cavity of the mouth, and of the clitoris (Fig. 372). To the same category belong the nerve corpuscles found in joints and in tendons, which are of large size in joints, and also the bodies found in the *glans penis*, *glans clitoridis*, and the *labia minora* (Fig. 373). The latter, *genital* or *sexual corpuscles*, vary in diameter from 14 to 20 μ, and are often grouped in clusters round the end of a nerve, giving rise to a mulberry-like appearance.

(*d*) **End Bulbs.**—These are elongated oval bodies, into one end of which a nerve fibre penetrates. There are two forms, a simple and a complex. The *simple* form consists, in great measure, of a modification of the external portions of the nerve fibre entering the bulb. We have (1) a fine covering of connective tissue, which is the continuation of the perineurium; and (2) an internal knob of finely granular matter, showing concentric stratification and a few nuclei. The nature of the knob has not yet been clearly explained, but if we regard it as a continuation of the white substance of the nerve, or of Henle's sheath, it should consist of flattened cells. In the centre of this we find the axis cylinder, which penetrates the lower end of the knob, runs through it like a delicate ribbon to the upper pole, and there ends in a little swelling or thickening. Such end bulbs are found in the basement membrane of certain mucous membranes, as in the conjunctiva covering the cornea, and in the mucous membrane of the mouth.

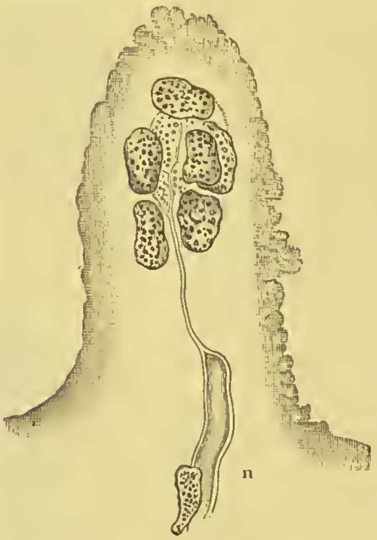

FIG. 372.—Genital corpuscles from clitoris connected with the nerve, *n*.

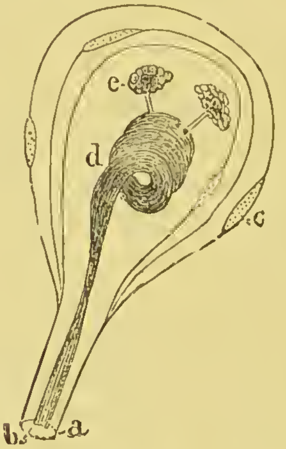

FIG. 373.—Genital corpuscles from glans penis. *a*, nerve; *b*, sheath of connective tissue; *c*, *d*, corpuscles.

The *complex* end bulbs are known as the *corpuscles of Vater*, or the *corpuscles of Pacini.* They are elongated, oval, translucent bodies, from 1 to 2 mm. in thickness, and from 2 to 3 mm. in length. Like the end bulbs above described, they show an external portion or integument, an internal knob, and an axis cylinder. The body consists of a large number of lamellæ or capsules, concentrically arranged, and each separated from its neighbour by a layer of flat endothelial cells. Each space between two lamellæ contains fluid, and it is crossed by connective tissue fibres running longitudinally or transversely through it. The lamellæ are continuous with the perineurium of the nerve. Each capsule is smaller as we approach the centre, and the capsules are all connected at the pole opposite the entrance of the nerve by a thickening, which has been termed an interlamellar ligament. A small artery enters the corpuscle and forms a network between the capsules.

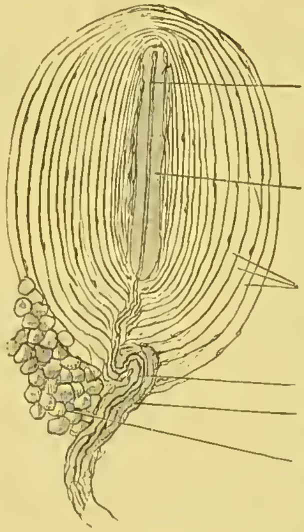

FIG. 374.—Small Pacinian corpuscles from mesentery of a cat. × 50 d. The endothelial cells between the capsules are recognizable by their darkly marked nuclei. Observe also the entrance of the nerve. (Method No. 123, Appendix.)

Pacinian corpuscles are found in the subcutaneous connective tissue of the palm of the hand and the sole of the foot, on the dorsal nerve of the penis and clitoris, in the deeper layers of connective tissue below the skin near joints, in the mesentery and in the connective tissue around the pancreas.

The *corpuscles of Herbst* in birds are small Pacinian corpuscles. They show a double row of nuclei in the rod-like nerve ending. The *corpuscles of Golgi* are long spindle-shaped bodies found in many tendons at their junction with the muscle. They are formed of connective tissue, and one or more medullated nerve fibres enter each corpuscle and end in small granular swellings near its surface.

CHAP. II.—TACTILE IMPRESSIONS.

Touch may be defined as a sense of pressure, referred to the surface of the body. It is often understood as a sensation of contact as distinguished from pressure, but it is evident that, however gentle be the contact, a certain amount of pressure exists between the sensitive surface and the body touched. Mere contact is gentle pressure; a greater amount of force causes a feeling of resistance referred to the skin; a still greater amount causes a feeling of muscular resistance, as when a weight is supported on the palm of the hand; whilst, finally, the pressure may be so great as to cause pain. The force may not be exerted vertically on the sensory surface, but in the opposite direction, as when a hair on a sensory surface is pulled or twisted. Touch is the sense by which mechanical force is appreciated, and it presents a strong resemblance to hearing, in which the sensation is excited by intermittent pressures on the auditory organ. Contact may also give rise to a sensation of temperature, according as the thing touched feels hot or cold. These sensations of contact, pressure, or temperature, are referred to the skin or integument covering the body, but they are experienced to a greater or less extent when any serous or mucous surface is touched.

Organs devoted to touch are usually very mobile, as, for example, the fingers of man, the tongue of all animals, the upper lip of the horse, the trunk of the elephant, and the antennæ of insects. The tactile sensibility of the feet is of great importance for firmness in standing and walking. The hoof of the horse even, by the skin enclosed in the capsule of horny substance, which is rich in nerves, enables the animal to judge of the quality of the ground on which it treads, so that it will walk securely when blind or in the dark. The tactile hairs of the felines and of the dog and its allies are important organs of touch, and the soft hairs of the skin all over the body are also devoted to the sense.

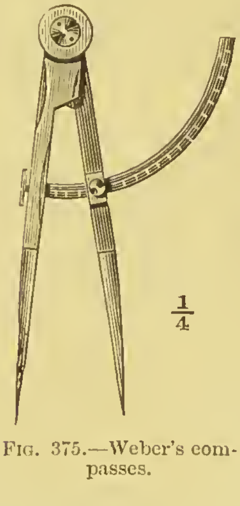

Fig. 375.—Weber's compasses.

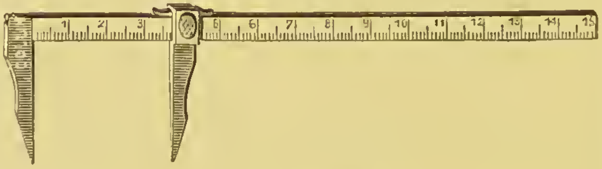

Fig. 376.—Æsthesiometer.

Sensitiveness and Sense of Locality.—The degree of sensitiveness of the skin is determined by finding the smallest distance at which the two points of a pair of compasses can be felt. The following table shows the sensitiveness in millimetres for an adult:—

	Millimetres.
Tip of tongue,	1·1
Third phalanx of finger, volar surface,	2-2·3
Red part of the lip,	4·5
Second phalanx of finger, volar surface,	4-4·5
First phalanx of finger, volar surface,	5-5·5
Third phalanx of finger, dorsal surface,	6·8
Tip of nose,	6·8
Head of metacarpal bone, volar,	5-6·8
Ball of thumb,	6·5-7
Ball of little finger,	5·5-6
Centre of palm,	8-9
Dorsum and side of tongue; white of the lips; metacarpal part of the thumb,	9
Third phalanx of the great toe, plantar surface,	11·3
Second phalanx of the fingers, dorsal surface,	11·3
Back,	11·3
Eyelid,	11·3
Centre of hard palate,	13·5
Lower third of the forearm, volar surface,	15
In front of the zygoma,	15·8
Plantar surface of the great toe,	15·8
Inner surface of the lip,	20·3
Behind the zygoma,	22·6
Forehead,	22·6
Occiput,	27·1
Back of the hand,	31·6
Under the chin,	33·8
Vertex,	33·8
Knee,	36·1
Sacrum (gluteal region),	44·6
Forearm and leg,	45·1
Neck,	54·1
Back of the 5th dorsal vertebra; lower dorsal and lumbar region,	54·1
Middle of the neck,	67·7
Upper arm; thigh; centre of the back,	67·7

These investigations show not only that the skin is sensitive, but that one is able with great precision to distinguish the part touched. This latter power is called the *sense of locality*, and it is influenced by various conditions. The greater the number of sensory nerves in a given area of skin, the greater is the degree of accuracy in distinguishing different points. Contrast in this way the tip of the finger and the back of the hand. Sensitiveness increases from the joints towards the extremities. It is doubtful if exercise improves sensitiveness, as Francis Galton found that the performances of blind boys were not superior to those of other boys, and he says that "the guidance of the blind depends mainly on the multitude of collateral indications, to which they give much heed, and not their superiority in any one of them." When the skin is moistened with indifferent fluids sensibility is increased. Stretching the skin, and baths in water containing carbonic acid or common salt, increase the power of localising tactile impressions. If the points of the compasses are unequally heated, the sensation of two contacts becomes confused.

Absolute Sensitiveness, as indicated by a *sense of pressure*, has been determined, by various methods, with the following general results: (1) The skin of the forehead, temples, and back of the hand and forearm detected a pressure of ·002 grm.; fingers, ·005 to ·015 grm.; the chin, abdomen, and nose, ·04 to ·05 grm. (2) Eulenberg found the following gradations in the fineness of the pressure sense: the forehead, lips, back of the cheeks, and temples, appreciate differences of $\frac{1}{40}$th to $\frac{1}{30}$th. The back of the last phalanx of the fingers, the forearm, hand, 1st and 2nd phalanges, the palmar surface of the hand, forearm, and upper arm distinguish differences of $\frac{1}{10}$th to $\frac{1}{20}$th. The front of the leg and thigh is similar to the forearm. Then follow the back of the foot and toes, the sole of the foot, and the back of the leg and thigh. (3) In passing from light to heavier weights, the acuteness increases at once, a maximum is reached, and then, with heavy weights, the power of distinguishing the differences diminishes. (4) A sensation of pressure after the weights have been removed may be noticed, especially if the weight be considerable. (5) If the finger is held against a blunt-toothed wheel, and the wheel rotated with a certain rapidity, a smooth margin is felt when the intervals of time between the contacts of successive teeth are less than from $\frac{1}{480}$th to $\frac{1}{640}$th of a second. (6) Vibrations of strings are detected, even when the number is about 1500 per second. By attaching bristles to the prongs of tuning forks, and bringing these into contact with the lips or tongue, sensations of a very acute character are experienced, which are most intense when the forks vibrate from 600 to 1500 per second. (7) Weber states that, if we place weights on the skin at intervals of more than 15 sec., we may distinguish weights that are in the ratio of 29:30. If more than ·5 minute elapse, then the ratio of the weights will be 24:40. (8) The sense of pressure may be retained by the mind for some time after the exciting cause has been removed, so that we may compare impressions of weight.

Information from Tactile Impressions.—These enable us to come to the following conclusions: (1) We note the existence of something touching the sensory surface. (2) From the intensity of the sensation we determine the weight, tension, or intensity of the pressure. (3) The locality of the part touched is determined, and from this the probable position of the touching body. Like the visual field, to which all retinal impressions are referred, point for point, there is a *tactile field*, to which all points on the skin surface may be referred. (4) By touching a body at various points, from the difference of pressure and from a comparison of the positions of various points in the tactile field, we judge of the configuration of the body. A number of "tactile pictures" are obtained by passing the skin over the touched body, and the shape of the body is determined by a knowledge of the muscular movements necessary to bring the cutaneous surface into contact with different portions of it. If there is abnormal displacement of position, a false conception may arise as to the shape of the body. Thus, if a small marble or pea is placed between the index and middle finger, so as to touch (with the palm downwards) the outer side of the index finger and the inner side of the middle finger, a sensation of touching one round body is experienced; but, if the fingers be crossed, so that the marble touches the inner side of the index finger and the outer side of the middle finger, there will be a feeling of *two* round bodies, because in these circumstances there is added to the feelings of contact a feeling of distortion (or of muscular action), like what would take place if the fingers, for purposes of touch, were placed in the abnormal position. Again, as showing that our knowledge of the tactile field is precise, there is the well-known fact that, when a piece of skin is transplanted from the forehead to the nose, in the operation for removing a deformity of the nose, arising from lupus or other ulcerative disease, the patient feels the new nasal part as if it were his forehead, and he may have the curious sensation of a nasal instead of a frontal headache. (5) From the number of points touched, we judge as to the smoothness or roughness of a body.

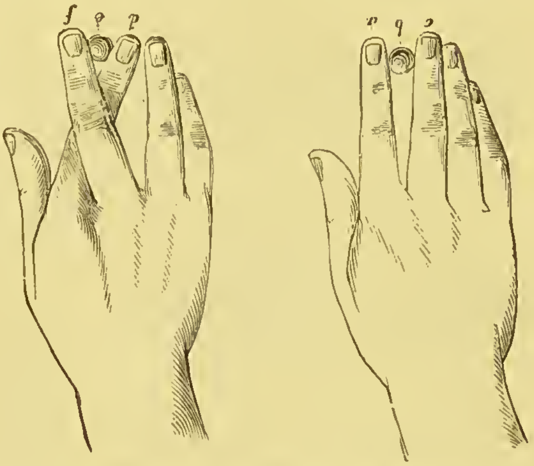

FIG. 377.—Aristotle's experiment. With the ball, as in figure to the right, there is a sensation of one contact, and as in figure to the left, there are sensations of two contacts.

Theories as to Touch.—The theory generally adopted is that of E. H. Weber, as restated by Lotze and others. It assumes that, whilst we refer every tactile sensation to a certain position in the tactile field, we do not refer it merely to a point, but to a circular or oval area in the skin, called a *circle of sensibility*. Further, it is assumed that if two such circles touch or overlap, they cannot be individually perceived, and that they can only be so individually perceived, when one or more

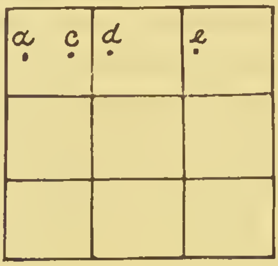

FIG. 378.

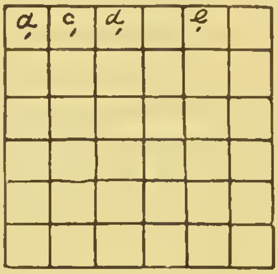

FIG. 379.

circles of sensibility intervene, or, in other words, when there is a sensory element between the two points touched that escapes irritation.

Each circle of sensibility is innervated by a single nerve fibre.

Thus, suppose the sensitive surface of the skin to be diagrammatically represented, as in Figs. 378 and 379, each square would be a "circle of sensibility." In more sensitive regions, the squares would be smaller, and the number of nerve terminations greater, than in less sensitive regions. In Fig. 378 the area contains nine "circles," and has nine nerve terminations, whilst in Fig. 379, although the total area is the same, there are thirty-six "circles" and thirty-six nerve filaments.

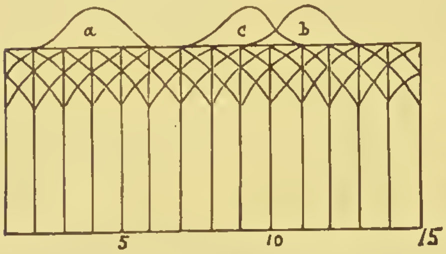

FIG. 380.

If the points of the compasses be placed at *a* and *c*, in Fig. 378, the sensation will be that of one point; there would also be a sensation of one point if they were placed at *c* and *d*; but if the points touch *c* and *e* there will be a double sensation because the "circle," *d*, intervenes. Again in Fig. 379, where the "circles" are much smaller and more numerous, the minimum distance at which two sensations are experienced is much less than in Fig. 378, for this would happen when the compasses touch *a* and *d*. It will also be observed that the same distance, *d e*, in Fig. 378, would give a single sensation, whilst it would give a double sensation in Fig. 379. But *c e* in Fig. 378 gives a double sensation, and yet the same distance would give a single sensation if the points of the compasses touched adjoining "circles." A "circle of sensibility," however, cannot be regarded as an anatomical magnitude or "cutaneous sensory unit," or, in other words, the area of distribution of a single nerve fibre. The extent of any such hypothetical circle can be altered by practice and attention, and we may therefore assume that the circles overlap, and that even the same area of skin receives numerous nerve filaments, and that consequently, when a body is touched, it excites at once many filaments. This is illustrated by Fig. 380. It will be seen that each area receives a certain number of nerve fibres, and each nerve fibre supplies fibrils that cross the fibrils of adjoining nerves. If the point of the compass touch at *a* it will irritate all the fibres from 1 to 7, but these will not be excited with equal intensity ; the excitation will be at a maximum at 4, more feeble for 3 and 5, and still more feeble for 2 and 6 ; so that the intensity of the excitation may be represented by the curve above *a*. In this case the sensation will be that of one point, because all the fibrils have been excited. If the other point of the compasses be placed at *b*, there will be an intermediary region not excited, and two points will be felt. Suppose now the second point of the compasses is moved to *c*, all the fibrils between the two points *a* and *c* are excited, and there is likely a sensation of single contact; but the excitation of the fibrils 7 and 8 is very feeble, and it is possible, by attention and practice to leave these out, and then there will be a sensation of two contacts (Beaunis). This mechanical theory has no anatomical basis, except it be the statement made by Krause that the distance of the two points of the compasses at which two points are felt, includes in the mean 12 tactile corpuscles. Whilst attention has been mainly directed to the skin as the locality where an anatomical explanation is to be sought for, it must not be forgotten that processes may be in operation in the nerve centres. It is well known that irradiation of the nervous impulses occurs in the nerve centres, and it is not unlikely that when a nervous impression reaches the brain from a particular area of skin, this may be diffused to neighbouring nerve cells, exciting these, and that then the effect on these cells, in accordance with the law that sensations in nerve centres are referred to the origins in the periphery of the sensory nerve fibres reaching them, will be referred to adjoining areas of skin, or, in other words, to adjoining points in the tactile field.

Sensations of Temperature.—The skin is also the seat of impressions of temperature. This depends on thermic irritation of the terminal organs, as proved by the fact that if the elbow is dipped into ice-cold water, the cold is only felt at the immersed part of the body; pain, however, is now felt in the terminal organs of the ulnar nerve, namely, in the finger points. If the sensation of cold were due to the irritation of a specific nerve fibre, the sensation of cold would be referred to the tips of the fingers. When any part of the skin is above its normal mean temperature, warmth is felt : in the opposite case, cold. The normal mean temperature of a given area varies according to the distribution of hot blood in it and to the activity of nutritive changes occurring in it. When the skin is brought into contact with a good conductor of heat there is a sensation of cold. A sensation of heat is experienced when heat is carried to the skin in any way. The following are the chief facts that have been ascertained regarding the temperature sense :—

(1) With a skin temperature of from 15·5° C. to 35° C., the tips of the fingers distinguish a difference of ·25° C. to ·20° C. (2) The thermal sense varies in different regions :—tip of tongue, eyelids, cheeks, lips, neck, belly. The *perceptible minimum* in degrees C. is :—breast, ·4° ; back, ·9° ; back of hand, ·3° ; palm, ·4° ; arm, ·2° ; back of foot, ·4° ; thigh, ·5° ; leg, ·6° to ·2° ; cheek, ·4° ; temple, ·3°.

(3) Sensations of heat and cold may alternate; thus when the skin is dipped first into water at 10° C. cold is felt, and if it be then dipped into water at 16° C. there is a feeling of warmth, followed by cold. There are probably different nerve fibres and different central organs for the tactile and thermal sensations.

Recent observations by Goldscheider and others show that on the cutaneous surface there are *temperature spots*, that is to say, little areas in which sensations of heat and cold are more acutely felt than in adjoining areas. These spots are found near hairs in many parts of the body. Certain of these areas are more sensitive to cold and hence are termed *cold spots*, and others are more sensitive to heat and are called *heat* spots. Cold spots are more abundant than heat spots, and both seem to be insensible to pressure. Irritation of such spots does not produce pain, but sensations of heat or cold. The spots are arranged in curved lines, but the curve uniting a number of cold spots does not coincide with the curve uniting a chain of heat spots. Cold spots are perceived as double at a shorter distance apart than heat spots. Thus, on the forehead, cold spots have a minimum distance of ·8 mm., and heat spots, 4 mm.; on the breast, cold spots = 2 mm. and heat spots = 5 mm.; on the back, cold spots = 1·5 mm. and heat spots = 4 to 6 mm.; on the back of the hand, cold spots = 3 mm. and heat spots = 4 mm.; on the palm, cold spots = ·8 mm. and heat spots = 2 mm.; and on the thigh and leg, cold spots = 3 mm. and heat spots = 3·5 mm. No terminal organ for temperature has yet been discovered.

Pain.—There is still a third kind of sensation, unlike touch and temperature, namely pain. This sensation cannot be supposed to be excited by irritations of the end organs of touch, or of specific thermal end organs (if such there be), but rather by irritation of ordinary sensory nerves. Painful impressions make their way to the brain along special tracts in the spinal cord. Irritation of a nerve, in accordance with the law of *peripheral reference of sensation*, will cause pain. Sometimes the irritation applied to the trunk of a sensory nerve may be so intense as to destroy its normal function, and loss of sensation or anæsthesia results. If then the stimulus is increased further, pain is excited which is referred to the end of the nerve, with the result of producing what has been called *anæsthesia dolorosa.* Pains frequently cannot be distinctly located, probably owing to the fact of irradiation in the nerve centres, and reference is made to areas of the body which are not really the seat of irritations. The intensity of pain depends on the degree of excitability of the sensory nerves, whilst its massiveness depends on the number of nerve fibres affected. The quality of the pain is probably produced by the kind of irritation of the nerve, as affected by the structure of the part and the greater or less continuance of severe pressure. Thus there are piercing, cutting, boring, burning, throbbing, pressing, gnawing, dull, and acute varieties of pain.

E.—The Sense of Hearing.

Chap. I.—GENERAL STRUCTURE OF THE EAR.

The simplest form of ear, as found in the lower invertebrates, consists of hair-like appendages, either on the free surface or in the form of a depression, more or less concealed from view. Such an ear exists in the medusæ, as shown in Fig. 381. In the higher animals it becomes a very complicated structure.

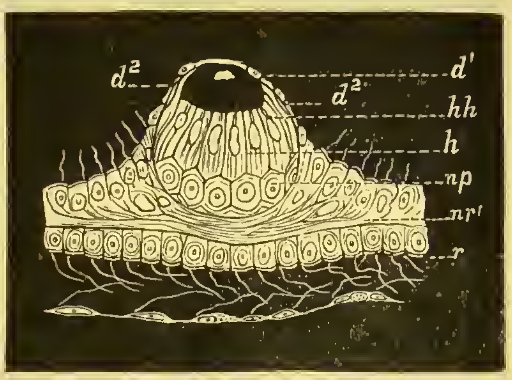

Fig. 381.—Auditory vesicle of *Phialidium*. d', epithelium of the upper surface of the velum; d^2, epithelium of the under surface of the velum; nr', upper nerve ring; h, auditory cells; hh, auditory hairs; np, nervous cushion formed of a prolongation of the lower nerve ring. Close to the nerve ring is seen a cell, shown black, containing an otolith. (Lankester and O. and R. Hertwig.)

The ear consists of an apparatus fitted for the transmission of sonorous vibrations to the terminal apparatus of the auditory nerve. Its various parts are shown in the following diagram (Fig. 382). It consists of the following parts: (1) the external ear, formed of the *concha*, and *external auditory canal;* (2) the middle ear, a cavity filled with air, communicating with the back of the throat by the *Eustachian tube*, and separated from the external ear by the *membrana tympani*, the latter being connected with the *fenestra ovalis* by a chain of bones, namely, the *malleus, incus*, and *stapes;* and (3) the internal ear or labyrinth, a complicated structure filled with fluid, and consisting of the *vestibule, semicircular canals*, and the *cochlea.*

The essential part of the auditory apparatus is the internal ear, or *labyrinth.* This is divided into three parts, as represented in Fig. 383. These are, the three semicircular canals on the one side, the cochlea on the other, and the vestibule between the two. The wall of the latter is pierced by an opening, the *fenestra ovalis, d,* closed by a membrane, into which is inserted the base of the stapes. Seven openings communicate with the vestibule, viz., the fenestra ovalis, five orifices of the semicircular canals, and an aperture communicating with the scala vestibuli of the cochlea. The vestibule contains masses of crystals of calcareous matter called *otoliths.* From its walls, hair-like bodies project, which arise from cells connected with the extremities of the vestibular division of the auditory nerve.

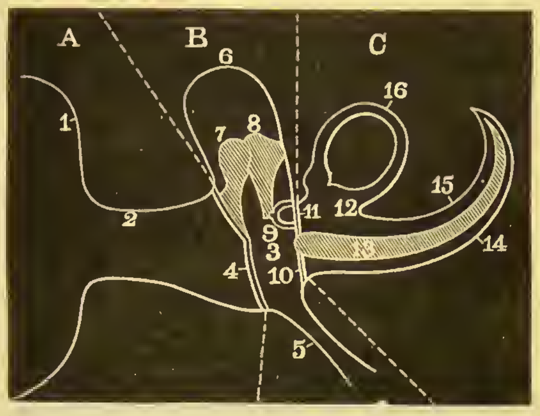

FIG. 382.—Diagrammatic view of the auditory apparatus. A, external ear; B, middle ear; C, internal ear. 1, *concha*; 2, external auditory passage; 3, *tympanum;* 4, *membrana tympani;* 5, Eustachian tube; 6, mastoid cells; 7, *malteus:* 8, *incus;* 9, *stapes;* 10, *fenestra rotunda;* 11, *fenestra ovalis;* 12, vestibule; 13, cochlea; 14, *scala tympani;* 15, *scala vestibuli;* 16, semicircular canal. (Beaunis.)

The osseous labyrinth contains a membranous structure, termed the membranous labyrinth, seen in Fig. 384. This consists of two sacs — the *utricle, u,* communicating with the *semicircular canals,* and the *saccule, s,* opening into *c,* the *ductus cochlearis.* It will be observed that *s* and *u* communicate by a forked canal which is said to be lodged in the *aqueductus vestibuli* of the temporal bone.

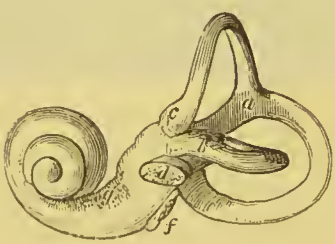

FIG. 383.—Diagrammatic view of the osseous labyrinth. See text.

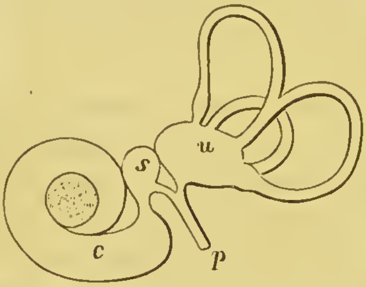

FIG. 384.—Membranous labyrinth. See text.

The semicircular canals have been termed the *anterior vertical,* a dilatation of which, termed the ampulla, is seen at *c;* the *posterior vertical, e;* and the *horizontal, b* (Fig. 383). It will be observed that the anterior and posterior vertical open into the vestibule by a common tube, *a.*

The cochlea is a tube, tapering towards one extremity, twisted round a central axis or *columella.* This tube is divided into two cavities by a spiral partition formed of two parts, one osseous, next the *columella,* and the other membranous, which completes the division. The view in Fig. 385 represents a section of the osseous part of the cochlea. In this figure, *b* is the *columella,* round which the spiral partition of

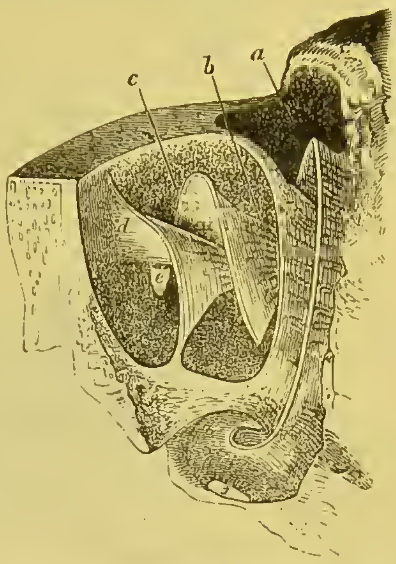

FIG. 385.—Section of the cochlea. See text

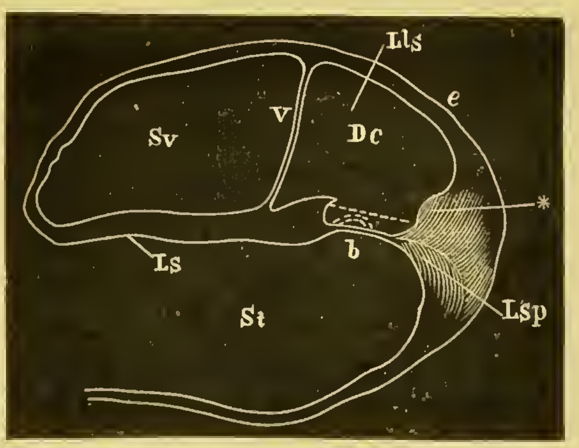

FIG. 386.—Diagram showing a section of the tube of the cochlea. See text.

bone, *a c*, is twisted. From the edge of the osseous partition (termed the *lamina spiralis*) two membranes pass obliquely, so as to cut off a triangular space, the *scala intermedia.* The position of this space, in which exists the most important part of the terminal apparatus of hearing, is indicated in the diagram, Fig. 386. From the free edge of the osseous *lamina spiralis*, Ls, a membrane, *b*, the *basilar membrane,* passes transversely across to a set of fibres, Lsp, sometimes called the ligament of the *lamina spiralis,* or *Bowman's muscle.* A second membrane, V, *Reissner's membrane,* passes from Ls to the osseous wall of the tube. The tube is thus divided into three parts, viz., *scala vestibuli,* Sv, communicating with the vestibule; *scala tympani,* St, communicating with the tympanum through the *fenestra rotunda* (see Fig. 382, 10); and between the two a third space, Dc. The space between *b* and V is frequently spoken of as the cochlear canal, and on *b*, the basilar membrane, we find the *rods of Corti,* forming a series of arches for the support of certain cells having hair-like appendages, which latter are the true vibratory organs of hearing. The general arrangement of the rods is seen in Fig. 387. The rods support a number of modified epithelial cells, termed *hair cells,* because they bear minute hair-like structures. In man, there are five rows of such cells over the external and one over the internal rods. In birds, the hair cells rest directly on the basilar membrane, no arches of Corti being present. In Fig. 388, hair-cells, *d*, are seen as found in the cochlea of a pigeon. It will be observed that they are connected by delicate filaments with nucleated cells, *b ;* also with such a multipolar nerve cell as *c*; and that they rest on a basilar membrane, *a*.

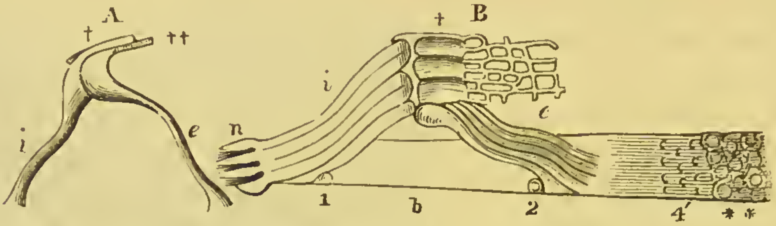

FIG. 387.—Corti's organ. A, profile view of two rods, *i* internal, *e* external. B represents in position five complete arches resting on the basilar membrane, *b*.

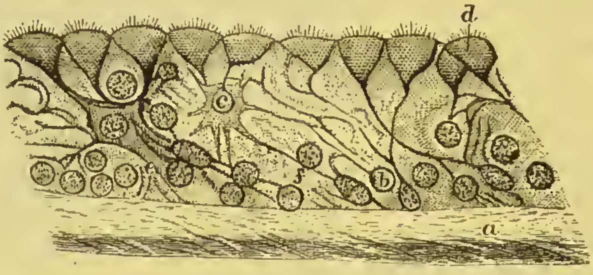

FIG. 388.—Portion of cochlea of pigeon, showing hair cells. See text. (Paul Meyer.)

CHAP. II.—THE MINUTE STRUCTURE OF THE EAR.

The Internal Ear consists of two membranous sacs which communicate with each other by a small duct, the *ductus endolymphaticus*. The smaller sac, the *utricle*, or *sacculus ellipticus*, is related to the membranous tubes, the *semicircular canals*, each of which shows a wider part termed the *ampulla*. The other sac, the *sacculus*, or *sacculus sphericus*, is connected with a long spirally wound tube, the *ductus cochlearis*. The utricle, saccule, canals, and cochlear duct, form the *membranous labyrinth*, enclosed in cavities in the petrous portion of the temporal bone of corresponding form, termed the *osseous labyrinth*. The fluid termed the *perilymph* lies between the membranous portion and the bony wall, while the *endolymph* is in the interior of the membranous labyrinth. The walls of the saccule, utricle, and semicircular canals, consist of three layers. Externally, there is a layer of connective tissue, rich in elastic tissue; within this, we have a hyaloid membrane showing small papillæ on its inner surface, and this last is covered by one layer of pavement epithelium. This simple structure is modified where the fibres of the auditory nerve come into contact with it, namely, on the saccule, utricle, and on the ampullæ of the semicircular canals — the *cristæ acusticæ*. Here both the connective tissue layer and the hyaloid membrane are thicker, the pavement epithelium passes into cylindrical epithelium, and this passes over into the neuro-epithelium of the *macula*. The *neuro-epithelium* consists of one layer of cells, but these are of two kinds: (1) *Thread cells*, which are elongated bodies, broadened somewhat both at their upper and lower ends, and containing an oval nucleus. These act as supporting cells. (2) *Hair cells*, oval, occupying only the upper half of the thickness of the epithelial layer and showing in their lower part a large globular nucleus, while the upper surface has a number of fine thread-like filaments cemented together to form *auditory hairs*. Nerve fibres come into relation with these hair cells. The medullated fibres of the vestibular branch of the auditory nerve lose their white substance where they enter the epithelium and run along the borders, as naked axis cylinders, of the hair cells, without, however, entering these. The hair cells are the terminal organs of the vestibular nerve. Both the *maculæ acusticæ* are covered with a soft substance enclosing numerous prismatic crystals, ·1 to 15 μ in diameter, termed *otoliths*. We also find on the *cristæ acusticæ*, a peculiar structure termed the *cupula*, the true nature of which is unknown. The saccule, utricle, and canals, are bound by bands of connective tissue to the inner surface of the osseous labyrinth, which is also lined by a thin periosteum clad with flat epithelial cells.

FIG. 389. — Otoliths from the saccule of a newly born child. (Method No. 124. Appendix.)

The membranous part of the cochlea, *ductus cochlearis*, is attached to the border of the osseous *lamina spiralis*, so that its upper wall is formed by *Reissner's membrane*, next the *scala vestibuli*, and its lower wall by the *lamina spiralis membranacea*, or *basilar membrane*, next the *scala tympani*. The angle at which the *lamina Reissneri* and the *lamina spiralis membranacea* meet is at the free border of the *lamina spiralis ossea*. The connective tissue of the *ductus cochlearis* is there strongly developed, forming a pad, known as the *limbus cristatus spiralis*, which rests on the *lamina spiralis ossea*, and ends in a short margin directed outwards. This margin is the *labium vestibulare*, the free edge of the *lamina spiralis ossea* is known as the *labium tympanicum*, and between both we have the *sulcus spiralis internus* (Fig. 390). The inner surface of the *ductus cochlearis* is covered with epithelium which varies in character in different situations. The outer surfaces directed towards the *scalæ* are covered with a delicate continuation of the periosteum lining the *scalæ*. On the outer wall of the cochlea, the periosteum is much thickened, so as to form a long strip, semilunar in section, the *ligamentum spirale* (Fig. 390). The external and the vestibular walls of the *ductus cochlearis* show a simple structure, but the tympanic wall (that is the basilar membrane) shows a very complicated mechanism. The connective tissue of the outer wall is, as already described, thickened, and becoming somewhat looser inwards, it forms the *ligamentum spirale*, first carefully described by Bowman. The epithelium is formed of a layer of cubical cells. A dense network of vessels, *striæ vasculares*, occupies three-fourths of the summit of the outer wall, and they end in a vein running towards the lumen of the cochlea, the *vas prominens* (Fig. 390). From the capillaries of the *striæ*, lying immediately below the epithelium, the fluid of the endolymph exudes. The vestibular wall, forming the *membrane of Reissner* (Fig. 390), is a continuation of the periosteum of the *scala vestibuli*, that is, of an endothelium, lying on delicate connective tissue. On the side next the *ductus* there is a single layer of polygonal cells.

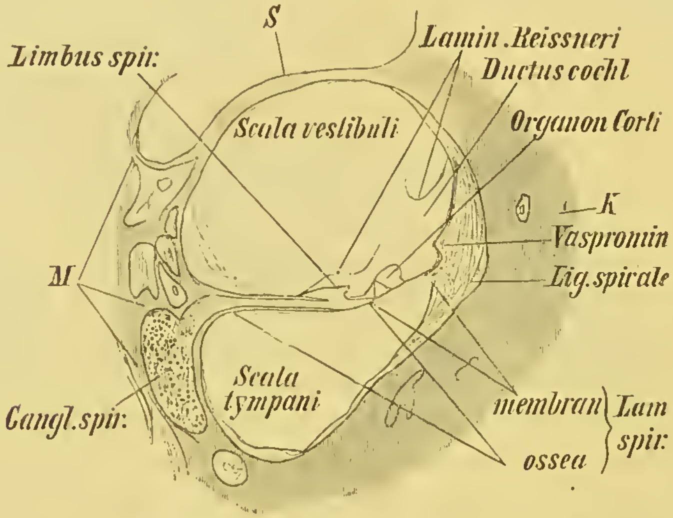

FIG. 390.—Section through the second turn of the cochlea of a new born child. × 25 d. *K*, external osseous wall. *M*, osseous axis, or *columella*, or *modiolus*, containing longitudinal canals cut obliquely. *S*, osseous wall between the second and third turns of the cochlea. The membrane of Reissner is torn and has fallen in. (Method No. 125, Appendix.)

The tympanic wall of the *ductus*, or, as it is termed, the *membrana basilaris*, is divided into two portions: (1) the *limbus spiralis*, with the free border of the *lamina spiralis ossea*, and (2) the *lamina spiralis membranacea*. (1) The *limbus spiralis* is formed of dense connective tissue, rich in spindle-shaped cells, connected underneath with the periosteum of the *lamina spiralis ossea*, and having peculiarly formed papillæ on its upper surface. These latter are irregularly hemispherical, extending towards the *labium vestibulare* in the form of long narrow plates, the *auditory teeth of Huschke* (Figs. 391 and 394). A single layer of flat epithelial cells covers the upper surface of the *limbus*, and passes over at the corner of the *labium vestibulare* into the cubical epithelium of the *sulcus* *spiralis.* The free margin of the *lamina spiralis ossea* is broken on its upper surface by a series of slits through which the nerves pass in their course towards the epithelium of the *lamina spiralis membranacea.* For this reason, this zone is termed the *zona* or *habenula perforata.*

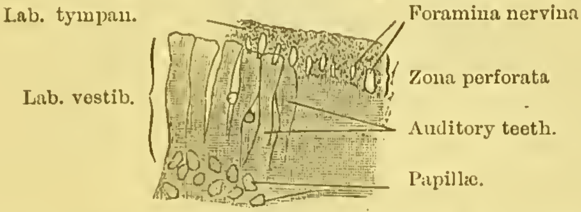

FIG. 391.—Upper surface of the *lamina spiralis* of a cat. × 24 d. The *labium vestibulare* seen from above; between the auditory teeth, observe two nuclei of the epithelial cells. On the left, we see the auditory teeth, and on the right the flat portion of the *zona perforata.* (Method No. 126, Appendix.)

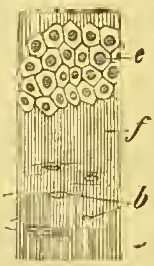

FIG. 392. — Surface of the *lamina spiralis membranacea* of a cat. × 240 d. The strata of the *zona pectinata* are indicated by changing the position of the tube of the microscope; *e*, high position showing the indifferent epithelium, or *cells of Claudius*, of the *ductus cochlearis*; *f*, mid position, showing the fibres of the *membrana basilaris*; *b*, deep position showing the nuclei of the layer next the *scala tympani.* (Method No. 127, Appendix.)

The *lamina spiralis membranacea* consists of the *membrana basilaris*, that is the continuation of the *limbus spiralis*, and of the periosteum of the *lamina spiralis ossea*, and also of the border continued from the periosteum of the *scala tympani.* The *membrana basilaris* is formed of a structureless membrane composed of straight stiff fibres running transversely from the *labium tympanicum* as far as the *ligamentum spirale.* Among the fibres we observe elongated nuclei, and the membrane has a delicately striated appearance.

The tympanic border stratum consists of delicate connective tissue containing spindle-shaped cells, the fibres of which run at right angles to the direction of those forming the *membrana basilaris* (Fig. 392, *b*). The epithelium on the side next the axis at the cochlea is neuroepithelium and forms the *organ of Corti*, and that next the side of the *ligamentum spirale* is composed of indifferent epithelial cells. The *lamina spiralis membranacea* is divided into two zones, an inner, covered with Corti's organ, the *zona tecta*, and an outer, the *zona pectinata.*

The most remarkable structures of Corti's organ are the *pillar cells*, standing in two rows along the entire length of the *ductus cochlearis.* The inner pillars or rods form the inner row, and the outer pillars the outer row. Both being inclined obliquely towards each other, they form an arch, the *arcus spiralis*, which bridges over a three-sided space, the *tunnel*, directed towards the *membrana basilaris.* The tunnel is merely a large intercellular space, occupied during life by an intercellular substance. The inner pillar cells are stiff structures, showing a triangular broad foot, a narrow body, and a head, having a concavity

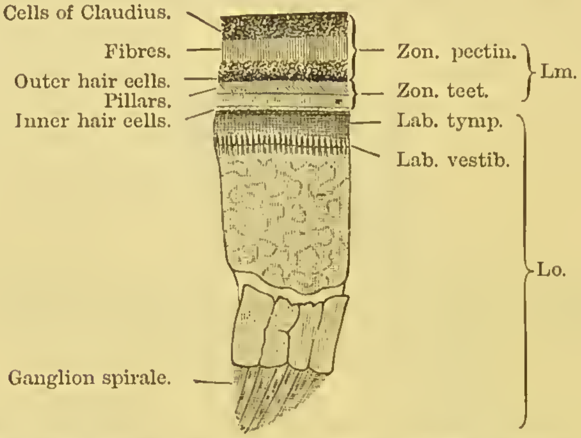

FIG. 393.—*Lamina spiralis* of a cat, seen from the vestibular surface. The *membrana tectoria* has been removed. × 50 d. Lo, *lamina spiralis ossea*, cracked and broken in the inner half; the cells of the *ganglion spirale* are seen on the posterior margin. Lm, *lamina spiralis membranacea*; the cells of Claudius have partly fallen off, so that we see the delicate striation due to the fibres of the *membrana basilaris*. (Method No. 128, Appendix.)

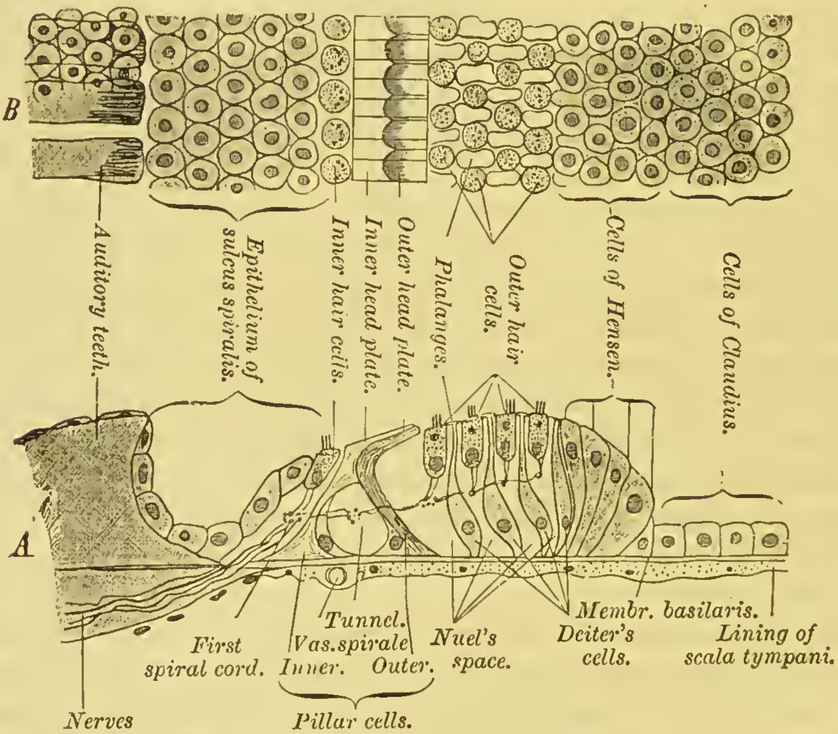

FIG. 394.—Diagram of the structure of the tympanic wall of the canal of the cochlea. *A*, seen from the side; *B*, seen from the surface.

directed outwards. The head carries a narrow flattened portion, called the head plate. The body and foot of the cell show a little protoplasm, and this is more abundant near the nucleus. The external pillar cells or rods show much the same structure. The roundish head rests in a concave depression of the inner pillar cell, and its head plate is covered by the head plate of the inner pillar. The *membrana tectoria* is not shown in Fig. 393. See also Fig. 394. Passing internally from the inner pillars, we find a series of cells, called the *inner hair cells.* These are short and cylindrical in form; their bases are rounded and do not extend to the *membrana basilaris*, and their free surfaces show about twenty stiff hairs on each cell. Still more internally to the inner hair cells, we find the cubical epithelium of the *sulcus spiralis internus.* Externally to the outer pillars lie the *outer hair cells*, which resemble the inner ones, only that they have a peculiar dark body in the upper part of the cell, called *Hensen's spiral body*, and shown in Fig. 394, A, by a dark spot immediately below the cilia. The outer hair cells are usually four rows deep, and they are kept apart by peculiar elongated cells, called *Deiter's cells.* These are elongated bodies, having on their upper end a cuticular appendage, shaped like the phalanx of a finger. The chasms between the phalanges are occupied by the upper ends of the outer hair cells. Deiter's cells are supporting structures, similar in general characters to the pillar cells, only the metamorphosis of soft protoplasm into stiff substance is not so far advanced. By the connections of the phalanges a reticulated membrane is formed, the *membrana reticularis* (Fig. 395).

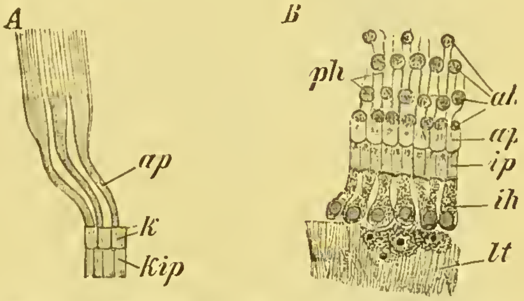

FIG. 395.—Surface of the *lamina spiralis membranacea* of cat. × 240 d. *A*, outer pillars; *k*, head plates; *ap*, body and foot; *kip*, portions of head plates of inner pillars. *B*, *lt*, *labium tympanici* partially covered with epithelium of the *sulcus spiralis*; *ih*, inner, *ah*, outer, hair cells; the phalanges, *ph*, form the *membrana reticularis*; *ap*, head plates of the outer, *ip*, of the inner pillars. (Method No. 129, Appendix.)

The external hair cells do not reach so far down as the *membrana basilaris*, and they thus fill up only the upper half of the spaces between Deiter's cells, the lower halves of the spaces remaining open, and termed the *space of Nuel.* This space is intercellular, and it is connected with the tunnel. Externally to the last row of Deiter's cells, we find elongated cylindrical bodies, termed the *cells of Hensen*, which, becoming shorter, merge into the indifferent epithelium of the *ductus cochlearis*, whose cells are called the *cells of Claudius* (Figs. 394 and 396).

Above the *sulcus spiralis* and the organ of Corti we find a soft elastic cuticular structure, termed the *membrana tectoria*. It is fixed to the *labium vestibulare* and extends as far as the outermost row of hair cells.

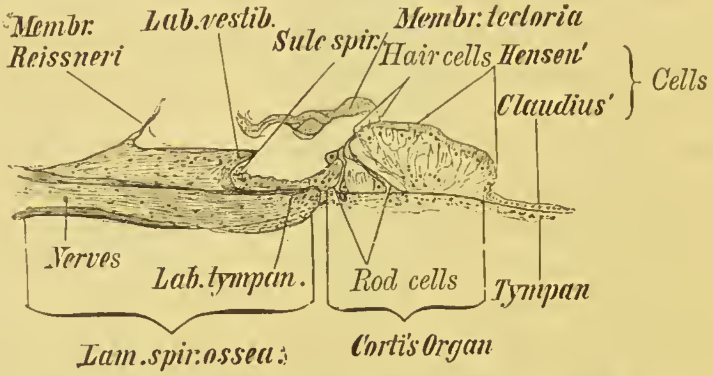

FIG. 396. — Vertical section through the peripheral half of the *lamina spiralis membranacea* of a newly born child. × 80 d. The *membrana tectoria* is torn from its point of attachment to the *labium vestibulare*. (Method No. 130, Appendix.)

The cochlear branch of the auditory nerve enters the axis of the cochlea, and gives off branches which pass to the root of the *lamina spiralis ossea*. Here the fibres enter a ganglionic mass of cells, the *ganglion spirale*, winding round the axis of the cochlea. From the ganglion the nerves pass out, forming a wide-meshed plexus, towards the *limbus tympanicus*, where, losing their white substance, they enter the *foramina nervina* and end in the epithelium. In this region they run as spiral cords, the first internal to the inner pillar cell, the second into the tunnel, the third between the outer pillar cell and the first Deiterian cell, and the remaining three between the Deiterian cells. Still finer fibres pass from these cords to the hair cells (Fig. 394).

The arteries of the labyrinth originate from the auditory artery and the stylomastoid artery. A branch passes to the *fenestra rotunda* and to the cochlea. From the auditory artery we have (1) branches to the utricle and saccule and the semicircular canals, supplying the *maculæ* and *cristæ;* (2) a branch to the cochlea, which gives off twigs to the *Reissnerian membrane* and to the osseous wall of the cochlea. The veins collect at the *vas prominens* and at the *vas spirale*, and the latter discharges itself through the *aqueductus cochleæ* into the internal jugular vein. The endolymph communicates with the lymph in the lymphatic vessels. The perilymph is discharged through the *aqueductus cochleæ* into a lymphatic vessel accompanying the internal jugular vein.

The Middle Ear.—The mucous membrane of the tympanum consists of connective tissue. A single layer of ciliated epithelium covers it except on the roof, the promontory, the ossicles, and the surface of the *membrana tympani*. Minute follicular glands, ·1 mm. in length, are found in small numbers. The mucous membrane of the *Eustachian tube* is formed of fibrillar connective tissue, interspersed with leucocytes, especially near the pharyngeal opening, and it is lined by stratified cylindrical epithelium, the ciliary current being directed to the pharynx. The cartilage of the tube where attached to the bone is hyaline, with here and there deposits of fibres, which are not elastic, but, farther on, many elastic networks are found in the cartilage. The blood-vessels in the cavity of the tympanum form a wide-meshed network, but the meshes are much narrower in the tube, and minute vessels twist spirally round glands. The lymphatics of the tympanum run in the periosteum.

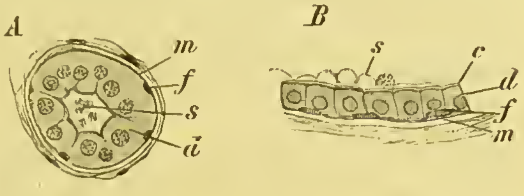

FIG. 397.—*A*, transverse section of the duct of a ceruminous gland in the external auditory passage. *B*, Longitudinal section of the same. From a boy, 12 years of age. × 240 d. *s*, secretion; *c*, cuticular layer; *d*, cells; *f*, nuclei of smooth muscle; *m*, *membrana propria*. (Method No. 131, Appendix.)

The External Ear.—The *membrana tympani* (drum-head) consists of a plate or layer of connective tissue, *lamina propria*, the bundles of which run radially on the upper surface, then bend slightly, and are continuous with the periosteum of the *sulcus tympanicus.* Bands of circular fibres run on the surface next the tympanum. The *membrana* is covered internally by the mucous membrane of the tympanum and externally by a fold of the lining membrane of the auditory meatus. Both coverings, firmly attached to the *lamina propria*, are smooth and have no papillæ, At the spot to which the malleus is attached there is a thin plate of hyaline cartilage.

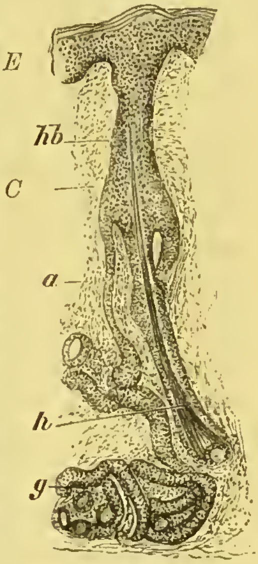

FIG. 398.—Vertical section through the lining of the external auditory canal of a newly born child. × 50 d. *E*, epidermis consisting of a thin *stratum corneum*, and a thicker *stratum mucosum*. *C*, tissue of cutis; *hb*, hair follicle, containing a young hair, *h*; *g*, ceruminous glands, with the duct, *a*, opening into hair follicle. (Method No. 132, Appendix.)

The external auditory passage shows in great numbers the *ceruminous* or *wax glands* of the ear. Somewhat resembling sweat glands, their ducts possess several layers of epithelial cells, while the coiled up part of the gland has a single layer of cubical cells, resting on a *membrana propria*, outside of which we find bands of smooth muscle. They are distinguished from sweat glands by their lumen being wider and by the cells containing pigment granules and numerous fatty globules. The *wax* consists of pigment, fat globules, and fatty cells. The *cartilage* of the cartilaginous part of the auditory passage and of the *concha* of the ear is of the elastic variety (Figs. 397 and 398).

Vessels of the Membrana.—A small artery descends close to the handle of the *malleus* and sends radial branches to the circumference of the membrana, and the blood is returned by veins running parallel to the handle of the *malleus*. The superficial vessels on the external surface belong to the outer lining. The inner lining has also a dense capillary network, anastomosing by minute branches with the vessels of the membrana. *Lymphatics* occur chiefly in the outer lining, and *nerves* are found in the form of delicate plexuses under both linings.

CHAP. III.—THE PHYSICAL CAUSES OF SOUND.

Sonorous vibrations consist of the regular to-and-fro oscillations of any elastic body. When such vibrations are communicated to the ear with sufficient rapidity and intensity, the result is an auditory sensation called a sound. Sound is usually conveyed to the ear by the air, at a rate of 350 metres per sec., but it may also be conveyed through solids and liquids. Sound travels 4 times faster in water than in air, and about 17 times faster in wire and pine wood. The to-and-fro movements of the molecules of any elastic body constitute a vibration. Different points of a medium traversed by a vibratory movement pass successively through the same phases, and in applying the term *wave*, it is important not to confound it with the vibrations of the individual molecules. The term *wave-length* is the distance which separates two points of a vibrating body, found at the same *instant* in the same phase. The wave-length is constant for a given number of vibrations in a second in the same medium, and it is proportional to the duration of the vibration, and in the inverse ratio to its rapidity.

Sounds may be classified into *noises* and *musical tones*. A noise is a sensation produced by non-periodic motions against the ear, or by a number of musical tones clashing together, so as to cause dissonance, as when we bring the palm of the hand down at random on the key-board of a piano.

A *tone* is produced by a periodic movement of the air or of the sounding body. Its production is illustrated by the double syren of Von Helmholtz, shown in Fig. 399.

It consists of two brass boxes, a_0 a_1, communicating with a powerful bellows by the tubes, g_0 and g_1. The lids of these boxes are perforated by a number of holes. Adjusted to the lids, there are two perforated brass discs, moving on a common spindle, k. The holes in the lower disc are seen over the lower box in the figure, but not in the upper. These holes pass through the lid of the box and through the discs obliquely in opposite directions, so that when air is forced by the bellows out of the boxes, the discs are driven round. As the discs revolve, when the holes in the disc and in the lid of the box coincide, the air escapes; the disc is driven onwards, thus bringing its unperforated parts over the holes, so that the air cannot escape. Hence the continuous stream of air from the bellows is converted into a series of discontinuous puffs, which, when they follow one another with sufficient rapidity, gather themselves into a tone. Thus it can be shown that a *tone* depends on a regular series of equal impulses reaching the ear, or on a periodic movement of the air. By this instrument, also, the relations of sounds, as expressed by *intervals*,

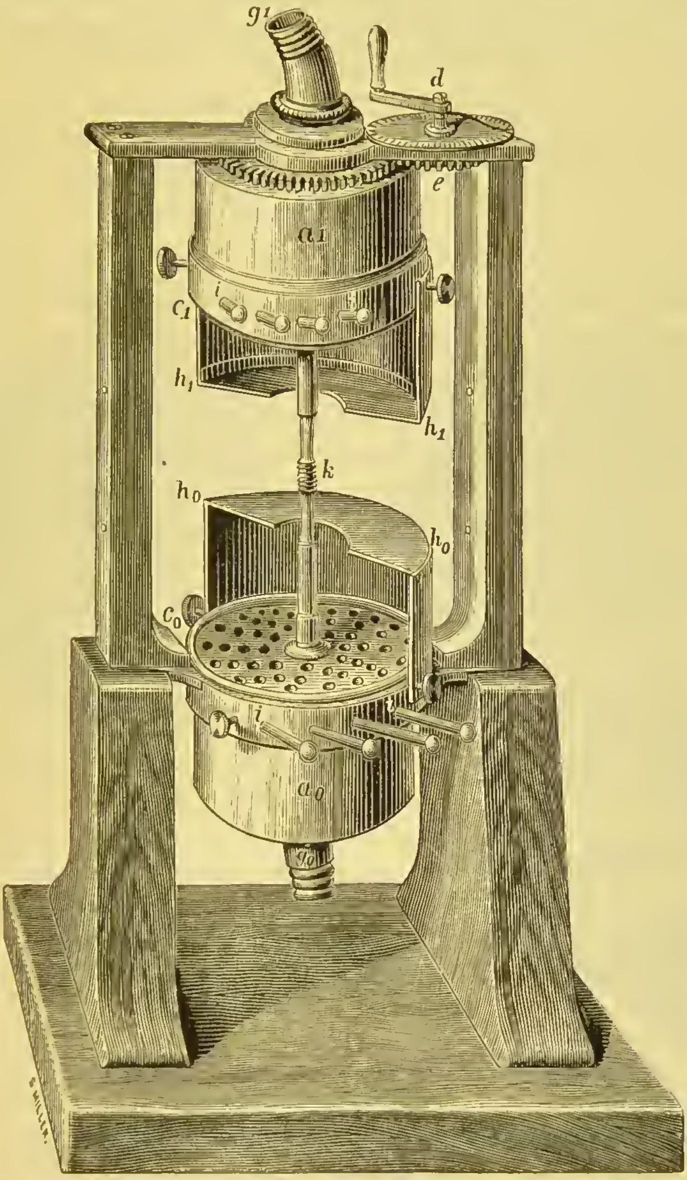

FIG. 399.—Double syren of Helmholtz. See text.

can be shown. In each disc there are four concentric rows of holes, and by means of the stops, marked *i* and *i*, any of these may be opened. In the lower box, the stops are marked 8, 10, 12, 18, and in the upper, 9, 12, 15, and 16, indicating the number of holes respectively. Suppose the row marked 16 is opened, at first a series of puffs are heard, but these soon fuse together in consciousness, so as to cause the sensation of a *pure tone*. When the puffs come at the rate of about thirty per second, a tone is heard. Again, we can use any one of the eight series of holes, or combine them as we wish. Suppose we open the row of holes marked 8 and the row marked 16, then we have two sounds produced in the relation of an octave.

Chap. IV.—ARRANGEMENTS FOR TRANSMISSION OF VIBRATIONS TO THE TERMINAL ORGAN.

Hearing is a special sensation, the cause of which is an excitation of the auditory nerves by the vibrations of sonorous bodies.

(*a*) **Transmission in External Ear.**—The external ear consists of the *pinna* or auricle, and the *external auditory meatus* or canal, at the bottom of which we find the *membrana tympani* or drum-head. In many animals the auricle is trumpet-shaped, and, being freely movable by muscles, serves to collect sonorous waves coming from various directions. The auricle of the human ear presents irregularities of surface. If these are abolished by filling them up with a soft material such as wax or oil, leaving the entrance to the canal free, experiment shows that the intensity of sounds is weakened, their quality somewhat altered, and that there is more difficulty in judging of their direction. The auricle, also, to some extent, and especially in some of the lower animals, prevents the entrance of dust, insects, etc., into the outer canal, and we often find strong hairs developed in this region. The outer ear is absent from the mole and from cetacea. When waves strike the auricle, they are partly reflected outwards, whilst the remainder, impinging at various angles, undergo a number of reflections, so as to be directed into the auditory canal. Vibrations are transmitted along the auditory canal, partly by the air it contains, and partly by its walls, to the *membrana tympani*. The absence of the auricle, as the result of accident or intentional injury, has not caused marked

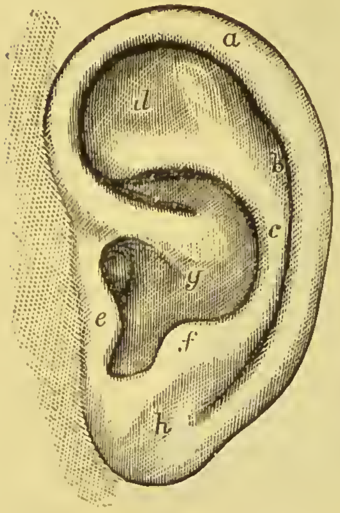

Fig. 400.—Left auricle. *a*, helix; *b*, fossa of helix; *c*, antihelix; *d*, fossa of antihelix; *e*, tragus; *f*, antitragus; *g*, concha; *h*, lobule.

diminution of hearing. In the auditory canal, waves of sound are reflected from side to side, until they reach the *membrana tympani.* From the obliquity in position and peculiar curvature of this membrane, most of the waves must strike it nearly perpendicularly, that is, in the most advantageous direction.

(*b*) **Transmission in Middle Ear.**—The middle ear is a small cavity, the walls of which are rigid, with the exception of the portions consisting of the *membrana tympani* and the membrane of the *fenestra rotunda,* and of the apparatus filling the *fenestra ovalis.* This cavity communicates with the pharynx by the Eustachian tube, which forms an air-tube between the pharynx and the tympanum, for regulating pressure on the *membrana tympani.* During rest the tube is closed, and it is opened during the act of deglutition (see p. 69). As this action frequently takes place, when food or drink is introduced, and when saliva is swallowed, the pressure of the air in the tympanum is kept in a state of equilibrium with that of the external air, exerted on the outer surface of the *membrana tympani,* and thus the latter is rendered independent of variations of atmospheric pressure, such as may occur within certain limits, as when we descend the shaft of a mine or ascend a high mountain. By a forcible expiration, the oral and nasal cavities being closed, followed by an act of deglutition, air may be driven into the tympanum, and a peculiar crackling noise will be heard in the ear. This is the *positive experiment of Valsalva.* A forcible inspiration, accompanied by deglutition, will draw air from that cavity, again causing a crackling noise. This is the *negative experiment of Valsalva.* In the first case, the *membrana tympani* bulges

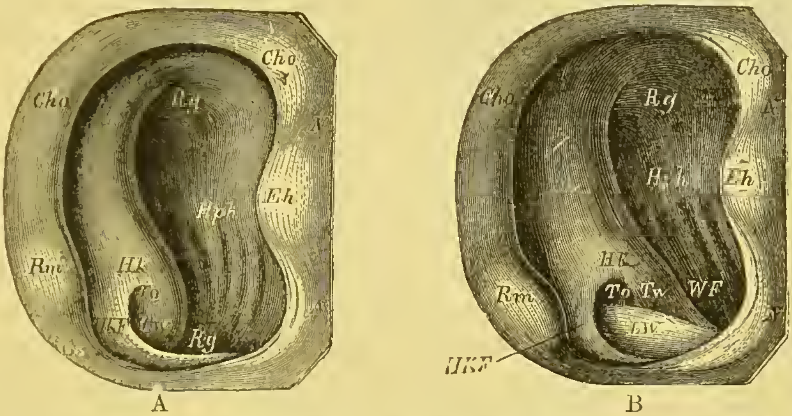

FIG. 401.—Semi-diagrammatic view of the pharyngeal opening of the Eustachian tube. *A*, tube closed ; *B*, tube open ; *N*, wall of nasal passage ; *Eh*, prominence of same ; *Cho*, inner nasal opening ; *Rm*, lower nasal muscle, here very rudimentary ; *Hph*, wall of pharynx ; *Rg*, fossa of Rosenmüller ; *Tw*, tuberosity of the tube ; *To*, opening of tube ; *Hk*, hook or hamulus ; *Hkf*, fold of the hook ; *Wf*, fold of the tuberosity ; *Lw*, levator of the tuberosity. (Hensen.)

outwards; in the second case, inwards; and in both, from excessive stretching of the membrane, there is partial deafness, especially for sounds of high pitch. Permanent occlusion of the tube is one of the most common causes of deafness. In such cases, the tension in the tympanum becomes less from absorption of oxygen, a transudation of serum from the vessels may take place, and mucus may increase in quantity. Closure of the tube, except in deglutition, is necessary for the transmission of sound waves from the drum-head to the inner ear. If the tube were always open, our own voices would cause too much resonance in the ear, and there would be a variation of pressure on the inner surface of the drum-head with each inspiration and expiration.

FIG. 402. — Horizontal section through tympanum and labyrinth. *d*, *membrana tympani;* *e*, anterior wall of cavity of tympanum; *f*, stapes, with its base attached to the *fenestra ovalis;* *g*, *stapedius* muscle; *h*, a portion of the facial nerve; *i*, situation of *tensor tympani* muscle; *k*, vestibular division, and *l*, cochlear division, of the auditory nerve in the internal auditory canal; *m*, section of the cochlea; *n*, nerve going to ampullæ of semicircular canals; *o*, section of utricle; *p*, section of saccule; *r*, section of a semicircular canal. (Rüdinger.)

The *membrana tympani* is set into vibration by a sound of any pitch included in the range of perceptible sounds. It responds exactly, as to number of vibrations (pitch), intensity of vibrations (loudness), and form of vibration (quality or timbre). Consequently, we can hear a sound of any given pitch, of a certain intensity, and of its own specific timbre or quality. Generally speaking, high tones are heard more easily than low tones of the same intensity. As the *membrana tympani* (Fig. 403) is not only fixed by its margin to a ring or tube of bone, but is also adherent to the handle of the malleus (*manubrium*), which follows its movements, its vibrations meet with considerable resistance. This diminishes the intensity of its vibrations, and prevents also the continued vibration of the *membrana* after an external vibration has ceased, so that a sound is not heard much longer than the moment when the exciting cause ceases. The tension of the membrane may be affected (1) by differences of pressure on the two surfaces of the *membrana tympani*, as may occur during forcible expiration, or inspiration, or in a pathological condition; and (2) by muscular action due to contraction of the *tensor tympani* muscle. This small muscle arises from the apex of the

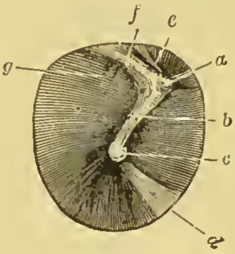

FIG. 403. — Outer aspect of the right *membrana tympani*, double natural size. *a*, short process; *b*, middle of *manubrium* (handle of *malleus*); *c*, umbo; *d*, cone of light; *e*, *membrana flaccida*; *f*, posterior fold; *g*, long process of the incus shining through the membrane. (Barr.)

petrous portion of the temporal bone and the cartilage of the Eustachian tube, enters the tympanum at its anterior wall, and is inserted into the malleus near its root. The handle of the malleus is inserted between the layers of the *membrana tympani*, and as the malleus and incus move round an axis, as seen in Fig. 404, passing through the neck of the malleus, from before backwards, the action of the muscle is to pull the *membrana tympani* inwards towards the tympanic cavity, in the form of a cone, the meridians of which, according to Von Helmholtz, are not straight but curved, with the convexity outwards. When the muscle contracts, the handle of the malleus is drawn still farther inwards, and thus a greater tension of the tympanic membrane is produced. On relaxation of the muscle, the membrane returns to its position of equilibrium, by its own elasticity, and by the elasticity of the chain of bones. This power of varying the tension of the membrane is a kind of accommodating mechanism for receiving and transmitting sounds of different pitch. With different degrees of tension, it will respond more readily to sounds of one pitch than to sounds of another. Thus, when the membrane is tense, it will readily respond to high sounds, while relaxation will be the condition most adapted

Fig. 404.—Diagram showing the axis of rotation of the bones of the ear. *m*, malleus; *e*, incus; *a*, short process of incus, abutting against tympanic wall; *r*, long process of incus, bearing the stapes; *p*, handle of the malleus; *a b*, axis of movement.

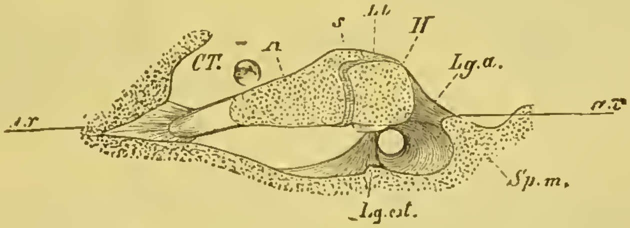

Fig. 405.—Horizontal section through cavity of the tympanum of the right ear to show the relations and connections of the chain of bones. × 4 d. *H*, head of malleus; *A*, incus showing the short process passing to, and connected with, the wall of the tympanum. Observe the bands of fibres. From the *spina major*, *Sp.m.*, of the tympanic wall passes the *ligamentum anterius*, *Lg.a.*; *ligamentum laterale* passing to processes of the malleus and incus, at the joint *Ll*; *Lg.ext.*, *ligamentum externum* passing from the wall of the tympanum to the head of the malleus. The canal-like space between the ligaments is the *membrana flaccida*; *ax.-ax.*, axis of rotation. (Von Helmholtz.)

for low sounds. In addition, increased tension of the membrane, by increasing the resistance, will diminish the intensity of vibrations. This is especially the case for sounds of low pitch. Von Helmholtz has also pointed out that the peculiar form of the *membrana tympani* in man (the arrangement of the radiating fibres being such that while the membrane, as a whole, has its convexity towards the tympanum, each band of fibres is curved so that the convexity is towards the external auditory canal) has the effect of increasing the force of its vibrations at the expense of their amplitude.

The vibrations of the *membrana tympani* are transmitted to the internal ear partly by the air which the middle ear, or tympanum, contains, and partly by the chain of bones consisting of the malleus, incus, and stapes (Figs. 405, 406 and 407). Of these, transmission by the chain of bones is the more important. In birds and in the scaly amphibia, this chain is represented by a single rod-like ossicle, the *columella*; but in man the two membranes, *membrana tympani* and the membrane of the *fenestra ovalis*, are connected by a compound lever, consisting of three bones, namely, the *malleus* or hammer, inserted into the *membrana tympani*; the *incus* or anvil, and the *stapes* or stirrup, the base of which fits into the oval window. The lever thus formed has its fulcrum at the short process of the

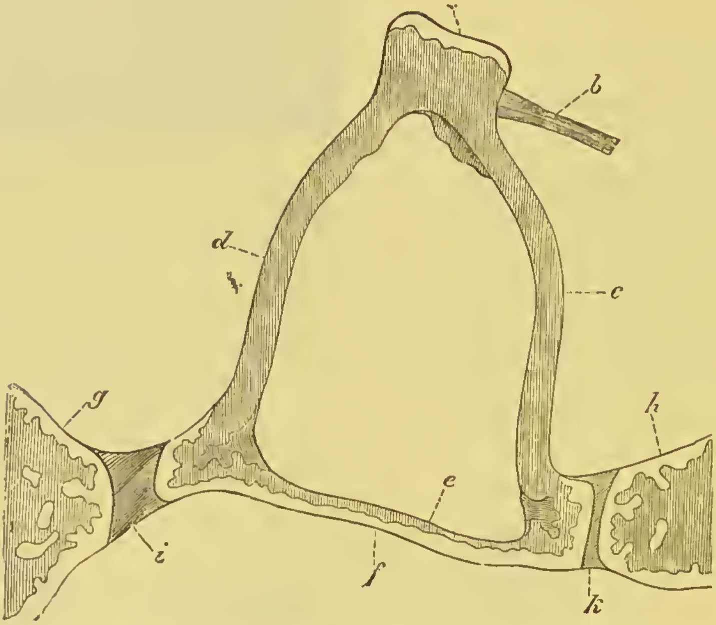

FIG. 406.—Section of the stapes. *a*, head of stapes which unites with the long process of the incus; *b*, tendon of the *stapedius* muscle; *c*, posterior, *d*, anterior, limb of stirrup; *e*, foot plate; *f*, thin layer of cartilage; *g*, anterior, and *h*, posterior, part of the *fenestra*; *i*, anterior, and *k*, posterior, portion of the *ligamentum annulare proprium*. (Eysell.)

incus, which abuts against the tympanic wall; the power is applied to the handle of the malleus, and the resistance is at the base of the stirrup. Von Helmholtz has shown that, by this arrangement, vibrations are diminished in extent, but are increased in force. Thus, the length of the handle below the axis of the malleus is 1·5 times that of the head above the axis. But the amplitude of the excursion of the head is only two-thirds that of the handle and of the drum-head. On the other hand, the power of the movement of the head of the malleus will be 1·5 times more than that of the handle. Again, the size of the drum-head is 20 times that of the oval window, and thus the energy of the movement of the drum-head is concentrated on a membrane 20 times smaller, that is to say, the movement of the membrane of the oval window is smaller in amplitude but about 30 times greater in power (1·5 × 20). Considering the great resistance offered to excursions of the stapes, and the small dimensions of the internal ear, such an arrangement must be advantageous. It must also be noted that in the transmission of vibrations of the *membrana tympani* to the fluid in the labyrinth or internal ear through the oval window, the chain of ossicles vibrates as a whole, although its length is only a small fraction of the wave-length of the sound transmitted. The mechanical arrangements of the ossicles may be studied with the aid of the model devised by Von Helmholtz, shown in Fig. 408. It is important to notice carefully the mechanism of the chain of bones. When pressure, by a sound wave, is made on the tympanum, the drum-head moves inwards and carries the handle of the malleus with it. But as the malleus turns round its axis, the parts above the axis make a movement in the opposite direction, that is, the head of the malleus swings outwards. This movement is accompanied by the incus. The body of the incus therefore swings outwards, while its long process (the short process touching the tympanic wall) passes inwards, that is, in the same direction as the handle of the malleus. This pushes the stapes into the oval window. The joint between the malleus and incus is of

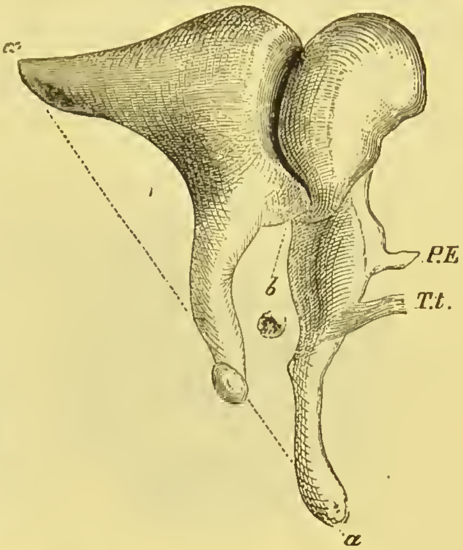

Fig. 407.—Diagram to illustrate the lever-like action of the chain of bones; *a a*, hypotenuse; *P.E.*, *processus Folianus* of malleus; *T.t.*, *tensor tympani*; *b*, tooth of the incus by which it interlocks with the malleus. The bones are seen from the tympanic cavity. (Von Helmholtz.)

such a shape that a movement of the head of the malleus must take the incus with it, and it has a peculiar interlocking action when the push on the drum-head is inwards. When the drum-head moves outwards, in consequence of the diminished pressure of the sound wave on its outer surface, a reverse series of actions occurs, but the head of the malleus and the incus fall away, as it were, from each other, the incus, carrying the stapes, slowly follows, and thus the danger is avoided of a sudden outward movement of the drum-head rudely pulling the base of the stirrup out of the round window.

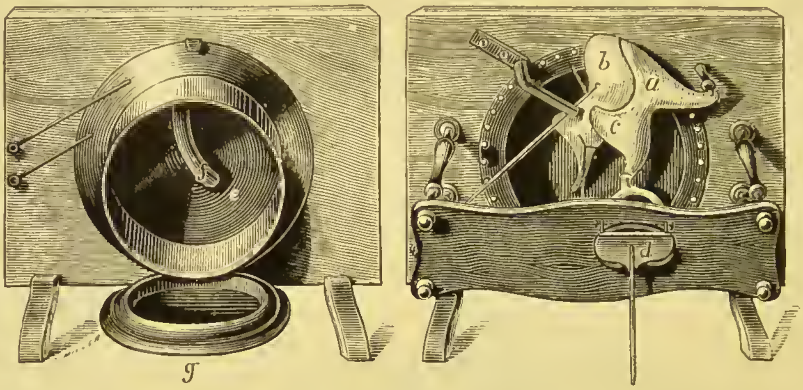

FIG. 408.—Model of the mechanical arrangements of the bones of the ear. External view to the left, internal to the right. *e*, in left-hand figure, outer surface of drum-head, made of leather ; *g*, cap, having india-rubber edge fitting over *c*, so that by compression, *e* may be caused to move. *a*, in right-hand figure, incus, showing its short process attached to tympanic wall, and its longer process, bearing the stapes ; *b*, malleus ; *d*, piece of wood bearing a wire, attached to oval window.

The peculiar form of the drum-head must also be noticed. A flat drum-head when struck gives out its proper tone, the pitch of which will be higher as the tension of the drum-head is increased. Such a membrane, also, will only vibrate sympathetically with its own tone, so that if many tones are produced near it, it will pick out its own tone. The drum of the ear, however, cannot so act because it must be affected by variations of pressure corresponding to tones produced by from 30 to 40,000 vibrations per second. Von Helmholtz has shown that the funnel-shaped form of the drum-head of the ear enables it to act as if it were a mosaic of many small membranes, that is to say, its different parts are not under the same tension. The tension is greatest in the middle where the membrane is thinnest, and it diminishes to the periphery. Thus the drum-head can transit many tones, or, in other words, it has no specific tone of its own. Further, it is so rigid and so weighted by the ossicles that it ceases vibrating when the cause of vibration ceases

The ossicles act as dampers. The damping is also assisted by the action of the tensor tympani.

Sounds are also conducted to the internal ear through the bones of the head. Thus the ticking of a watch is strongly heard when placed between the teeth, even when both ears are stopped. As shown by Rinne, we hear a sound longer when transmitted through the air than through the bones of the head. Sound a tuning fork of low pitch, hold it against the teeth till no sound is heard, then place the prongs near the ear, and the sound will still be heard.

Sonorous vibrations may reach the fluid in the labyrinth by three different ways: (1) by the osseous walls of the labyrinth; (2) by the air in the tympanum acting on the round window; and (3) by the base of the stapes inserted into the oval window.

When the head is plunged into water, or brought into direct contact with any vibrating body, vibrations are transmitted *directly*. Vibrations of the air in the mouth and in the nasal passages are also directly communicated to the walls of the cranium, and thus pass to the labyrinth. In like manner, we may experience peculiar auditory sensations, such as blowing, rubbing, and hissing sounds, due to muscular contraction or to the passage of blood in vessels close to the auditory organ. It has not been satisfactorily made out to what extent, if any, vibrations may be communicated to the fluid in the labyrinth by the round window. There can be no doubt, however, that in ordinary hearing, vibrations are communicated chiefly by the chain of bones. When the base of the stirrup is pushed into the oval window (Fig. 409), the pressure in the labyrinth increases, the impulse passes along the *scala vestibuli* to the *scala tympani*, and as the only mobile part of the wall of the labyrinth is the membrane covering the round window, this membrane is forced outwards; when the base of the stirrup passes outwards; a reverse action takes place. Thus, the fluid of the labyrinth may receive a series of pulses or vibrations isochronous with the movements of the base of the stirrup, and these pulses affect the terminal apparatus in connection with the auditory nerve.

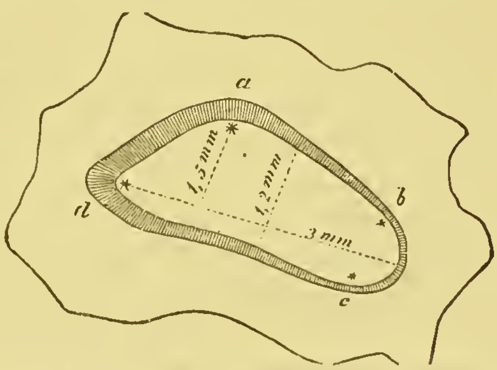

FIG. 409.—Base of the right stapes fitted into the *fenestra ovalis*, seen *in situ* from the vestibule. *a-b*, upper, *b-c*, posterior, *c-d*, under, and *d-a*, anterior wall. The figures give the measurements. (Eysell.)

Since the size of the membranous labyrinth is small, measuring in man not more than $\frac{1}{10}$th of an inch in diameter at its widest part, and since it is a chamber consisting partly of conduits of irregular form, it is impossible to state precisely the course of vibrations transmitted to it by impulses communicated from the base of the stirrup. In the cochlea, vibrations must pass from the saccule along the *scala vestibuli* to the apex, thus affecting the membrane of Reissner, which forms its roof; then passing through the opening at the apex (the *helicotrema*), they must descend by the *scala tympani* to the round window, and affect in their passage the *membrana basilaris*, on which, as already stated, the organ of Corti is situated. From the round window, impulses may be reflected backwards, but how they affect the advancing impulses is not known. The problem is even more complex when we take into account the fact that impulses are transmitted simultaneously to the utricle and to the semicircular canals.

CHAP. V.—PHYSIOLOGICAL CHARACTERS OF AUDITORY SENSATIONS.

Certain conditions are necessary for excitation of the auditory nerve sufficient to produce a sensation. In the first place, the vibrations must have a certain *amplitude:* if too feeble, no impression will be produced (see p. 566). In the next place, an impulse must have a certain *duration*. It must be less than $\frac{1}{30}$th of a second, and greater than $\frac{1}{30000}$th or $\frac{1}{40000}$th of a second.

Lastly, as already stated, a certain *number* of impulses must be made in a given interval of time to excite a sensation of a *tone*. By the syren, it may be shown that the lower limit is marked by about 30 vibrations per second. It has been ascertained by various methods that the upper limit is somewhere about 30,000 vibrations per second. Beyond this limit, few ears can detect any sound, and none range beyond 45,000 per second. König has constructed a series of steel cylinders slung on a wooden framework, by which, when they are struck so as to elicit sound, the upper limits of sensibility to pitch may be tested. The wave-length of the highest audible tone is about 10 mm. The most powerful high tones are produced by small tuning forks, and by these a tone of 40,000 vibrations has been heard by Preyer. The majority of persons detect a tone of 30,000 vibrations easily, but many are deaf to tones of 20,000 vibrations, or even 15,000 vibrations. A few may not hear tones of only 5,500 vibrations.[1]

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[1] J. Kerr Love, "An inquiry into the limits of hearing." *Glasgow Medical Journal.* 1888.

The sensation of a *simple tone* is caused by a *variation of pressure* of the air in the neighbourhood of the ear according to a simple harmonic function of the time. The vibrations of the air caused by a simple harmonic vibrator, however, may be either simple harmonic or in circular or elliptic orbits, resulting from the composition of two simple harmonic motions, and the change of air pressure near the ear follows the simple harmonic law if the maximum velocity of the vibrator and of the air near it is infinitely small in comparison with the velocity of sound. The more nearly this condition is observed, the nearer the sound is to a simple tone, but if the air rushes with great velocity past the edges of a vibrating body in a narrow aperture as a harmonium reed (Fig. 410), the motion of the vibrator itself is not simple harmonic, and the tone is rich in overtones, giving it a rich or harsh character. (Sir William Thomson.)

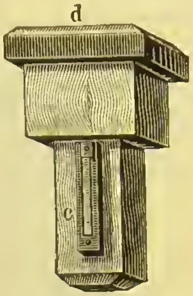

FIG. 410.—Vibrating reed, *c*; *d*, top of wooden frame.

A sound may or may not be loud, or it may appear to be higher or lower as regards pitch; but, in addition, it may have a certain quality, timbre, or klang, or the peculiar characteristic of a musical sound by which we identify it as proceeding from a particular instrument or from a particular human voice. *Intensity*, as may be proved optically, depends upon a greater or lesser amplitude of the vibration. Consequently there will be a corresponding amount of excitation of the terminal apparatus. Thus, a feeble sound will cause a smaller excursion of vibratory hairs than a loud sound. *Pitch*, as a sensation, depends on the number of vibrations in a given interval of time, or, in other words, on the length of time occupied by a single vibration. It may be absolute or relative. Most individuals can determine the relative pitch of a sound by referring it to the pitch of another sound which they have just heard. By the few who possess what may be termed a strong memory of sounds, an approximately correct estimation of the pitch of any tone may be given; but no experiments prove that any individual can at once detect absolute pitch. An experiment with the syren shows that variations in pitch glide into each other by insensible gradations. It has been stated that practised musicians may detect the $\frac{1}{64}$th of a semitone, but this is far beyond average attainment. In musical composition, the sounds range from about 40 to 4,000 vibrations per second, that is, a range of about six octaves.

The third peculiarity of musical tone is *quality*, *timbre*, or "*klang*," by which we identify it as proceeding from a particular instrument or from a particular human voice. This appears to be related physically to what is called the *form* of the wave. Many waves of sound that reach the ear are compound waves, built up of simple waves, so that the wave has a special form. This is illustrated by Fig. 411, which shows by the continuous line the form of the wave resulting from the combination of the two waves represented by dotted lines. The same fact is still further illustrated by the following diagrams given by Von Helmholtz, Fig. 412.

FIG. 411.—Form of wave produced by combining two simple waves.

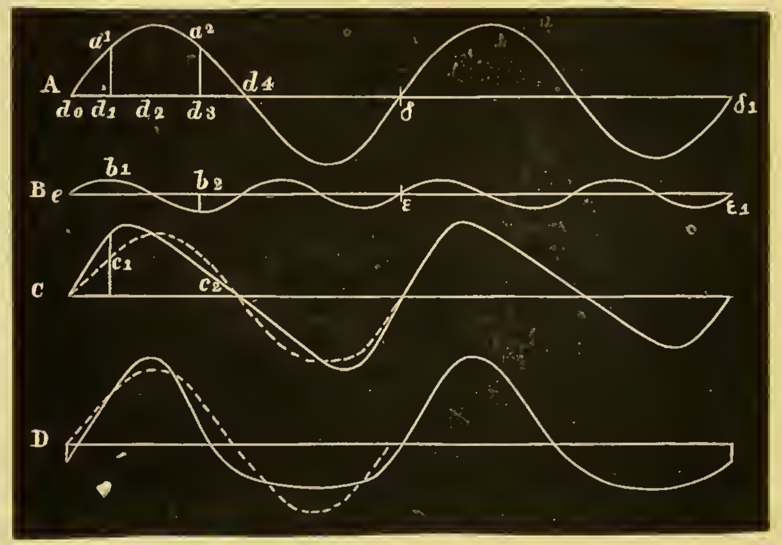

FIG. 412.—Various forms of wave curves.

A and B represent waves of simple tones, B having twice the number of vibrations of A, or, in other words, an octave higher in pitch. By superimposing B on A, the curves C and D are produced. The curves in C and D are representations of the compound wave form produced by superposing B on A so that *e* coincides with *do*, or is a little later or earlier.

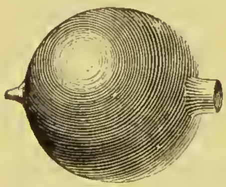

FIG. 413.—Resonator of Von Helmholtz.

Each of these constituent waves may so affect the organ of hearing as to be perceived as an individual sound, more especially with the aid of an instrument called a *resonator*, shown in Fig. 413. This consists essentially of a brass globe, having two openings, the narrower of which is placed in the external ear. Each resonator contains a mass of air which responds sympathetically to a particular tone. By using a number of such resonators, a compound tone may be analysed into its constituents, the action of an individual resonator being to strengthen the intensity of the tone to which it corresponds. Even without the aid of resonators, a sensitive ear may detect in the tone of a piano or harmonium some of its constituent tones. Thus, it appears that the ear must have some arrangement by which it resolves any wave-system, however complex, into *simple pendular vibrations.* When we listen to a sound of any quality, we recognize that it is of a certain pitch. This depends on the number of vibrations of one tone predominant in intensity over the others, called the *fundamental* or first partial tone. Quality depends on the number and intensity of other tones, called *partials*, or *harmonics*, or *overtones*, added to it. The relation of these to the first tone is very simple, their vibrational numbers being multiples of that of the fundamental tone, thus:

	Fundamental Tone.	Upper Partials or Harmonics.								
Notes, ...	do^1	do^2	sol^2	do^3	mi^3	sol^3	si♭^{3}	do^4	re^4	mi^4
Partial tones, .	1	2	3	4	5	6	7	8	9	10
Number of Vibrations,	33	66	99	132	165	198	231	264	297	330

A *harmony* is a sound which, without being a *simple tone*, has the variations of air pressure strictly periodic, and according to Fourier's analysis of periodic variations (harmonic analysis), any periodically varying quantity may be looked on as the sum of quantities varying separately according to the simple harmonic law, in periods respectively equal to the main period, half the main period, a third of the main period, a fourth of the main period, and so on. Thus, the variation of the air pressure of a harmony is the sum of the variations of simple tones, one having a period equal to the period of the harmony, a second $\frac{1}{2}$, a third $\frac{1}{3}$, and so on. A harmony is therefore composed of simple tones. On listening to such a complex tone, or sound, a tone may predominate in the sensory impression, and the pitch of the sound is referred to the main period of this tone, the other tones merely giving a special character to the sound. In musical harmony, however, one tone does not thus predominate, and a sound of two, three, or four, or more tones, having commensurable periods is heard, and the period of the harmony is the least common multiple of the period of its constituent tones. The harmonic number of a tone in a harmony is denoted by the number of times that the period of the harmony contains this particular tone. Again, the quality of a harmony depends on the amplitudes of the tones forming it, the periods of these tones, and the relation of their phases. It is important to observe the effect of *phase.* Thus, the instants of maximum pressure or of minimum pressure may coincide, or there may be a coincidence of the maximum pressure of one tone, with the minimum pressure of the other. If, now, the tone of a perfect binary harmony be very slightly sharpened or flattened, and if the two tones are sustained so as to secure perfect uniformity as to pitch and intensity, the effect is an imperfect harmony, with a slow change of phase relation through a cycle, and there is a variation of the quality of the tone recurring periodically on the imperfect harmony. This variation is the *beat* on the imperfect harmony. (Sir William Thomson.)

The relations of tones physically and physiologically may be studied with the aid of tuning forks, such as is shown in Fig. 414. By combining the sounds of a series of such forks, the vibrational numbers of which are multiples of the first, various qualities of tone may be produced, and the effect of increased intensity of one tone over the others may also be illustrated. Thus, quality of tone may be studied *synthetically*. As already stated, compound tones may be analysed by means of resonators applied to the ear; but the same may be done optically with the aid of apparatus devised by König.

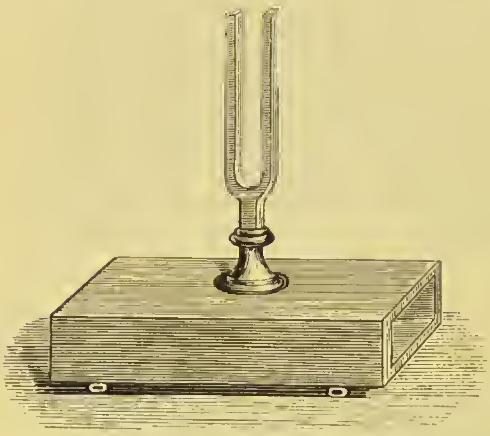

FIG. 414.—Tuning fork mounted on resonance box, for increasing intensity of tone. The best tuning forks for the purpose are made by König.

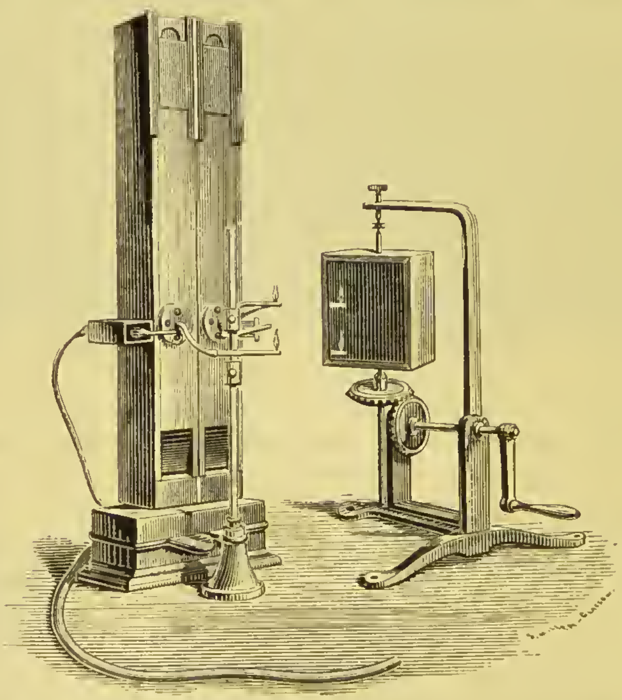

FIG. 415.—König's apparatus for studying optically the vibrations of the air in organ pipes.

The principle of his method will be readily understood with the aid of Fig. 415.

A small wooden capsule, the base of which is formed of thin india-rubber membrane, is screwed over a circular hole in the side of an organ pipe. By means of tubes, ordinary gas is led into and from the capsule, and the tube leading from it is connected with a small gas burner. Thus, the air in the organ pipe is separated from the gas by the thin membrane, so that the latter responds to every movement of the air, and consequently affects the pressure of the gas in the capsule. When such a pipe is sounded, the flame appears unsteady and of a pale blue colour, and if we then rotate a rectangular mirror, as suggested by Wheatstone, in front of the flame, a picture of the movements of the air in the pipes is seen on the mirror, such as is represented in Figs. 416 and 417.

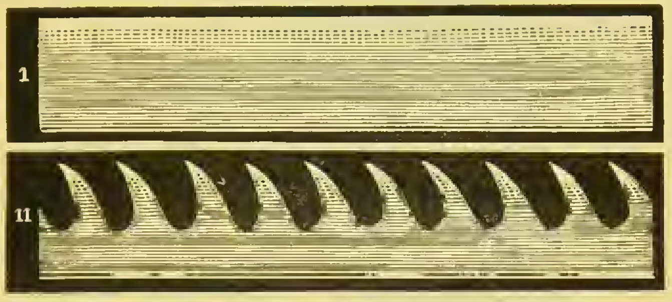

FIG. 416.—Appearance of the flame in the mirror of König's apparatus. 1, organ pipe not sounding; 2, organ pipe sounding—the teeth representing individual vibrations of the air in the pipe.

If two organ pipes of the same pitch be employed, the teeth of the flame picture will be equal in number; but by using pipes giving the various intervals of the scale, the relations of these intervals may be shown optically. Thus, by combining a tone with its octave, the flame picture shown in Fig. 417 will be produced.

Taking advantage of this method of what he terms *manometric flames*, König has devised an ingenious apparatus, shown in Fig. 418, by which any compound tone, whose fundamental tone is $\text{UT}_2 = 256$ vibrations per second, may be analysed. No apparatus with which the author is acquainted shows to the student more clearly the physical conditions upon which quality depends. It consists of a series of resonators, each connected with its special flame, mounted on a cast-iron framework, the flames being reflected by an elongated rectangular mirror.

On sounding any of the tuning forks in the harmonic series of UT_2, in front of this instrument, at the same time rotating the mirror, a special flame is affected, and appears segmented as represented in Fig. 416; and on producing any compound tone, the fundamental of which is UT_2, or which contains any harmonies of this series, it is at once analysed optically by the segmentation of the individual flames; also, on singing loudly in front of the instrument, the tones of the human voice may be analysed.

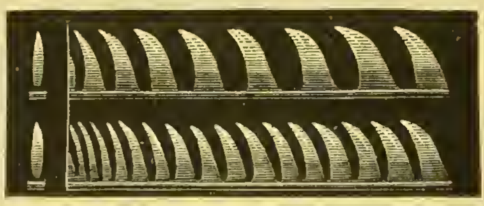

FIG. 417.—Flame picture of two organ pipes sounding an octave. It will be observed that the teeth are in the ratio of 2 : 1. The erect figures to the left are reflections from a small stationary mirror, for purposes of comparison.

When a simple tone, or one free from partials, is heard, it gives rise to a soft, somewhat insipid, sensation, as may be obtained by blowing across the mouth of an open bottle, or by a tuning fork. The lower partials added to the fundamental tone give softness combined with richness ; while, the higher, especially if they are very high, produce a brilliant and thrilling effect, as is caused by the brass instruments of an orchestra.

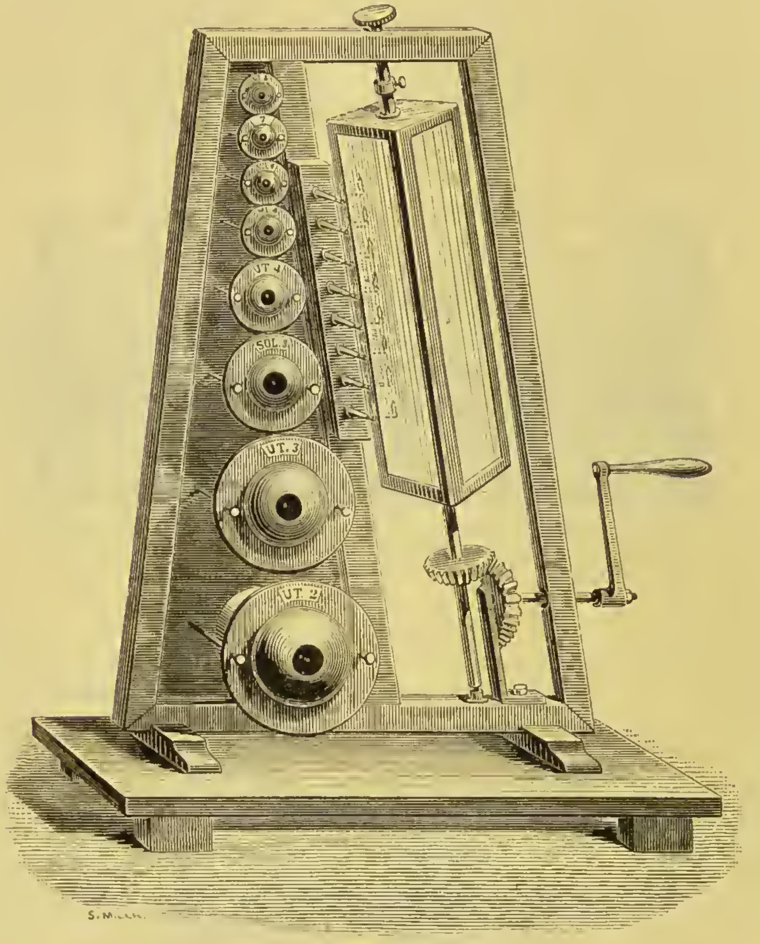

Fig. 418.—König's apparatus for the analysis of a compound tone, the fundamental of which is UT$_2$.

The phenomenon of interference may be illustrated by using the arrangement shown in Fig. 419. A sound is directed, as first carried out by Wheatstone, into a tube which divides into two U-shaped branches. Each branch, after running a length of two or three metres, is brought into relation with the manometric capsules, *c* and *c′*, mounted on a wooden frame, *p*, supplied by a gas tube, T, and furnished with stopcocks, C and B. The capsule, *c*, is connected with the gas jet, *d′*, and the capsule, *c′*, with the jet, *d″*, while both capsules are connected by a ⊥-shaped arrangement with the middle jet, *d*. The three flames are seen in the mirror, M. If, now, the two limbs of the U-shaped tubes are of the same length, the images of the three flames in the mirror will be dentated, but if one of the U-shaped tubes is lengthened, so that its length is half a wave-length longer than that of the sound employed in the experiment, complete interference will occur at the point where the two waves meet, and the image of the middle flame will be continuous, while the others will be dentated, as shown in Fig. 420.

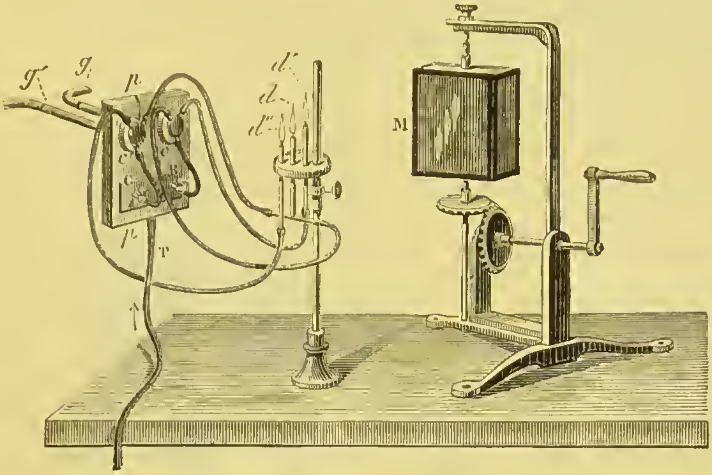

FIG. 419.—Wheatstone's experiment of interference shown by manometric flames.

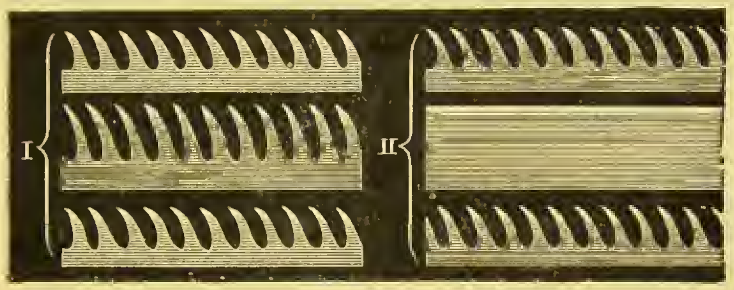

FIG. 420.—Manometric flames in Wheatstone's experiment. I, no interference: II, complete interference.

An interesting experiment may also be performed, in which the cat's tympanum is used as a manometric capsule. Small glass tubes are fixed with sealing wax into holes trephined in the tympanic bulla, and a tube is also inserted into the external meatus (Fig. 421).

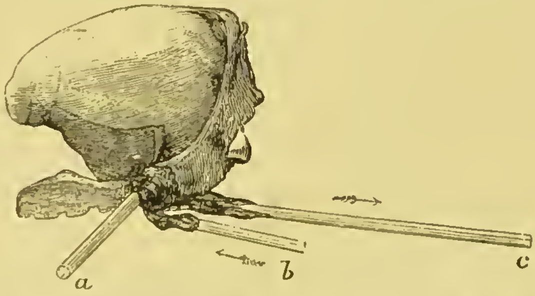

FIG. 421.—Temporal bone of cat. *a*, tube in external meatus; *b*, tube for entrance of, and *c*, tube for exit of, gas. The tube, *c*, is brought into connection with a small gas jet.

A funnel may be placed on tube, *a*, and on speaking into the funnel, and rotating Wheatstone's mirror, the flame picture will be seen. The preparation may be arranged as shown in Fig. 422.

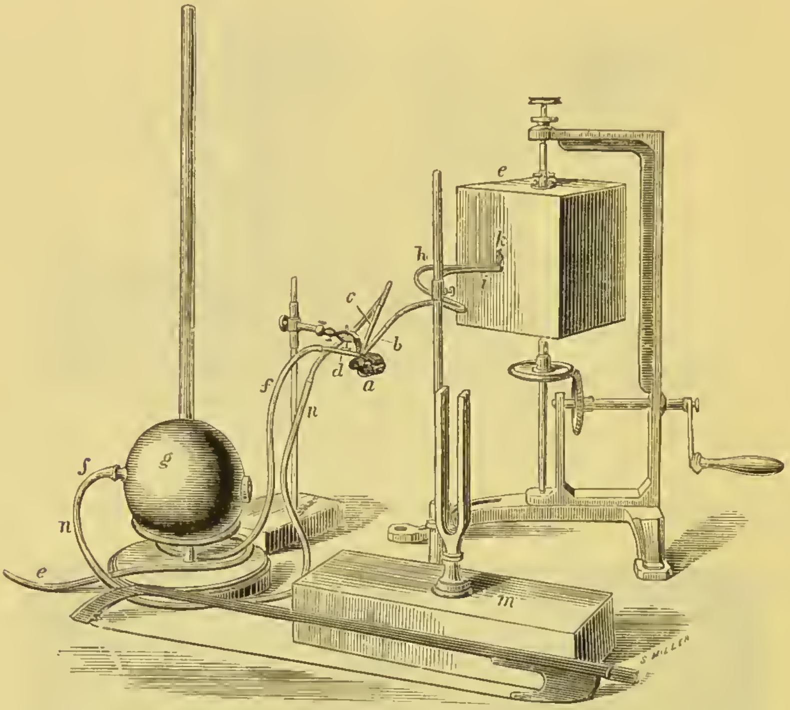

Fig. 422.—Experiment with cat's ear. *a*, temporal bone; *b*, tube carrying gas from tympanum to burner, *i k*; *c*, tube carrying gas into tympanum; *d*, tube connected with *n f*, conveying sound from resonator, *g*, acted on by tuning fork, *m*.

Chap. VI.—PHYSIOLOGICAL ARRANGEMENTS FOR THE APPRECIATION OF QUALITY OF TONE.

Little is known regarding the mode of action of the vibrations of the fluid in the labyrinth upon the terminal apparatus connected with the auditory nerve. There can be no doubt that it is a mechanical action, a communication of impulses to delicate hair-like processes, by the movements of which the nervous filaments are irritated. In each human ear, it has been estimated that there are about three thousand small arches formed by the *rods of Corti.* Each arch rests on the basilar membrane (see Fig. 387), and supports rows of cells, having minute hair-like processes, somewhat resembling cilia. It would appear also that the filaments of the cochlear division of the auditory nerve terminate in the hair cells, which are related to the basilar membrane (p. 668.) At one time, it was supposed by Von Helmholtz that these fibres of Corti were elastic, and that they were tuned for particular tones, so as to form a regular series, corresponding to all the tones audible to the human ear. Thus, two thousand eight hundred fibres, distributed over the tones of seven octaves, would give four hundred fibres for each octave, or nearly thirty-three for a semitone. Von Helmholtz put forward the ingenious hypothesis that, when a pendular vibration reaches the ear, it excites, by sympathetic vibration, the fibre of Corti which is tuned for its proper number of vibrations. If, then, different fibres are tuned to tones of different pitch, it is evident that we have here a mechanism which, by exciting different nerve fibres, will give rise to sensations of pitch. When the vibration is not simple, but compound, in consequence of the blending of vibrations, corresponding to various harmonics or partial tones, the ear has the power of resolving this compound vibration into its elements. It can only do so by different fibres responding to the different vibrations of the sound, one for the fundamental tone being stronger, and giving the sensation of a particular pitch or height to the sound; and the others, corresponding to the upper partial tones, being weaker, and causing special, though undefined, sensations, which are so blended together in consciousness as to terminate in a complex sensation, or a tone of a certain quality or timbre. It would appear, at first sight, that thirty-three fibres of Corti for a semitone are not sufficient to enable us to detect all the gradations of pitch in that interval, since, as has been stated above, trained musicians may distinguish a difference of $\frac{1}{64}$th of a semitone. To meet this difficulty, Von Helmholtz states, that if a sound be produced, the pitch of which may be supposed to come between two adjacent fibres of Corti, both of these will be set into sympathetic vibration, but the one which comes nearer to the pitch of the sound will vibrate with greater intensity than the other, and that consequently the pitch of that sound would be thus appreciated. These theoretical views of Von Helmholtz have derived much support from experiments by Hensen, who observed that minute hairs on the antennæ of *Mysis*, a Crustacean, when viewed with a low microscopic power, vibrated with certain tones produced by a keyed horn. It was seen that certain tones of the horn set some hairs into strong vibration, and other tones other hairs. Each hair responded also to several tones of the horn. Thus, one hair answered strongly to *d*♯ and *d′*♯, more weakly to *g*, and very weakly to G. It was probably tuned to some pitch between *d″* and d″♯.

Histological research has led to a modification of this hypothesis. It has been found that the rods or arches of Corti are stiff structures, not adapted for vibrating, but apparently forming a supporting structure for the hair cells. It is also known that there are no rods of Corti in the cochlea of birds, which apparently are capable nevertheless of appreciating pitch. Hensen and Von Helmholtz have suggested the view, that not only may the segments of the *membrana basilaris* be stretched more in the radial than in the longitudinal direction, but different segments may be stretched radially with different degrees of tension, so as to resemble a series of tense strings of gradually increasing length. Each string would then respond to a vibration of a particular pitch, and would communicate it to the hair cells. The exact mechanism of the hair cells and of the *membrana reticularis*, which suggests the idea of a damping apparatus, is unknown.

A conception of the minute size of the parts of this remarkable structure may be obtained from the following measurements :—I. *Breadth of membrana basilaris* (*a*), at ·2 mm. from base of cochlea, ·04 mm. ; (*b*), at ·8 mm. from base, ·08 mm. ; (*c*), in middle of first spiral, ·169 mm. ; (*d*), end of first spiral, ·300 mm. ; (*e*), middle of second spiral, ·4125 mm. ; (*f*), end of second spiral, ·450 mm. ; (*g*), at *hamulus*, ·495 mm. II. *Length of inner rod* (*a*), at fenestra ovalis, ·048 mm. ; (*b*), at *hamulus*, ·0855 mm. III. *Length of outer rod* (*a*), at fenestra ovalis, ·048 mm. ; (*b*), at *hamulus*, ·098 mm.

The ultimate analysis of auditory sensations must take place in the auditory centre of the brain. Each fibre of the auditory nerve coming from the cochlea will be stimulated by the vibrations of its own hair cells, or set of hair cells, and each filament will conduct impressions proportional in number to the vibrations of these hair cells. Thus, as suggested by Rutherford, different cells in the brain will receive varying numbers of nervous impulses, and thus sensations of sounds of different pitch will be produced.[1]

Considerable difference of opinion exists as to whether the *phase of vibration*, when two or more tones are sounded together, can be detected by the ear. It is evident that phase produces an alteration in the form of the wave reaching the ear, or, in other words, a variation of the pressure on the drum-head. The question thus is—does the ear take any cognizance of different wave forms, produced by the same pendular vibrations, or is it simply affected by these pendular vibrations without taking cognizance of wave form ? Von Helmholtz supports the latter view, and endeavours to prove it experimentally by means of an apparatus, usually termed the *vowel-tone apparatus*, a diagram of which is shown in Fig. 423. By sounding the forks of this series at different times, and opening to a greater or less extent the resonators, it is evident that by varying the phase, the form of the resultant wave may be almost

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[1] W. Rutherford, Address to British Association for Advancement of Science. *Proceedings*, 1887.

infinitely varied, and it is usually stated that the resultant sensation is always the same, that is to say, no difference can be detected in the quality of the tone. To this the objection may be urged that the sensation produced by any given form of wave can only be compared with one that has just passed away. On the other hand, Sir William Thomson maintains, from a study of the beats of imperfect harmonies, that the ear does take cognizance of phase. Thus, with an even binary harmony, periods 1 : 2, four distinct wave forms are produced, and Sir William Thomson states that "the ear distinguishes the quality of the sound represented by the sharp-topped and flat-hollowed curve from that represented by the flat-topped and sharp-hollowed curve. In the one case the pressure of air close to the ear rises very suddenly to, and falls very suddenly from, its maximum, and (as in cases of tides in which there

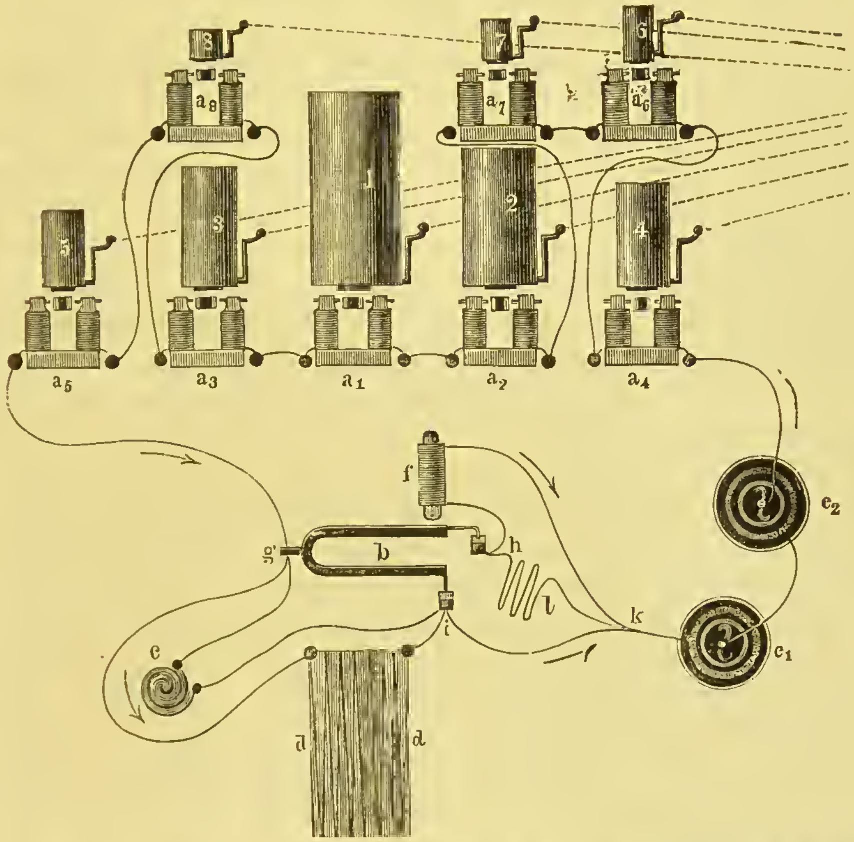

FIG. 423.—Von Helmholtz's vowel-tone apparatus. a_1 to a_8, tuning forks, in a harmonic series, worked by electro-magnets. The current from e_1 to c_2 is interrupted by the fork, b, worked by the electro-magnet, f, and furnished with a condenser, dd, so as to diminish the noise of the sparks at hi; g, end of fork; l, wire throwing resistance into current of fork. Each fork is supplied with a resonator, 1 to 8, the orifices of which may be opened by cords, represented by the dotted lines, attached to handles. The fork, b, has the same number of vibrations as the first tone of the series, a_1, and a_2 has twice the number of vibrations of a_1, and so on for the rest.

is a long hanging on low water) there is a comparatively slow variation of pressure for a few ten-thousandths of a second on each side of the instant of minimum pressure ; in the opposite phase relation there is a slow change before and after the time of maximum pressure, and a rapid change before and after the time of minimum pressure."[1] The ear apparently discriminates between push and pull on the tympanum, and Sir William Thomson states that it distinguishes between various configurations appropriate to the harmonies 2 : 3, 3 : 4, 4 : 5, 5 : 6, 6 : 7, 7 : 8, 1 : 3, and 3 : 5.

CHAP. VII.—PSYCHICAL CHARACTERS OF AUDITORY SENSATIONS.

Under ordinary circumstances, auditory sensations are referred to the outer world. When we hear a sound, we associate it with some external cause, and it appears to originate in a particular place, or to come in a particular direction. This feeling of *exteriority* of sound seems to require transmission through the *membrana tympani.* Sounds which are sent through the walls of the cranium, as when the head is immersed in, and the external auditory canals are filled with, water, appear to originate in the body itself. It is probable that the external character of auditory sensations may be more the result of habit than due to any anatomical peculiarity of the ear itself.

An auditory sensation lasts a short time after the cessation of the exciting cause, so that a number of separate vibrations, each capable of exciting a distinct sensation if heard alone, may succeed each other so rapidly that they are fused into a single sensation. If we listen to the puffs of a syren, or to vibrating tongues of low pitch, the single sensation is usually produced by about 30 or 35 vibrations per second ; but there can be no doubt, as was first pointed out by Von Helmholtz, that when we listen to *beats* of considerable intensity, produced by two adjacent tones of sufficiently high pitch, the ear may follow as many as 132 intermissions per second.

The sensibility of the ear for sounds of different pitch is not the same. It is more sensitive for acute than for grave sounds, and it is probable that the maximum degree of acuteness is for sounds produced by about 3,000 vibrations per second, that is near fa^5♯. Sensibility as to pitch varies much with the individual and with the training to which he has subjected himself. The power of appreciating differences of pitch is

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[1] Sir William Thomson on "Beats of Imperfect Harmonics." *Proc. Royal Soc. Edin.*, 1877-8.

termed a correct or just ear, and there can be no doubt of its improvement by practice (p. 681).

Binaural Audition.—Hearing with two ears does not materially influence auditory sensation, but probably the two organs are fitted for aiding us in determining the locality from which a sound originates. It is asserted by Fechner that one ear perceives the same tone at a slightly higher pitch than the other, but this was probably due to a pathological condition. If two tones, excited by two tuning forks of equal pitch, are produced, one near each ear, there is a uniform single sensation; if one of the tuning forks is then made to revolve round its axis in such a way that its tone increases and diminishes in intensity, neither fork is heard continuously, but both sound alternately, the fixed one being audible only when the revolving one is not. It is difficult to decide whether excitations of corresponding elements in the two ears can be distinguished from each other. It is probable that the sensations may be distinguished, if one of the generating tones differs from the other in intensity or quality, although it may be the same in pitch. Beats, due to interference, may be produced in the head by acting on the two ears *directly* by two tones of nearly the same pitch. This experiment is striking when the sounds of two forks, slightly different in pitch, are conveyed to two telephones, one placed opposite each ear.

Musical Sensations.—Hitherto we have considered only the action of a single sound, but it is possible also to have simultaneous sensations, as in musical harmony and composition. It is impossible to ascertain what is the limit beyond which distinct auditory sensations may be perceived. When we listen to an orchestra, there is a multiplicity of sensations, and a total effect, but, at the same time, we can single out and attentively notice the tones of one or two special instruments. Thus, the pleasure of music may arise partly from listening to simultaneous, and partly from the effect of contrast or suggestion in passing through successive, auditory sensations.

The principles of harmony belong to the department of music, but it is necessary to refer briefly to a few of these, from the physiological point of view. If two musical tones reach the ear at the same moment, an agreeable or disagreeable sensation is experienced, which may be termed a *concord* or a *discord.* It may be shown by the syren that *consonance* and *dissonance* depend upon the ratio of the vibrational numbers of the two tones. The octave (1 : 2), the twelfth (1 : 3), and double octave (1 : 4), are absolute consonant sounds; the fifth (2 : 3), is said to be perfectly consonant; then follow in the direction of dissonance, the fourth (3 : 4), major sixth (3 : 5), major third (4 : 5), minor sixth (5 : 8), and minor third (5 : 6). Von Helmholtz has attempted to account for this effect, more especially as regards compound tones, by the influence of *beats.*

Beats are observed when two tones of nearly the same pitch are produced together, and the number of beats per second is equal to the difference of the vibrational numbers of the two tones. They give rise to a disagreeable intermittent sensation, comparable to what is experienced in watching a flickering light, an effect probably due to intermittent stimulation of the auditory nerve. Beats may be so rapid as not to be distinguished individually, but their existence gives a certain roughness to the tone. According to Von Helmholtz, the maximum roughness is attained by 33 beats per second. Above 132 per second, they are inaudible. When two notes are sounded, say on a piano, not only may the first, fundamental, or prime tones beat, but partial tones of each primary may beat also. Thus there may be a certain roughness of tone. If the partial tones of the prime tones coincide, there will be no beats : but if they do not coincide, the beats produced will give a peculiar character to the sensational effect of the interval. Thus, in the octave and twelfth, all the partial tones of the acute sound coincide with the partial tones of the grave sound; in the fourth, major sixth, and major third, only two pairs of partial tones coincide; while in the minor sixth, minor third, and minor seventh, only one pair coincides. This explanation of Von Helmholtz accounts for the peculiar roughness of intervals sounded by vibrating reeds, as in a harmonium, but it does not meet the obvious difficulty, that sensations of dissonance and consonance are experienced even when tones are sounded which are destitute of harmonics.

Chap. VIII.—THE SEMICIRCULAR CANALS.

Although these structures form a part of the labyrinth, physiologists have always had a difficulty in associating them with the function of hearing. The oldest theory connected them with the perception of the *direction* of sound, and it rested on the observation that the three canals lie in planes representing the three dimensions of space. The planes of the three canals are nearly at right angles to each other, and they are named from their position, the horizontal, the superior, and the posterior. The plane of the horizontal canal is almost horizontal in the ordinary position of the head in all animals, and it is always at right angles to the mesial plane. The planes of the other two make nearly equal angles with the mesial plane. The view that they are connected with the appreciation of the direction of sound must be abandoned, because, as a matter of fact, we can only know the direction of a sound by making two or more simultaneous or successive observations. If the sound is heard louder in the right ear than in the left, we turn the head to the right, and by repeated observations judge of the direction, and if the sound be produced at any point equidistant from both ears, we cannot tell its position unless we see what produces it.

In 1828, Flourens observed that division of a membranous canal caused rotatory movements of the animal round an axis at right angles to the plane of the divided canal, that is to say the body of the animal always moved in the direction of the cut canal. As injury to the canal produces phenomena somewhat similar to those following injury of the cerebellum, Flourens suggested that the canals might be concerned in the co-ordination of movement. Goltz was the first, in 1870, to advance a theory explaining how they might thus act. In different positions of the head, he said, the endolymph would press upon the part of the canal at the lowest point, and by stimulating the nerves of each region, localised pressure would give rise to special sensations corresponding to the positions of the head. Any disturbance by which this mechanism was injured would interfere with the sense of equilibrium on which the movements of the body depend.

Two years later, in 1872, Cyon re-investigated the subject and formulated the following theory : The semicircular canals give us a series of unconscious sensations as to the position of our heads in space ; the loss of equilibrium and the other disturbances of locomotion caused by the section of the canals are solely due to the disorder of these sensations.

The next step was taken almost simultaneously, in 1875, by Mach,[1] Breuer, and Crum Brown. The theories advanced by these observers differ only in certain details, and they may be held to constitute a dynamical theory as opposed to the statical one of Goltz. Suppose the three canals to be full of fluid, a rotation of the head in one direction will cause currents of fluid in the canals in the opposite direction, and the amount of flow in each canal will depend on the plane in which the head is turned and on the rate of the rotation. As the auditory hairs in the *crista acustica* are at the *ampullæ*, we can conceive that they will be affected by the currents of the fluid and produce a sensation of rotation of the head in the plane of the canal in which the flow takes place, and

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[1] Mach. Grundlinien der Lehre von den Bewegungsempfindungen. Leipsig, 1875.

in a direction opposite to it. If the rotation of the head continue, the flow of the endolymph backwards will be arrested by friction, and if the head then suddenly stop, the endolymph will continue to flow in the direction in which the head was previously rotated, and a sensation will be felt of a rotation of the head and body in a direction opposite to that of the first rotation. Crum Brown sums up the matter thus :—

> "We have two ways in which a relative motion can occur between the endolymph and the walls of the cavity containing it :—(1) when the head begins to move, here the walls leave the fluid behind ; (2) when the head stops, here the fluid flows on. In both cases the sensation of rotation is felt. In the first, this sensation corresponds to a real rotation, in the second it does not, but in both it corresponds to a real acceleration (positive or negative) of rotation, using the word acceleration in its technical kinematical sense." [1]

Mach attributes the effects to variations of pressure in the canals rather than to an actual flow of fluid, as held by Breuer, and Crum Brown differs from both in two important points : (1) in attributing movement or variations of pressure not merely to the endolymph, but also to the walls of the membranous canals and to the surrounding perilymph ; and (2) in regarding the two labyrinths as one organ, all the six canals being required to form a true conception of the rotatory motion of the head. Crum Brown has shown by numerous measurements that the six canals are sensibly parallel, two and two. The two horizontal canals are on the same plane, while the superior canal on one side is nearly parallel with the posterior canal of the other.

> "Further, in each of these three pairs (right and left horizontal, right superior and left posterior, right posterior and left superior), the two canals are so placed that when rotation takes place about the axis to which they are perpendicular, one of the two canals moves with its ampulla preceding the canal, so that the flow, or tendency to flow [or pressure] is from ampulla to canal, while in the other the ampulla follows the canal and the flow or tendency to flow [or pressure] is from canal to ampulla. If, then, we suppose that flow from ampulla to canal—or, adopting Mach's view, *increase* of pressure in the ampulla—alone stimulates the hair cells, while no effect is produced by flow in the opposite direction—or by *diminution* of pressure in the ampulla—we have in the six canals a mechanical system capable of giving us an accurate notion of the axis about which rotation of the head takes place, and of the sense of rotation." [2]

I have been favoured by Crum Brown with the following description of his method of making the requisite measurements, and the illustrations are from photographs taken for this work :—

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[1] A. Crum Brown, "Cyon's Researches on the Ear." *Nature*, 1878.

Crum Brown, *op. cit.* p. 635.

1. **Preparation of the Skull.**—Having first marked out, with pencil, the part of the temporal bone to be removed, two saw-draughts were carried across the pencil line, cutting about half through the thickness of the skull. Two steel plates were then cut so that their edges fitted exactly the bottom of the saw-draughts, and the position of each steel plate was marked as accurately as possible. The steel plates were then removed, and the portion of bone marked out by the pencil line was sawn out. The steel plates were then fitted to the portion of bone so removed, and firmly fixed by wires. I could thus quite accurately replace the removed piece of bone, by putting the ends of the steel plates into the parts of the saw-draughts remaining on the part of the skull outside the pencil line. The removed piece of bone, containing the internal ear, was then immersed in a bath of fusible metal, and placed under the receiver of an air-pump. On exhausting, air came out of all the cavities in the bone, and on air being again admitted to the receiver, fusible metal was, by atmospheric pressure, forced into these cavities. This operation was repeated, with the bone in different positions, until all the air was hunted out of the cavities and these filled with fusible metal. I now arranged clamps by means of which the piece of bone removed could be firmly retained in its original position when replaced. The external part of the removed piece of bone and the steel plates were now thickly coated with paraffin, and the part of the bone left unprotected was dissolved away by means of dilute hydrochloric acid. What now remained consisted of the steel plates, the external part of the bone, and casts, in fusible metal, of the cavities in the part of bone dissolved away. By means of a hot wire I removed the casts of the internal meatus and of the aqueducts and small tunnels originally filled by nerves and vessels ; the cast of the cochlea ought strictly to

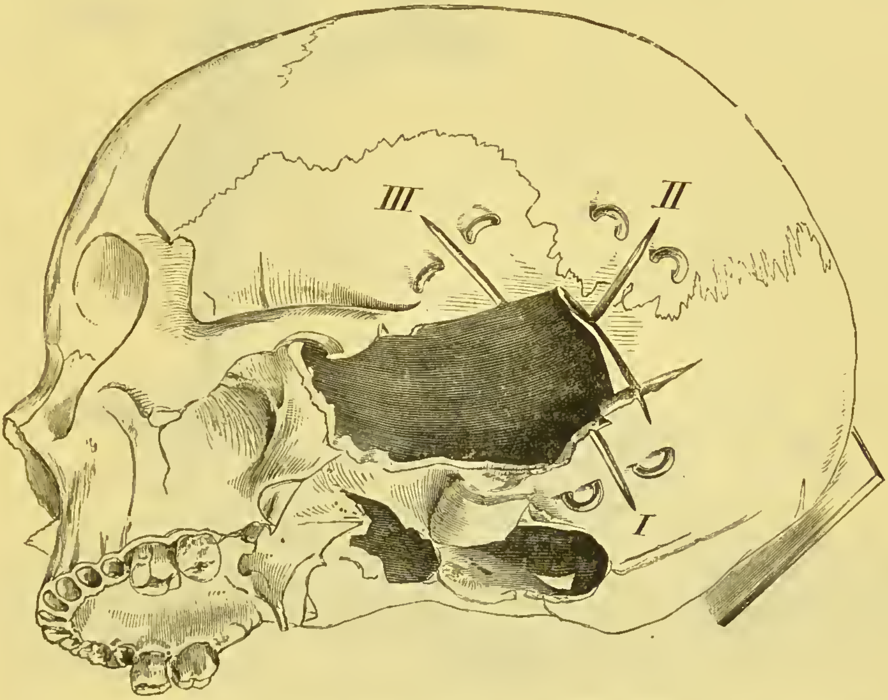

Fig. 424.—Skull showing the gap left when the bone containing the internal ear had been removed and the saw-draughts for the steel plates.

have been removed also, but it was so beautiful, and interfered so little with my measurement, that I allowed it to remain. I next soldered a cylindrical brass pin to the mastoid portion near the position of the external meatus (Fig. 426).

I shall now describe the apparatus used for the measurements. This is essentially a large goniometer, with a horizontal divided circle, two slide-rests at right angles to one another, and a jointed rod ending in a socket into which the pin already mentioned as soldered to the detached piece of the skull can be fitted and held securely in one position by a wire passed through a hole drilled through a socket and pin (Fig. 425).

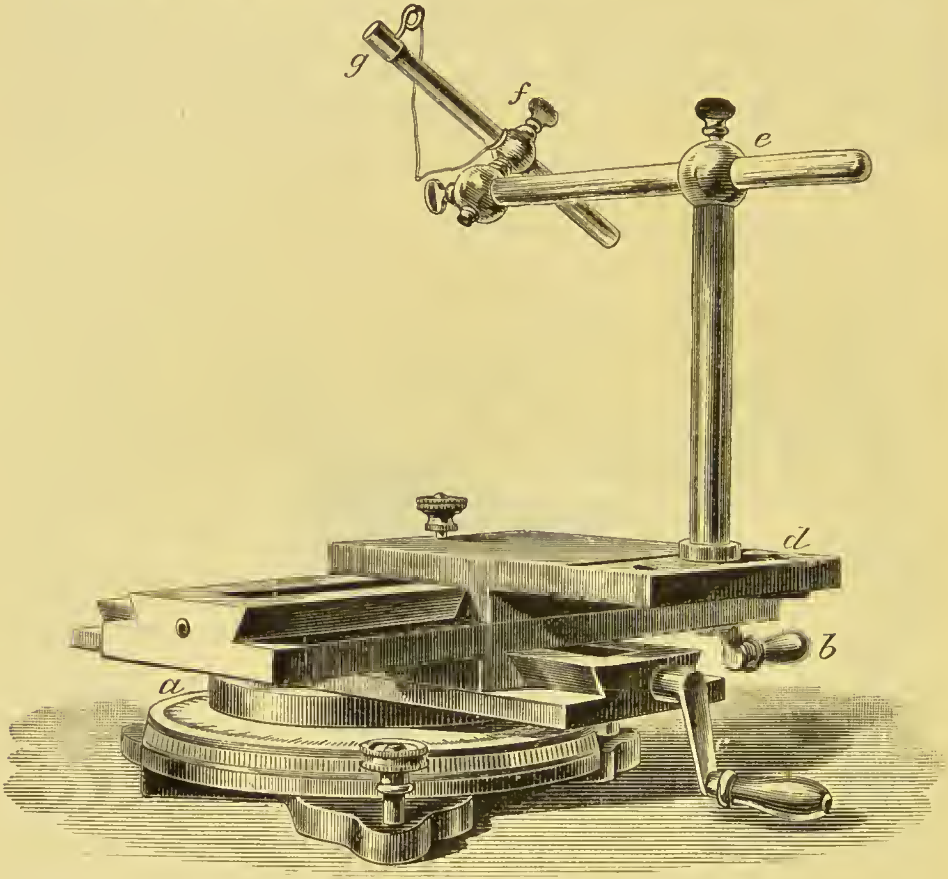

FIG. 425.—Apparatus used for making measurements.

To make a measurement, the detached piece of bone is fixed by its pin to the end of the jointed rod, and, then by moving the joints and slide-rests, brought into such a position that, 1st, the plane of one of the canals is as nearly as possible horizontal, and 2nd, the axis of rotation of the instrument passes as nearly as possible through the centre of curvature of the said canal. This is at first attained roughly by eye alone, and then more exactly by looking from some distance through a telescope while the apparatus is slowly turned round by an assistant. This position is shown for the horizontal canal in Fig. 427, H. All the joints being now screwed tight, the skull is fitted to its place on the detached piece of bone and clamped firmly; as shown in Fig. 427. A glass plate is now fastened with sealing wax to what is now the upper part of the skull, and, while it is warm, made as horizontal as possible by the help of a spirit-level. This glass plate is now sensibly parallel to the plane of the canal in question—in this case the left horizontal. The same thing is then done for the other canals. Lastly, the skull, fixed on the apparatus, is placed so that its mesial plane is horizontal; this is ascertained to be the case by turning round the apparatus and looking through the telescope, when mesial objects are seen to pass the cross wires of the telescope. A glass plate is then fixed horizontally, and therefore parallel to the mesial plane. The angles between these glass plates, and therefore the angles between the planes to which these glass plates are respectively parallel, can now be measured, either by using the apparatus as a reflecting goniometer, or by means of a carpenter's square.

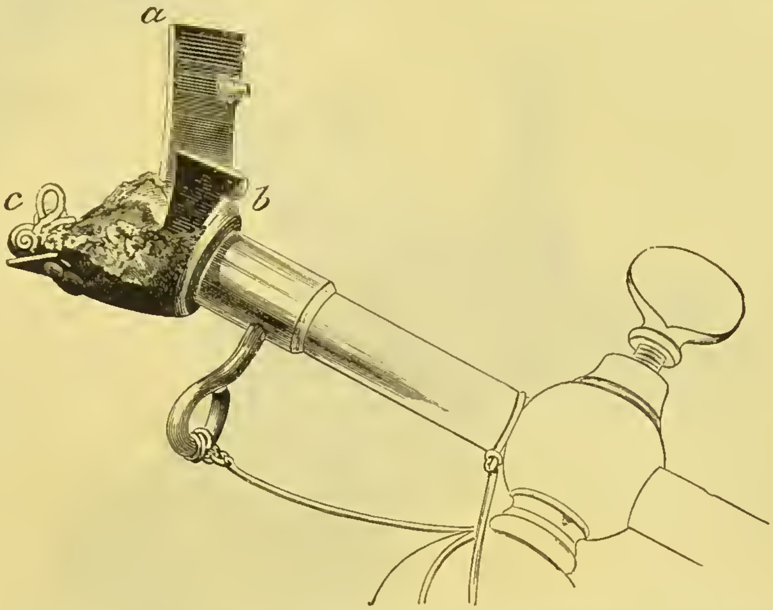

FIG. 426.—Portion of apparatus holding bone and cast of internal ear in position.

The result of Crum Brown's measurements may be briefly summarized as follows:—(1) The horizontal canal has its plane sensibly at right angles to the mesial plane, and therefore the two, right and left, horizontal canals are sensibly in the same plane. (2) The planes of the superior and posterior canals of the same side make *nearly* the same angle with the mesial plane, but the right superior and the left posterior canals are not quite parallel—the posterior making with the mesial plane a somewhat greater angle than the superior—as much as 8° more in one instance. Thus the $\substack{\text{right}\\\text{left}}$ superior canal is nearly parallel to the $\substack{\text{left}\\\text{right}}$ posterior and in each pair of approximately parallel canals the ampulla of one canal is at the one end and that of the other, at the other end.

In 1877, Cyon again re-investigated the whole question, criticised adversely the Breuer-Mach-Crum-Brown theory, and re-stated with some modifications the theory first advanced by him in 1872.[1] Certain of his experiments are irreconcilable with the dynamic theory. Thus he modified the pressure in the canals, reducing it by allowing the perilymph to escape, and by evacuating the endolymph, and increasing it by introducing small rods of dry laminaria into the canals which swelled by imbibing moisture. These variations in pressure produced no disturbance of equilibrium, as seen in Flouren's experiments. He

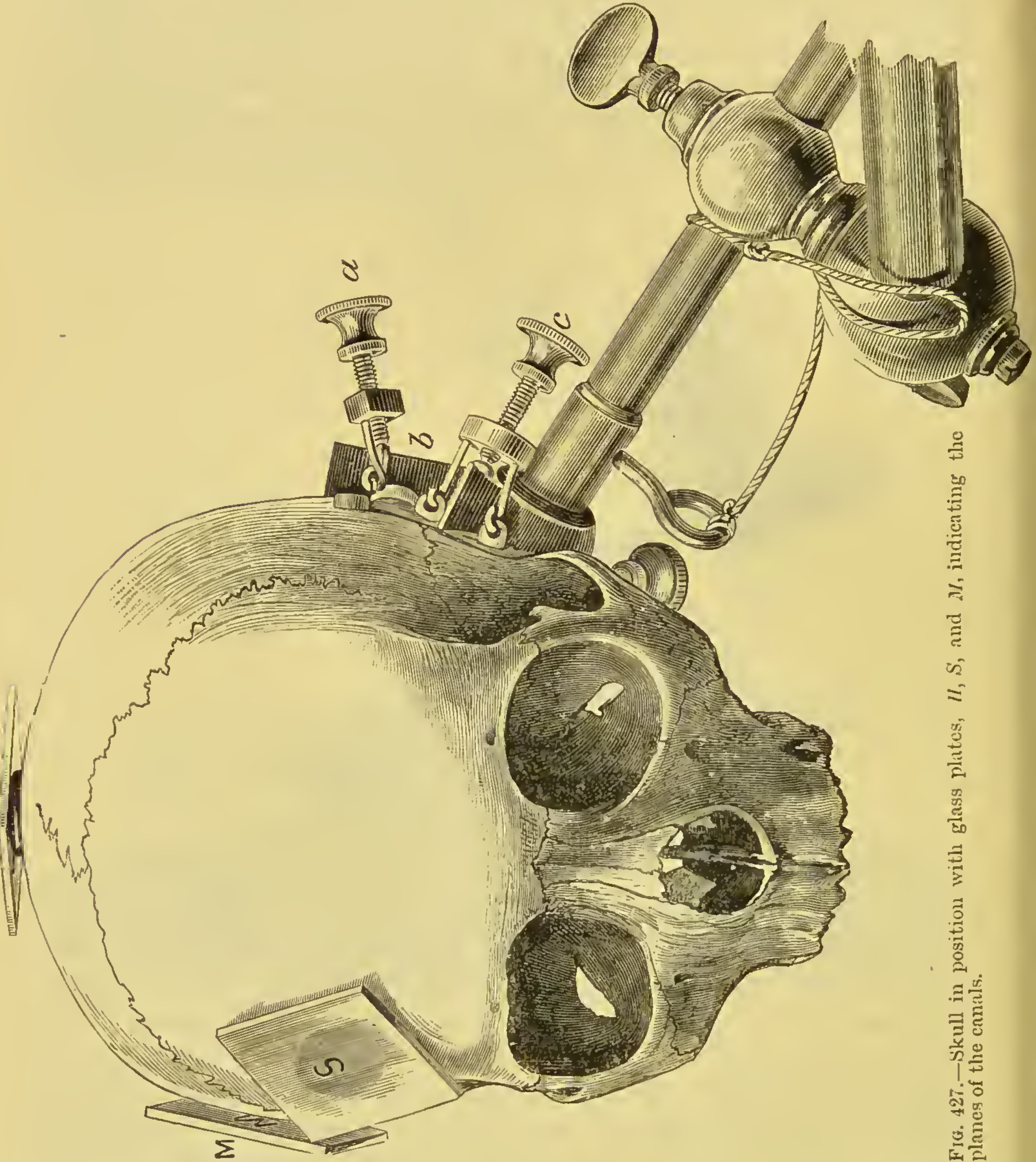

Fig. 427.—Skull in position with glass plates, *H*, *S*, and *M*, indicating the planes of the canals.

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[1] Elié de Cyon, Recherches expérimentales sur les Fonctions des Canaux semi-circulaires et sur leur Rôle dans la Formation de la Notion de l'Espace.

also divided the auditory nerve in rabbits, and states that when the animals were subjected to rotation, symptoms of vertigo came on as in normal rabbits. If this last experiment is correct, the inference is fatal to the Breuer-Mach-Crum-Brown theory, and it merits repetition. Finally, Cyon states his own theory as follows :—The semicircular canals are the peripheric organs of the sense of space ; that is to say, the sensations caused by excitation of the nervous terminations in the ampullæ form our notions of the three dimensions of space. The sensations of each canal correspond to one of these dimensions. By these sensations we form in the brain an ideal space to which we refer all those perceptions of our other senses which concern the positions of objects, and we turn the body towards these objects. The weakness of Cyon's theory is that it offers no explanation of the mechanism of the canals.

In connection with this subject, we may briefly refer to two interesting experiments, carefully described by Purkinje. 1. Stand up and rotate round a vertical axis for some minutes, and then stop. Surrounding objects appear still to move round and there may be a feeling of vertigo. The direction of the apparent motion depends on the direction of the preceding real motion, and is always opposite to it, and the axis about which the apparent motion takes place is always that line in the head which was the axis of the preceding real rotation. Bend the head forwards, rotate, and then stop. In this case the apparent motion is round a vertical axis. Bend the head forwards, rotate, stop, and then raise the head so as to look forward, and the apparent motion will take place round a horizontal axis, the horizontal axis having been vertical when the real rotation occurred, and the floor will seem to rise on one side and to fall on the other. Purkinje attributed these phenomena to rotational movements of the brain.

2. During real rotation round a vertical axis, at first the eyes move by a series of jerks, that is to say, they remain fixed for an instant, then follow the head, again they remain fixed, again move with a jerk and so on. After a little time, however, if the rotation is continued, the eye does not continue fixed for even an instant, but moves more slowly than the head, then quickly makes up to it in speed, then falls behind. At last both head and eye move together. If, then, the rotation stops, the movements of the eyeballs are renewed, and gradually become less and less until they cease. The oscillatory movements of the eyeballs are the effects of the visual vertigo. When the real rotation ceases, the person has still a sensation that his head is turning round, but he feels also that his body is at rest relatively to his head ; he sees that objects are at rest relatively to his head, and he concludes that as his head is turning round, his body, and external objects must be rotating also, and his eyes oscillate exactly as they would do if these movements were real. That these oscillations of the eyeballs may be related to irritations of the semicircular canals is rendered probable by the observation of Cyon that irritation of the canals excites oscillatory spasms from 20 to 150 per minute of the ocular muscles. The eyeballs oscillate about an axis perpendicular to the plane of the irritated canal. Oscillatory movements of the eyeballs of a similar kind may be observed in rapid railway travelling when the person looks at near objects, and

probably they form no inconsiderable part of the cause of fatigue in such circumstances.

F.—The Muscular Sense.

By the muscular sense is understood the sensation of pressure, or of resistance to pressure, produced by movements of muscles. This sensation may be either the perception of a voluntary effort being put forth to perform a certain movement, or it may be a feeling referred to various groups of muscles which are at the time in a state of movement. By means of it, we may gain information regarding the following points: (1) the *energy* of contraction; (2) the *extent* of contraction, by which we judge of precision of movement; (3) the *rapidity* of contraction; (4) the *duration* of contraction; (5) the *position* of the members and of the body. The sense of *direction* of movement is complex, being made up of notions furnished by tactile, visual, and muscular sensations. By the muscular sense, also, we have a feeling of stability or equilibrium, a sensation which plays an important part in all movements. A feeling of muscular resistance aids us in the movements of locomotion, and in those adjustments of muscular effort which have to be made in delicate manipulations. We are aided by what may be termed a "guiding sensation." This may be derived from visual impressions or from muscular sensations, or from both combined. When the muscular sense is paralysed, as in *locomotor ataxia*, the patient guides his movements by looking at his feet, and when his attention is diverted, by causing him to look at something else, his gait becomes unsteady, or he may totter and fall (see p. 500).

The sensory nerves distributed to the muscles carry impressions to the nerve centres, and excite sensations of muscular resistance. By the muscular sense, Weber was able to distinguish weights—having the ratio of 39 : 40, while the sense of pressure *on the skin* enabled him to discriminate those having a ratio of 29 : 30. To account for the phenomena of the muscular sense, three theories have been advanced: (1) that we judge of the state of the muscles by the amount of effort necessary to cause a certain amount of contraction, that is, we perceive the intention or volition and not the phenomena following these; (2) that what we term *muscular sensations* are due to the excitation of nerves in the skin or membranes, serous or mucous, covering the muscles; and (3) that there are special sensory nerves distributed to the muscles which convey impressions directly to the nerve centres. The latter view is the one most generally adopted.

G.—SLEEP, DREAMS, SOMNAMBULISM, ETC.

Like other organs, the brain manifests periodicity of function, so that we have the two states of wakefulness and sleep. The desire for sleep comes on at more or less regular intervals, and is accompanied by many sensations which scarcely even require enumeration: the heaviness of the eyes—in other words, the muscular sensations referable to the *levator palpebræ superioris*; the sensations referred to the muscles of the throat which precede a yawn; the heaviness of the head and of the limbs, and the apparently enfeebled effect of sensory impressions. Then ensues a more or less unconscious state, which affects to a certain degree all the other functions. Thus, the pulse is slower, the respiratory movements fewer in number and more profound, the amount of carbonic acid eliminated is diminished, and digestion goes on more slowly. This state continues for several hours, or perhaps only for a few minutes; but, whether of long or short duration, the period of its access and the period of its disappearance have the same psychological characters, namely, lessened acuteness to sensory perception, a confusion of ideas, and a loss of mental control.

The physiological cause of sleep cannot at present be stated. So far as one can judge from observations made during sleep on the surface of the brain and on the retinal expansion, there appears to be a state of cerebral anæmia, that is, less blood is found in the vessels. No hypothesis at present advanced explains all the phenomena of sleep.

Dreams are indications of partial cerebral activity. During profound sleep there are no dreams; they occur when slumber is light, and consequently they are more apt to happen during the time when the person passes from profound sleep to wakefulness. In dreaming, the ideas are under no control; old sensations crowd upon the mind in confusion and unconnected; notions of time and space are vague or entirely absent; in our supposed actions, we are guided by transient impulses, without definite moral notions, so that when we awake there is a feeling of relief that it was all a dream. If we watch a dreamer, he may be seen to move his lips or even to utter sounds, or to toss his arms to and fro—actions indicating the influence of his partially active cerebral centres. Here is the transitional step from dreaming to *somnambulism*. In some persons, the ideas of the dream become so intense and definite as to result in movements of locomotion. The walking dreamer may then perform very definite movements: he may be regarded as acting his dream. In such circumstances, he may be influenced by suggestions from without. By a word whispered into his ear in the tones of a well-known voice, if the suggestion coincide with the train of ideas in the dream, the dreamer may be led to another line of conduct.

During sleep which is not profound, the current of the dream may be affected by many kinds of bodily states. Those coming from the digestive organs may give rise to a feeling of intense oppression, referred to the chest, and usually associated with dreaming of a horrible character—a state known as *nightmare.*[1]

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[1] See articles "Sleep and Magnetism (Animal)," by the Author, in the *Encyclopædia Britannica*, 9th ed.

SECTION XIII.

VOICE.

The voice is produced by the vibrations of the vocal cords, two ligaments or bands of fibrous elastic tissue situated in the larynx. It is to be distinguished from speech, which is the production of sounds intended to express ideas. Many of the lower animals have voice, but none has the power of speech in the sense in which man possesses that faculty. There may be speech without voice, as in whispering, while in singing a scale of musical tones we have voice without speech.

The organ of voice, the larynx, is situated in man in the upper and fore part of the neck, where it forms a well-known prominence in the middle line. It opens below into the trachea or windpipe, and above into the cavity of the pharynx, and it consists of a framework of cartilages, connected by elastic membranes or ligaments, two of which constitute the true vocal cords. These cartilages are movable on each other by the action of various muscles, which thus regulate the position and the tension of the vocal cords. The trachea conveys the blast of air from the lungs during expiration, and the whole apparatus may be compared to an acoustical contrivance in which the lungs represent the wind chest and the trachea the tube passing from the wind chest to the sounding body contained in the larynx. Suppose two tight bands of

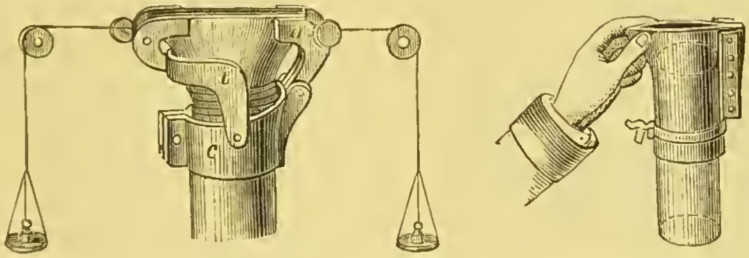

FIG. 428.—To the right, a simple artificial larynx is shown, consisting of two pieces of india-rubber tied firmly round the end of a tube. On stretching the upper orifice with the hand and blowing through the tube, sounds of various pitch may be produced. A more complicated apparatus devised by Müller, is shown to the left. *c*, a ring of metal, representing the cricoid cartilage; *t*, a movable piece of brass, representing the thyroid. The cords, or margins of the india-rubber membrane may be rendered more or less tense by weights.

any elastic membrane, such as thin sheet india-rubber, stretched over the end of a wide glass tube, so as to leave a narrow chink between the free borders of the membrane, and that a powerful blast of air is driven through the tube by a bellows. The pressure would so distend the margins of the membrane as to open the aperture and allow the air to escape; this would cause a fall of pressure and the edges of the membrane would spring back by their elasticity to their former position; again the pressure would increase, and again the edges of the membrane would be distended; and these actions would be so quickly repeated as to cause the edges of the membrane to vibrate with sufficient rapidity to produce a musical tone, the pitch of which would depend on the number of vibrations executed in a second of time. The condensation and rarefaction of the air thus produced are the chief cause of the tone, as Von Helmholtz has pointed out, and in this way the larynx resembles the syren in its mode of producing tone. It is evident also that the intensity or loudness of the tone would be determined by the amplitude of the vibrations of the margins of the membrane, and that its pitch would be affected by any arrangements causing an increase or decrease of the tension of the margins of the membrane. The pitch

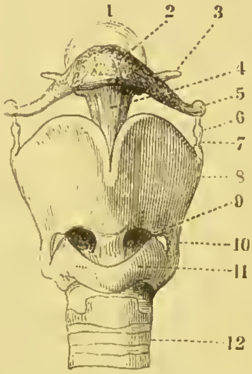

Fig. 429. — Cartilages and ligaments of the larynx seen from the front; half natural size. 1, epiglottis; 2, hyoid bone; 3, small cornu of hyoid bone; 6, small nodules of cartilage (cartilago triticea); 7, lateral thyro-hyoid ligament; 8, left lamina or wing of thyroid cartilage; 9, cricoid cartilage; 10, lower cornu of thyroid cartilage; 11, part of cricoid united to the thyroid by the middle crico-thyroid ligament; 12, second ring of trachea. (Krause.)

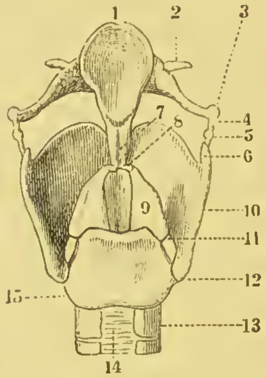

Fig. 430.—Cartilages and ligaments of larynx seen from behind; half natural size. 1, epiglottis; 2, lesser cornu of hyoid bone; 3, greater cornu of hyoid; 4, lateral thyro-hyoid ligament; 5, cartilago triticea; 6, upper cornu of thyroid; 7, thyro-epiglottic ligament; 8, cartilages of Santorini; 9, arytenoid cartilages; 10, right lamina of thyroid; 11, external process of arytenoid cartilage; 12, inferior cornu of thyroid; 13, first ring of trachea; 14, posterior membranous wall of trachea; 15, lamina of cricoid cartilage. (Krause.)

might also be raised by the strength of the current of air, because the greater amplitude of the vibrations would increase the mean tension of the elastic membrane. With tones of medium pitch, the pressure of the air in the trachea is equal to that of a column of mercury of 160 mm.; with high pitch 920 mm.; and with tones of very high pitch 945 mm.; whilst in whispering it may fall as low as that represented by 30 mm. of water. Such is a general conception of the mechanism of voice.

The cartilages forming the framework of the larynx are shown in Figs. 429 and 430.

The cartilages are connected by ligaments, some of which are seen in Figs. 429 and 430, whilst the remainder are represented in Fig. 431. The ligaments specially concerned in the production of voice are the inferior thyro-arytenoid ligaments, or true vocal cords. These are composed of fine elastic fibres attached behind to the anterior projection of the base of the arytenoid cartilages, *processus vocalis* (3 in Fig. 431), and in front to the middle of the angle between the wings or laminæ of the thyroid cartilage. They are practically continuous with the lateral crico-thyroid ligaments (6 in Fig. 431).

The cavity of the larynx is divided into an upper and lower portion by the narrow aperture of the glottis between the true vocal cords, called the *rima glottidis*. Immediately above the true vocal cords, between these and the false vocal cords, there is a recess or pouch termed the *ventricle of Morgagni*, and opening from each ventricle there is a still smaller recess, *the laryngeal pouch*, which passes for the space of half an inch between the superior vocal cords inside and the thyroid cartilage outside, reaching as high as the upper border of that cartilage at the side of the epiglottis. The ventricles permit a free vibration of the true vocal cords. They are of immense size in howling monkeys (*Mycetes*), and in the orang, chimpanzee, and gorilla, acting here as resonating cavities and strengthening the voice. The horse has large resonating cavities.

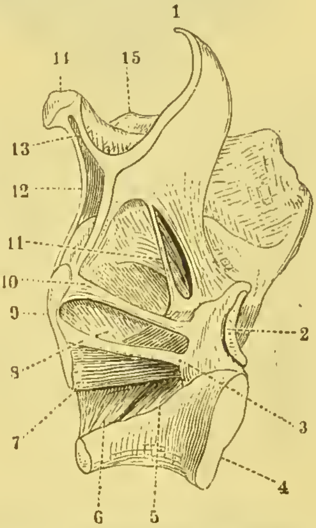

Fig. 431.—Right half of the larynx, from a vertical and slightly oblique section; two-thirds natural size. 1, epiglottis; 2, arytenoid cartilage; 3, processus vocalis of arytenoid; 4, cricoid cartilage; 5, crico-thyroid membrane; 6, lateral crico-thyroid ligament; 7, anterior crico-thyroid ligament; 8, inferior thyro-arytenoid ligament, or true vocal cord; 9, thyroid cartilage; 10, superior thyro-arytenoid ligament; 11, thyro-ary-epiglottideus muscle; 12, middle thyro-hyoid ligament; 13, hyo-epiglottic ligament; 14, body of hyoid bone; 15, smaller cornu of hyoid bone. (Krause.)

The upper aperture of the glottis is triangular, wide in front and narrow behind; and when seen from above by means of the laryngoscope it presents the view represented in Fig. 432. The aperture is bounded in front by the epiglottis, *e*, behind by the summits of the arytenoid cartilages, *ar*, and on the sides by two folds of mucous membrane, the aryteno-epiglottic folds, *ae*. The rounded elevations corresponding to the *cornicula laryngis* and cuniform cartilages, *c*, and also the cushion of the epiglottis, *e*, are readily seen in the laryngoscopic picture. The glottis, *o*, is seen in the form of a long narrow fissure, bounded by the true vocal cords, *ti*, whilst above them we have the false vocal cords, *ts*, and between the true and false vocal cords the opening of the ventricle, *v*. The *rima glottidis*, between the true vocal cords, in the adult male measures about 23 mm., or nearly an inch from before backwards, and from 6 to 12 mm. across its widest part, according to the degree of dilatation. In females and in males before puberty the antero-posterior diameter is about 17 mm., and its transverse diameter about 4 mm. The vocal cords of the adult male are in length about 15 mm., and of the adult female about 11 mm.

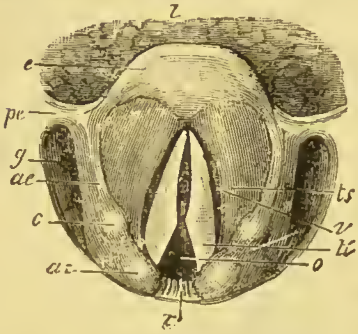

FIG. 432.—Laryngoscopic view of the glottis. *l*, tongue; *e*, epiglottis; *pe*, pharyngo-epiglottic fold; *c*, cuniform cartilage or cartilage of Wrisberg; *ar*, arytenoid cartilage; *r*, inter-arytenoid fold; *o*, glottis; *v*, ventricle; *ti*, inferior or true vocal cord; *ts*, superior or false vocal cord. (Mandl.)

The larynx is lined with a layer of epithelium which is closely adherent to underlying structures, more especially over the true vocal cords. The cells of the epithelium in the greater portion of the larynx, are of the columnar ciliated variety, and by the vibratory action of the cilia mucus is driven upwards, but over the true vocal cords the epithelium is squamous. Patches of squamous epithelium are also found on the ciliated tract above the glottis, on the under surface of the epiglottis, on the inner surface of the arytenoid cartilages, and on the free border of the upper or false cords. Numerous mucous glands exist in the lining membrane of the larynx, more especially in the epiglottis. In each laryngeal pouch there are sixty to seventy such glands, surrounded by adipose tissue.

We are now in a position to understand the action of the muscles of the larynx by which the vocal cords, forming the *rima glottidis*, can be tightened or relaxed, and by which they can be approximated or separated. Besides certain extrinsic muscles—sterno-hyoid, omo-hyoid, sterno-thyroid, and thyro-hyoid—which move the larynx as a whole, there are intrinsic muscles which move the cartilages on each other. Some of these are seen in Fig. 433. These muscles are (*a*) the crico-thyroid, (*b*) the posterior crico-arytenoid, (*c*) the lateral crico-arytenoid, (*d*) the thyro-arytenoid, (*e*) the arytenoid, and (*f*) aryteno-epiglottidean. Their actions will be readily understood with the aid of the diagrams in Fig. 434. (1) The crico-thyroid is a short thick triangular muscle, its fibres passing from the cricoid cartilage obliquely upwards and outwards to be inserted into the lower border of the thyroid cartilage and to the outer border of its lower horn. When the muscle contracts the cricoid and thyroid cartilages are approximated. In this action, however, it is not the thyroid that is depressed on the cricoid, as is generally stated, but, the thyroid being fixed in position by the action of the intrinsic muscles, the anterior border of the cricoid is drawn upwards, whilst its posterior border, in consequence of a revolution around the axis uniting the articulations between the lower cornua of the cricoid and the thyroid, is depressed, carrying the arytenoid cartilages along with it. Thus the vocal cords are stretched. (2) The thyro-arytenoid has been divided by anatomists into two parts—one, the internal, lying close to the true vocal cord, and the other, external, immediately within the ala of the thyroid cartilage. Many of the fibres of the anterior portion pass from the thyroid cartilage with a slight curve (concavity inwards) to the *processus vocalis* at the base of the arytenoid cartilage. They are thus parallel with the true vocal cord, and when they contract the arytenoids are drawn forwards, carrying with them the posterior part of the cricoid and relaxing the vocal cords. Thus the thyro-arytenoids are the antagonists of the crico-thyroids. Ludwig has pointed out that certain fibres (*portio-ary-vocalis*) arise from the side of the cord itself and pass obliquely back to the *processus vocalis*. These will tighten the parts of the cord in front and relax the parts behind their points of attachment. Some of the fibres of the outer portion run obliquely upwards from the side of the crico-thyroid membrane, pass through the antero-posterior fibres of the inner portion of the muscle, and finally

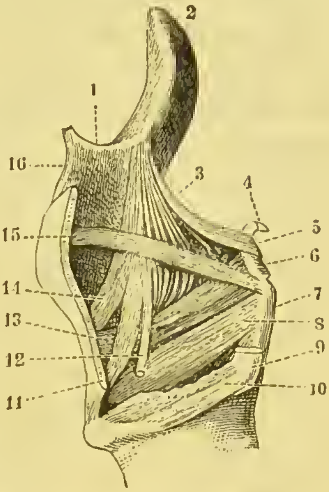

FIG. 433.—Muscles of the left side of the larynx seen from within; two-thirds natural size. 1, hyo-epiglottic ligament seen in profile; 2, epiglottis; 3, aryteno-epiglottic muscle; 4, Santorini's cartilage; 5, oblique arytenoid muscle; 6, transverse arytenoid muscle seen in profile; 7, posterior crico-arytenoid; 8, lateral crico-arytenoid; 9, lower cornu of thyroid cartilage cut through; 10, insertion of posterior portion of crico-thyroid muscle; 11, left lamina of thyroid cartilage cut through; 12, long thyro-epiglottic muscle (a variety); 13, inferior thyro-arytenoid; 14, thyro-epiglottic; 15, superior thyro-arytenoid; 16, median thyro-hyoid ligament. (Krause.)

end in the tissue of the false cord. These fibres have been supposed to render the edge of the cord more prominent. Other fibres inserted into the *processus vocalis* will rotate the arytenoid slightly outwards, whilst a few passing up into the aryteno-epiglottidean folds may assist in depressing the epiglottis. (3) The posterior and lateral crico-arytenoid muscles have antagonistic actions, and may be considered together. The posterior arise from the posterior surface of the cricoid cartilage, and, passing upwards and outwards, are attached to the outer angle of the base of the arytenoid. On the other hand, the lateral arise from the upper border of the cricoid as far back as the articular surface for the arytenoid, pass backwards and upwards, and are also inserted into the outer angle of the base of the arytenoid before the attachment of the posterior crico-arytenoid. Imagine the pyramidal form of the arytenoid cartilages. To the inner angle of the triangular base are

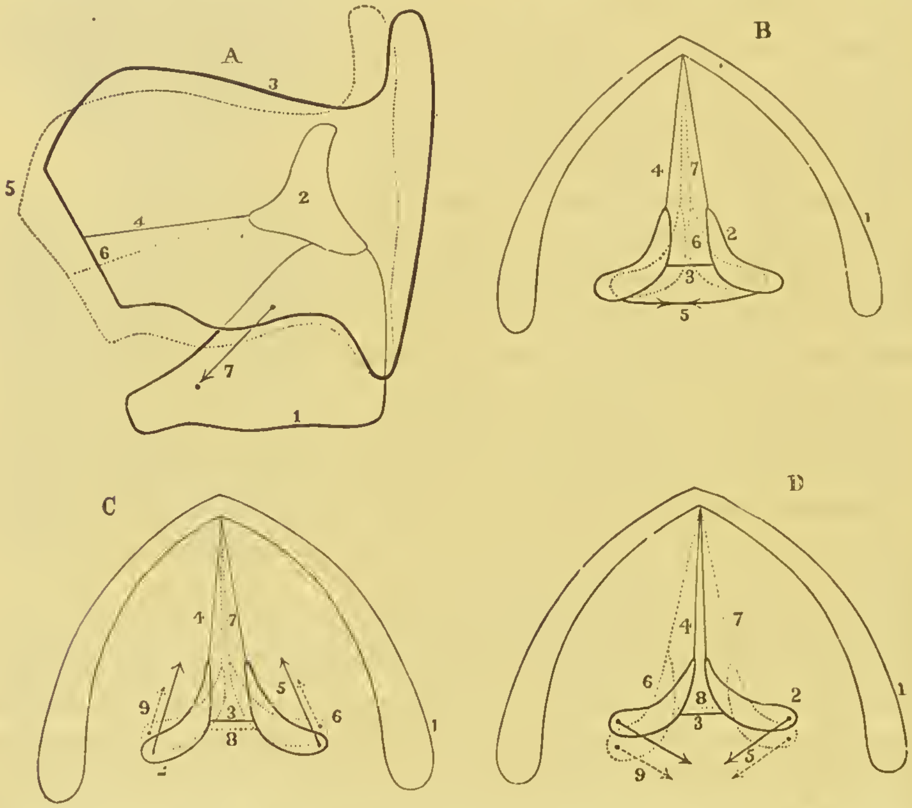

Fig. 434.—Diagrams explaining the muscles of the larynx. The dotted lines show the position taken by the cartilages and the true vocal cords by the action of the muscles, and the arrows show the general direction in which the muscular fibres act. A, action of crico-thyroid. 1, cricoid cartilage; 2, arytenoid cartilage; 3, thyroid cartilage; 4, true vocal cord; 5, thyroid cartilage, new position; 6, true vocal cord, new position. B, action of arytenoid. 1, section of thyroid; 2, arytenoid; 3, posterior border of epiglottis; 4, true vocal cord; 5, direction of muscular fibres; 6, arytenoid, new position; 7, true vocal cord, new position. C, action of lateral crico-arytenoid, same description as for A and B; 8, posterior border of epiglottis, new position; 9, arytenoid in new position. D, action of posterior crico-arytenoid, same description. (From Beaunis and Bouchard.)

attached, as already described, the true vocal cords, and to the outer angle the two muscles in question. The posterior crico-arytenoids draw the outer angles backwards and inwards, thus rotating the inner angles or *processus vocales* outwards, and when the two muscles act, widening the *rima glottidis.* This action is opposed by the lateral crico-thyroids, which draw the outer angle forwards and outwards, rotate the inner angles inwards, and thus approximate the cords. (4) The arytenoids pass from the one arytenoid cartilage to the other, and in action these cartilages will be approximated and slightly depressed. (5) The aryteno-epiglottidean muscles arise near the outer angles of the arytenoid; their fibres pass obliquely upwards, decussate, and are inserted partly into the outer and upper border of the opposite cartilage, partly into the aryteno-epiglottic fold, and partly join the fibres of the thyro-arytenoids. In action they assist in bringing the arytenoids together, whilst they also draw down the epiglottis, and constrict the upper aperture of the larynx. The vocal cords will be also relaxed by the elasticity of the parts.

1. **Physiological Characters of the Voice.**—As already stated, the intensity or loudness of voice depends on the amplitude of the movement of the vocal cords. Pitch depends on the number of vibrations per second; and the length, size, and degree of tension of the cords will determine the number of vibrations. The more tense the cords the higher the pitch, and the greater the length of the cords the lower will be the pitch. The range of the human voice is about three octaves, that is from fa_1 (87 vibrations per second) to sol_4 (768 vibrations). In men, by the development of the larynx, the cords become more elongated than in women, in the ratio of 3 to 2, so that the male voice is of lower pitch and is usually stronger. At the age of puberty the larynx grows rapidly, and the voice of a boy "breaks" in consequence of the lengthening of the cords, generally falling an octave in pitch. A similar change, but very much less in amount, occurs at the same period in the female. At puberty in the female there is an increase of about one-third in the size of the glottis, but it is nearly doubled in the male. The adult male larynx is about one-third greater than that of the female. In advanced life, the upper notes of the register are gradually weakened and ultimately disappear, whilst the character of the voice also changes, owing to loss of elasticity caused by ossification, which first begins about middle life in the thyroid cartilage, then appears in the cricoid, and much later in the arytenoid. Eunuchs retain the voice of childhood, and by careful training it is possible in normal persons to arrest the development of

the larynx, so that an adult male can still sing the soprano parts sometimes used in cathedral choirs. The ranges of the different varieties of voice are shown in the following diagram :—

FIG. 435.—Range of varieties of human voice.

A basso, named Gaspard Forster, passed from fa_{-1} to la_3; the younger of the sisters Sessi had a contralto voice from do_2 to fa_5; the voice of Catalani ranged three and a half octaves; a eunuch singer, Farinelli, passed from la_1 to re_5; Nilsson, in *Il Flauto Magico*, can take fa_5; and Mozart states that he heard in Parma, in 1770, a singer, Lucrezia Ajugari, range from sol_2 to do_6, which she gave purely, whilst she could execute trills on re_5. The latter is the most highly pitched voice referred to in musical literature, and far above the highest ordinary soprano. There is thus a range for ordinary voices of nearly two octaves, and certain rare voices may have a range of three and a half octaves.[1]

The quality of the human voice depends on the same laws that determine the quality, klang-tint, or timbre of the tones produced by any musical instrument. Musical tones are formed by the vibrations of the true vocal cords. These tones may be either pure or mixed, and in both cases they are strengthened by the resonance of the air in the air passages and in the pharyngeal and oral cavities. If mixed—that is, if the tone is compounded of a number of partials—one or more of these will be strengthened by the cavities above the cords acting as a resonator, and so strongly may these partials be thus reinforced that the fundamental tone may be obscured and a certain quality or timbre will be communicated to the ear. Further, Von Helmholtz has shown that special forms of the oral cavity reinforce, in particular, certain partials, and thus give a character to vowel tones—indeed to such an extent that each vowel tone may be said to have a fixed pitch. This may be proved by putting the mouth in a certain form, keeping

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[1] See Article, "Voice," by Author, in *Encyclopædia Britannica*, 9th ed.

the lips open, and bringing various tuning forks sounding feebly in front of the opening. When a fork is found to which the resonant cavity of the mouth corresponds then the tone of the fork is intensified, and by thus altering the form and capacity of the oral cavity its pitch in various conditions may be determined. Thus, according to Von Helmholtz, the pitch corresponding to the vowels may be expressed—

Vowels,	OU	O	A	AI	E	I	EU	U
Tone,	*fa*$_2$	*si*♭$_3$	*si*♭$_4$	*sol*$_5$ or *re*$_4$	*si*♭$_5$ or *fa*$_3$	*re*$_6$ or *fa*$_2$	*do*$_5$ or *fa*$_3$	*sol*$_5$ or *fa*$_2$
No. of Vibs.,	170	470,	940,	1536, or 576,	1920, or 341,	2304, or 170,	1024, or 341,	1536 or 170.

FIG. 436.—Pitch of vowel-sounds according to Von Helmholtz.

König has fixed the pitch of the vowels differently, thus—

Vowels,	OU	O	A	E	I
Tone,	*si*♭$_2$	*si*♭$_3$	*si*♭$_4$	*si*♭$_5$	*si*♭$_6$
No. of Vibs.,	235,	470,	940,	1880,	3760.

FIG. 437.—Pitch of vowel-sounds according to König.

Donders has given a third result differing from each of the above, and there is little doubt that much will depend on the quality of tone peculiar to different nationalities. By means of König's manometric flames with revolving mirror, the varying quality of tone may be illustrated; with a pure tone, the teeth in the flame-picture are equal, like the serrations of a saw, whilst usually the tone is mixed with partials which show themselves by the unequal serrations. It is thus certain that quality of voice depends not merely on the size, degree of elasticity, and general mobility of the vocal cords, but also on the form of the resonating cavities above, and there can be no doubt that very slight differences in these may produce striking results.

The quality of vowel tones may be illustrated with the aid of an apparatus devised by König, shown in Fig. 438.

It consists of a little capsule, *d*, divided by a thin india-rubber membrane. On one side of the membrane there is gas, led out to a small burner, and on the other there is a wide tube, terminating in a mouthpiece. On speaking or singing the vowels into the latter, a characteristic flame-picture will be obtained for each vowel, and even for the same vowel at a different pitch. The flame-picture of a pure tone consists of equal segments, whilst two or more tones acting on the *same* flame produce an irregular picture. This may be illustrated by causing two organ pipes, with the apparatus shown in Fig. 438, to act on the same flame. The following diagram shows the form of the flames which characterize the vowels A, O, OU, sung at the pitch of ut_1, sol_1, ut_2. Thus the harmonics produced in the larynx are strengthened or reinforced by the proper tone of the oral cavity for a particular vowel; and, consequently, quality of vowel-sound depends chiefly on the form of the oral cavity. The following points may be noted in an analysis of vowel-tones:—(1) The vowels U and O are not so rich in overtones as E and I; (2) to sound U the oral cavity is usually like a round bottle without a neck, opening widely into the pharynx and narrowly between the lips. The smaller the opening of the lips the deeper is the fundamental tone. (3) If the opening of the lips widens, U becomes O, and if the lips are opened still wider, O becomes A; (4) in A the larynx rises and the tongue lies flat. In sounding E and I there is a large space above the larynx by

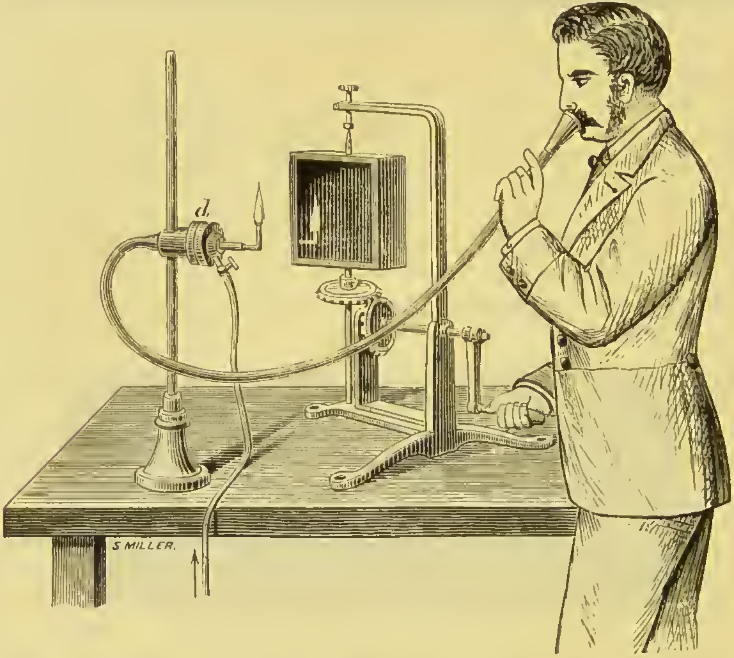

FIG. 438.—König's apparatus for illustrating the quality of vowel-tones by a manometric flame.

the posterior part of the tongue being lifted forwards. In I, this space is very large, so that the mouth is like a bottle, the body of the bottle being the space above the larynx, while the neck is the narrow space between the tongue and the hard palate. In sounding vowels, the nasal cavity is shut by raising the soft palate, as in swallowing. If defects of the soft palate exist, or if there is paralysis of the muscles of the palate, as may follow diphtheria, the vowel sounds are nasal in quality, and we have snuffled speech. In sounding I, the *velum palati* shuts off all communication with the nose, but with A some air always escapes into the nose, so that A is slightly nasal.

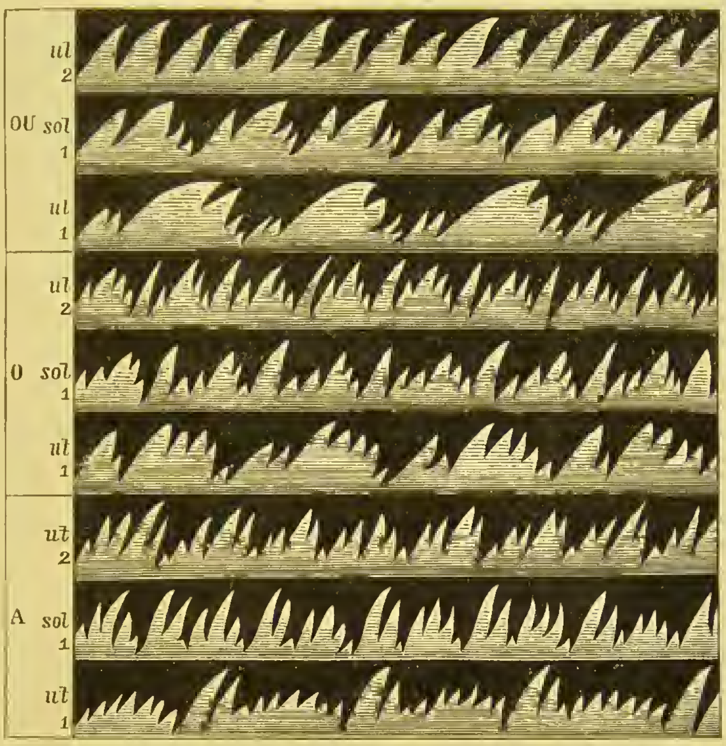

FIG. 439.—Flame-pictures of the vowels OU, O, and A, showing their different quality. (König.)

2. Condition of the Larynx in the Various Registers.—

In singing, the tone may appear to come chiefly from the chest, from the throat, or from the head, or it may show the peculiar quality of tone termed falsetto. Authorities differ much in the nomenclature applied to these varieties of the voice. Thus the old Italian music masters spoke of the *voce di petto*, *voce di gola*, and *voce di testa*. Madame Seiler describes five conditions, namely, the first series of tones of the chest register, the second series of tones of the chest register, the first series of tones of the falsetto register, the second series of tones of the falsetto register, and the head register. French writers usually refer to two registers only, the chest and the head; whilst Behnke gives three registers for male voices (lower thick, upper thick, and upper thin), and five for the voices of women and children (lower thick, upper thick, lower thin, upper thin, and small). These distinctions are of more importance practically than as implying any marked physiological differences in the mechanism of the larynx during the production of the tones in the different registers.

By means of the laryngoscope, it is possible to see the condition of the *rima glottidis* and the cords in passing through all the range of the voice. The laryngoscope is a small mirror about the diameter of a shilling, fixed to the end of a long handle at an angle of 125° to 130°. This mirror is gently pushed towards the back of the throat, and if sufficient light is thrown into the mouth from a lamp, and if the eye of the observer is in the proper position, by angling the small mirror it is not difficult to get a view of the glottis. The light from the lamp is reflected by the mirror down on the glottis, from this it is reflected back to the mirror, and then from the mirror it is finally reflected to the eye of the observer. Usually the observer has in front of his eye a mirror by which a powerful beam of light can be thrown from a lamp into the mouth and throat. In the centre of the mirror there is a small hole through which the eye of the observer sees the image in the small mirror at the back of the throat. By placing a second plane mirror in front of the face, an observer can easily study the mechanism of his own larynx. (See Fig. 350, p. 624.)

Suppose the picture of the larynx to be examined in the small mirror at the back of the throat, an image will be seen as in Fig. 440. During calm breathing the glottis is lance-shaped between the yellowish white cords. A deep inspiration causes the glottis to open widely, and in favourable circumstances one may look into the trachea (Fig. 444).

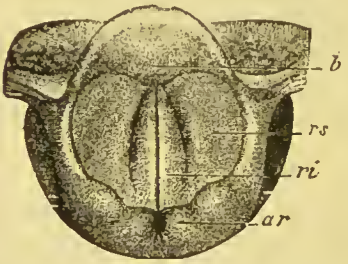

Fig. 440.—Arrangement of glottis previous to emission of a sound. *b*, epiglottis; *rs*, false cord; *ri*, true cord; *ar*, arytenoid cartilages.

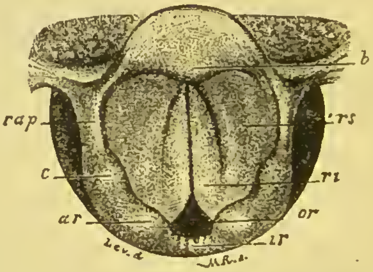

Fig. 441.—Closure of the ligamentous portion of glottis. *b*, epiglottis; *rs*, false cord; *ri*, true vocal cord; *ar*, space between arytenoids; *ar*, arytenoid cartilages; *c*, cuniform cartilages; *rap*, ary-epiglottic fold; *ir*, inter-arytenoid fold. (Mandl.)

When a sound is to be made, the vocal cords are brought close together, either along their whole length, as in Fig. 442, or only along the ligamentous portion, the space between the arytenoids being still open, as in Fig. 441. Thus, when the sound begins, the glottis opens (Fig. 443), the form of the opening influencing the kind of voice, whilst the degree of tension of the cords will determine the pitch.

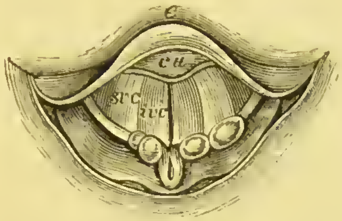

FIG. 442.—View of glottis with true cords. *ivc*, close together; *svc*, false cords; *ca*, base of epiglottis; *e*, fold above epiglottis.

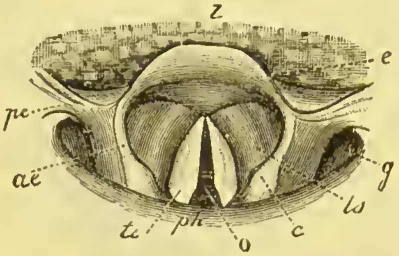

FIG. 443.—Closure of the glottis. *l*, tongue; *e*, epiglottis; *pe*, pharyngo-epiglottic fold; *g*, pharyngo-laryngeal groove; *ae*, ary-epiglottic fold; *c*, cuniform cartilage; *ar*, arytenoid cartilage; *r*, inter-arytenoid fold; *o*, glottis; *v*, ventricle; *ti*, inferior vocal cord; *ts*, superior vocal cord. (Mandl.)

During inspiration the edges of the true vocal cords may occasionally be close together, as in sobbing. It has been pointed out by various observers that during inspiration the false cords are easily separated, even when they touch, and during expiration, owing to dilatation of the ventricles, they come together and may readily close. Wyllie showed, in 1865, that the false vocal cords play the chief part in closure of the glottis during expiration.[1] Lauder Brunton and Cash have confirmed Wyllie's results, and have shown further that the function of the false cords is to close the glottis, and thus fix the thorax for muscular effort; and they adduce many facts from comparative anatomy in favour of this view, these cords being strongly developed in those animals whose habits render fixation serviceable, whilst, on the other hand, they are absent or weakly developed in animals where fixation is of little or no service.[2]

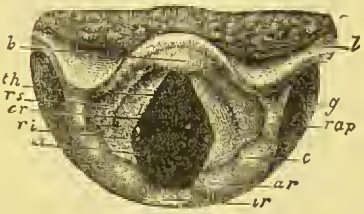

FIG. 444.—View of glottis widely opened. Same description as for Fig. 441.

During the production of the chest voice, the space between the arytenoid cartilages is open, and between the vocal cords there is an ellipsoidal opening which gradually closes as the pitch of the sound rises (see Figs. 445, 446, 447). During head voice the opening between the arytenoid cartilages is completely closed; the portion between the vocal cords is

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[1] J. Wyllie. *Edin. Med. Jour.* 1866.

[2] T. Lauder Brunton and T. Cash. *Jour. Anat. and Physiol.* vol. xvii.

open, but in place of being almost a narrow slit as in chest voice, it is wide open so as to allow an escape of more air (see Fig. 447). The condition of the cords during falsetto is, according to Müller, one in which the cords can only vibrate at their margins, and especially in the middle, in consequence of the false cords pressing downwards upon them. Oertel, on the other hand, states that in falsetto the cords vibrate throughout their length, but that they form nodal lines parallel to the free borders of the loops or bellies of vibration. Probably, in these circumstances, the membranes become much thinner. Oertel also found that during the falsetto voice the epiglottis became erect, the apices of the arytenoids were directed backwards, and the whole larynx became narrower but longer from before backwards. Behnke says that, in the production of the "small register," the mechanism "consists in the formation of an oval orifice in the front part of the glottis which contracts the more the higher the voice ascends, the vocal ligaments being, in the hinder part, pressed together so tightly that scarcely any trace of a slit remains."[1] Illingworth is of opinion that falsetto (and even the ordinary voice) is produced in the "same way as the mouth is used in whistling."[2] This view may be true to some extent as regards falsetto, but it will not hold good for the ordinary voice.

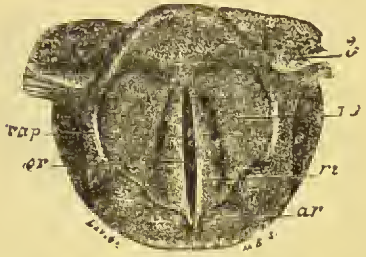

Fig. 445.—Chest voice deep tone. *b*, epiglottis; *or*, glottis; *rs*, false vocal cord; *ri*, true vocal cord; *rap*, ary-epiglottidean fold; *ar*, arytenoid cartilages. (Mandl.)

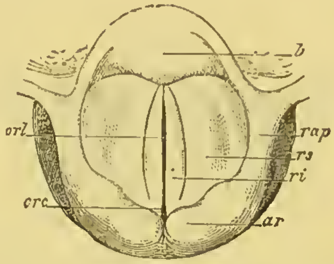

Fig. 446.—Chest voice, high tone. Description as in Fig. 441. (Mandl.)

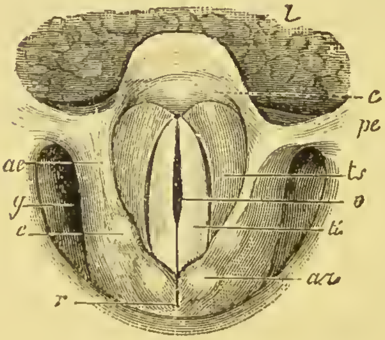

Fig. 447.—Head voice, deep tones. *l*, tongue; *e*, epiglottis; *pe*, pharyngo-epiglottidean folds; *ae*, ary-epiglottic folds; *ts*, false cords; *ti*, true vocal cords; *g*, pharyngo-laryngeal groove; *ar*, arytenoid cartilages; *c*, cuniform cartilages; *o*, glottis; *r*, inter-arytenoid folds. (Mandl.)

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[1] Lennox Brown and Behnke on "Voice," etc.

[2] Illingworth. See *Edin. Med. Jour.* 1876.

Voice sounds are subject to many modifications. *Sobbing* consists of short, broken, quickly following inspirations, caused by spasmodic actions of the diaphragm; the vocal cords vibrate, but not strongly. *Sighing* is a deep inspiration by which the air produces a sound in the oral cavity without the cords coming into action. *Yawning* is caused by a deep, slow inspiration, with a convulsive movement of the muscles of the face, followed by a sudden expiration, causing an oral and pharyngeal sound. *Laughing* consists of short sudden expirations, in which the vocal cords also vibrate. *Snoring* occurs when the curtain of the soft palate vibrates. *Coughing* and *Sneezing* are powerful expirations in which the air is driven through the oral cavity in the first, and through the nasal passages in the second. Mammals produce a great variety of sounds. Many monkeys and the anthropoid apes have deep resonant voices from the development of the ventricles of Morgagni. Large quadrupeds produce strong chest notes with short expirations and an extended neck and open mouth. The pitch of animals' voices varies much. Thus we have the deep grunt or shrill cry of the pig, the purring and mewing of cats, while dogs can bark, growl, moan, howl, or cry. In neighing, the horse produces the sound by expiration, but inspiration and expiration both come into play in the bray of an ass. Whales have no vocal cords, and they are dumb. (Munk.)

3. **Physiological Characters of Consonants.**—It may be said generally that consonants are sounds formed in the buccal cavity, and strengthened by the laryngeal sound, but the initial consonants P, T, and M, N, and NG, are not so formed. There appear to be three special regions of articulation: (1) *Guttural*, from the neighbourhood of the soft palate and base of the tongue; (2) *Lingual*, from the neighbourhood of the superior dental arch, the anterior part of the hard palate, and the tongue; and (3) *Labial*, from the lips. The different consonant sounds may be produced as follows: (1) The oral tube is contracted in the guttural, lingual, or labial regions, and at the same time the air is expelled—thus, *gutturals*, CH and J; *linguals*, S, SCH; and *labials*, V and F; (2) there is complete and instantaneous closure in the region of articulation, the sound being produced either before the moment of closure, as *a*B, or at the moment of opening, B*a*—such are *gutturals*, G, K; *linguals*, D, T; and *labials*, B, P; G, D, and B may also be sounded after the closure and before they are separated on opening them; (3) there is a kind of vibratory movement given to the articulating region, such as the guttural or lingual R; and (4) the consonant sound acquires a *nasal* quality, from part of the breath passing into the nasal passages, which it does not do in the three preceding cases—such are the *guttural* nasal sounds NG, the *lingual* N, and the *labial* M. In the English language, CH and J are not gutturals but linguals. There are three modes of trilling R; the first and second are both lingual, and the third is uvular. The first mode is caused by a vibration of the tip of the tongue (initial R) and the second by vibrating the

dorsal part of the tongue (final R). The combination NG is a simple sound and its vocal cognate J is also simple. The sound of H is caused by the air escaping through a narrowed glottis and a snapping movement of the jaws. These facts are shortly classified in the following table :—

Varieties of Consonants.			Regions of Articulation.		
			Labials.	Linguals.	Gutturals.
Continuous,	Hard,		F	S	Ch
	Soft,		V W	Sch Z	J
Explosives,	Simples,	Hard,	P	T	K
		Soft,	B	D	G
	Aspirates,	Hard,	PH	TH	KH
		Soft.	BH	DH	GH
Trilling,			R	R	R
Nasal,			M	N	NG

SECTION XIV.

ANIMAL LOCOMOTION.

MECHANISM OF THE ATTITUDES AND THE MOVEMENTS OF MAN.

1. **Static Equilibrium of the Body.**—The skeleton constitutes a firm, partly rigid, and partly movable framework of support, suitable for posture and locomotion in the erect position. The different bones, more especially those of the limbs, are moved by the muscles in directions determined by the form of the joints and the points of insertion of the muscles.

The term *posture* is applied to those states of equilibrium of the body which may be maintained for a certain time without displacement, such as standing, sitting, or lying. The essential condition of stability is, that the centre of gravity of the body fall within the basis of support. The *centre of gravity*, in the prime of life, is about 112 mm. above the middle distance, or, in the sacro-lumbar articulation, 1·5 mm. in front of the promontory of the sacrum. The basis of support is contained in the erect posture between the feet, and will vary according to the distance separating the feet. In standing erect, the feet are apart, the knees extended, the legs slightly rotated outwards, the pelvis and trunk bent a little backwards, and the arms hanging down. The weight is transmitted to the feet, each of which touches the ground at three points: the heel, the ball of the little toe, and the ball of the great toe. The heels may touch in the erect posture, the feet forming an angle of 50°. When the basis is limited to one foot, or to the point of one foot, there is of course a diminution in the equilibrium, so that the slightest oscillation of the line of gravity outside of the basis may cause a fall. To secure the line of gravity falling within the basis, muscular action may be necessary, as in crouching, but fatigue soon supervenes. In the erect posture, however, the anatomical arrangements are such as to ensure stability to a large extent by the action of gravity. Thus, the head is in equilibrium upon the atlas, the centre of gravity falling a little in front of the axis of rotation of the occipito-atloid articulation, muscular action being necessary only to a small extent. The muscles of the back assist in maintaining the straightness of the spine. The centre of gravity of the trunk passes behind the axis of rotation of the femurs, but the body is kept from falling backwards by the tension of the structures in front of the thigh and hip-joint, more especially the ilio-femoral ligament and the fascia lata. In the erect posture, all the body, from the tibio-tarsal articulation upwards, forms a more or less rigid structure. It may be observed that the slightest movement at the articulation causes a considerable oscillation of the head and upper parts of the body ; and even when the body appears to be quite steady, minute oscillations, of which the individual is unconscious, may be traced graphically. There would thus appear to be a series of limited muscular contractions, now in front, now behind, on the one side or the other, by which the body is so steadied as to prevent the risk of the line of gravity falling outside the base of support. These muscular movements probably contribute to the production of the muscular sense, or feeling of pressure or resistance, by means of which guiding sensations precede and are related to our movements. The greater the sensibility of the soles of the feet, the more securely one can stand. This was proved by Vierordt. By placing a light recording lever on the vertex of the head, he obtained tracings of the oscillatory motions of the body in the erect posture, and then he ascertained that by benumbing the soles of the feet with cold water or chloroform, the oscillations became much greater.

2. **Mechanism of Joints.**—The bones are firmly united by sutures, as in the skull, or they may be bound together by cartilage, as in the *synchondroses* between the sacrum and the iliac bones. The latter form of joint does not admit of much movement, but it offers great resistance to disruptive forces and it is very elastic, so that, if a strain acting on the joint is removed, the parts readily return to their original position. In the case of the joints between the bodies of adjacent vertebræ, while the amount of movement between each pair is slight, the movement of the vertebral column as a whole is very considerable in man. In ordinary joints, friction between the ends of the bones, which usually are in close apposition, is diminished by the cartilaginous surfaces. The forms of joints vary much, but they are either ball and socket or arthrodial, saddle-shaped or ginglymoid, rotating or trochoidal, rigid or amphiarthrosic. Ball and socket joints admit of movements in all directions. The ball is the segment of a sphere fitting accurately into a cup-shaped depression, and if a line were drawn from the centre of the ball, cutting the surface exactly in the centre of the spherical surface, this line will describe during rotation a cone, the apex of which is the point where the line leaves the spherical surface. The area of the base

of the cone will depend on the size of the surface of the joint, and thus it will be large in proportion to the degree of flatness and smallness of the cup-shaped surface in which the ball rotates, in comparison with the size of the ball. Such joints we see in the shoulder and hip. A saddle-shaped joint exists between the *trapezium* in the wrist and the first metacarpal bone. It permits of a movement with reference to two axes, one from before backwards and the other from side to side. A hinge joint permits of movement only in a single plane, and it consists of a segment of a cylinder moving in a corresponding segment of a hollow cylinder. Such a joint is found between the humerus and ulna, and in the maxillary joint of carnivora. The joint between the lower end of the tibia and the astragalus is not a simple hinge joint, so that movement is possible not only round a transverse axis, but there may be movement of the surfaces of the joint in the direction of the axis. It thus resembles a screw, the surface of the astragalus being the section of a screw surface, while the joint surface of the tibia is a corresponding section of the nut of the screw (Fick). An example of a pivot joint is found between the atlas and axis. A modified form of this kind of joint is seen in the radio-ulnar articulation, by which pronation and supination are effected. The hand can rotate thus through 180°, in every possible position of the elbow. In rigid joints, like those of the carpus and tarsus, the surfaces are flat or slightly convex, and they are firmly held together by rigid ligaments. In a position of rest, and also in movement, the surfaces of all joints are in close contact, and they are thus held together by bands of connective tissue forming a capsule, or by distinct bands and ligaments. Between the cartilaginous surfaces we find a very thin layer of synovial fluid secreted by a serous membrane, termed a synovial membrane. The membrane often shows villous prominences. Synovia is a clear or yellowish alkaline fluid, containing 96·97 per cent. of water, and 3 to 4 per cent. of solids; the latter contain about ·3 per cent. of mucin, 1·1 per cent. of salts, and 1·6 per cent. of extractives.

As first shown by the Webers, the pressure of the air maintains the apposition of the surfaces of joints. Thus the pressure on the outer surface of the hip joint is about 12 kilogs., about the weight of the bones, muscles, skin, etc., connected with the joint, so that these may be cut without the head of the femur falling out of its place, the acetabulum. If air is allowed to get into the joint by boring a hole from the inner surface of the os innominatum, the surfaces of the joint at once separate. If the pressure of the air is removed by the air pump, one can observe a converse result, the ball dropping from the acetabulum when the external pressure has been sufficiently lowered. Thus it is that the leg may be suspended from the hip joint, without a feeling of weight or dragging, the air pressure being sufficient to support it. The tonicity of the muscles and the adhesion between the joint surfaces also tend to keep them in apposition without much, if any, muscular effort.

Ligaments either strengthen the capsule between the ends of the bones or they form distinct bands for checking movements in certain directions. We have examples of the latter in the ilio-femoral ligament which prevents excessive rotation of the leg outwards, and the ligamentum teres in the hip joint which prevents too great abduction. The joint between the condyle of the lower maxilla and the glenoid fossa is a peculiar joint in man, and especially in herbivora, permitting of vertical, lateral, and antero-posterior movements. Between the bones, we find an interarticular cartilage, thinner in the middle than at the edges, so that in movement of the lower jaw forwards or backwards the cartilage slides with it. The knee joint is not a simple hinge joint, but presents spiral-shaped surfaces. The joint possesses two lateral ligaments, an external and an internal, and between the bones we have the semilunar cartilages. When the leg is extended, the external lateral ligament is put on the stretch, and as the internal lateral ligament is broader than the external, in stretching it becomes still broader, so that in consequence of the tension of these ligaments, no rotation of the knee joint is possible when the leg is extended. When the knee is flexed, these ligaments become loose and a certain amount of pronation and supination is possible. Pronation occurs when the great toe is directed inwards, and then the outer condyles of the tibia describe almost a semicircle round the inner condyles, and by the action of the check ligaments even in this movement the condyles of the femur glide upon those of the tibia and are never separated from them. The anterior crucial ligament prevents too great extension and the posterior too great flexion. The cartilages, according to Weber, distribute the pressure of the weight of the trunk over a greater surface, and the form of the articular surfaces permits of a certain amount of rolling movement from before backwards and from side to side.

Muscles do not act directly upon the bones but indirectly through tendons. If the tendon is narrow in comparison with the breadth of the muscle connected with it, the pulling power of the latter is concentrated on one point of the bone to be moved, and on the other hand, if the muscular fibres are attached to an aponeurosis the power of the muscle is spread over a greater surface.

3. Mechanism of the Muscles and Bones.—In the human body, there are different adaptations of the muscles to the bones, corresponding with the three varieties of lever movement. The movable bone represents a lever, of which the *fulcrum* is the articulation with the fixed bone, the *power* is employed at the point of insertion of the contracting muscle, and the *resistance* may be of various kinds, according to the obstacles which tend to prevent displacement of the movable bone.

(1) *Levers of the First Order.*—Here we find the fulcrum between the power and the resistance. As an example, take the balancing of the head on the vertebral column: the fulcrum is the articulation between the occipital bone and the atlas; the resistance is the weight of that part of the head and face in front of the articulation, and the power is behind, at the point of insertion of the muscles of the neck. The construction of the vertebral column, the balancing of the trunk on the pelvis, and of the leg on the foot, represent levers of the same kind. Usually, in man, this kind of lever is for the purpose of *stability*, but we find it also in certain movements. For example, in extending the fore-arm upon the arm—the fulcrum is the elbow joint, the power, applied behind the articulation, is the insertion of the triceps, and the resistance is the weight of the fore-arm in front of the articulation.

(2) *Levers of the Second Order.*—Here the resistance is between the power and the fulcrum. In this lever, the power arm[1] is always longer than the resistance-arm. As the forces are inversely proportional to the length of the arms of the lever, a comparatively weak force will overcome considerable resistance, and consequently this lever is advantageous as regards expenditure of force. But it is disadvantageous as regards rapidity of movement, for the displacements of the two points of application are proportional to the lengths of the arms of the lever. For example, if the length of the power-arm = 10, and that of the resistance-arm = 1, a force of 1 lb. would move a resistance of 10 lbs., but the point of application of the power would be displaced 10 feet, while that of the resistance would be displaced only 1 foot. This lever may be termed the lever of *power*. It is not common in the body. As an example, take the action of standing on tiptoe. Here the fulcrum is the contact of the toes with the ground; the power is at the insertion of the tendo Achillis, the strong ligament fixed into the *os calcis*, or heel-bone; and

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[1] The term *arm of the lever* is the distance which separates the fulcrum from the point of application of the power or of the resistance. The one may be called the *power-arm* and the other the *resistance-arm*.

the resistance is the weight of the body transmitted to the articulation between the tibia and astragalus.

(3) *Levers of the Third Order.*—The power is between the resistance and the fulcrum. In this lever, the resistance-arm is always longer than the power-arm, and while it is advantageous as regards swiftness, it is disadvantageous as regards expenditure of force. It may be termed the lever of *rapidity*. It is the one common in the movements of man. For instance, in the flexion of the fore-arm upon the arm—the fulcrum is the articulation at the elbow, the power is at the insertion of the flexors (*brachialis anticus* and *biceps*), and the resistance is the weight of the fore-arm. The power is usually applied in the body near the fulcrum, and the power-arm is thus much shorter than the resistance arm, and hence only small weights can be moved, but with great speed. Thus the various movements of the body are rapidly performed, and the clumsy form of the limb, which would have resulted had the power been applied near the resistance, is obviated.

In a lever, the power exerts the greatest effect when it pulls at right angles to the direction of the lever. Such an arrangement is found in the body in the case of certain of the muscles of mastication, in the flexors of the head, and in the muscles of the calf of the leg. In many other cases, the muscular fibres pull obliquely and their power can be estimated by the application of the parallelogram of forces, in which one side corresponds with the direction of the bone, and the other to a line perpendicular to this from the point of attachment of the muscle. The amount of pull is proportional to the latter, and consequently the more acute the angle formed by the muscular fibres, or tendon, with the line of the bone, the smaller will be the effective pull. This is most evident at the beginning of the pull, but as the arm, for example, is flexed, the effective power of the flexor muscle becomes greater and greater.

Simple movements, such as are above described, rarely take place. Usually the movements which one bone makes on another are not effected by one muscle, but by several, which may be regarded as associated together or *co-ordinated* for that movement. Thus, in moving the arm, say from pronation to supination, with a slight degree of flexion or extension, many muscles act. Frequently muscles are doubled for particular movements. Thus, in the upward movement of the lower jaw we have the temporal and the masseter, for flexion of the fore-arm on the arm, the biceps and the brachialis anticus, and for flexion of the foot, the soleus and gastrocnemius. Usually a muscle passes over only one joint, like the brachialis anticus, but sometimes over two, as in the case of the biceps.

In many instances, considerable loss of power is caused by the oblique direction in which the tendons of muscles are inserted into the bones, by the combination of several muscles acting in different directions, and by the obliquity of the direction of the fibres in individual muscles. The degree of the obliquity of attachment is, in a number of bones, diminished by the enlargement of their heads, the existence of projecting parts, and still more by the occurrence of sesamoid bones and pulleys (*e.g.*, digastric muscle and the superior oblique muscle of eyeball), changing the direction of tendons. The patella thus increases the efficiency of the quadriceps extensor cruris, as without it the muscle would simply pull the bones of the leg against the lower end of the femur. The patella brings the fibres of the tendon forwards, and thus they are attached obliquely to the tibia. Nevertheless, the adaptation of the muscles to the bone, in the human body generally, may be regarded as attended with considerable loss of power, some part of which loss, however, is compensated by greater extent and velocity of motion. It has already been pointed out (Vol. I. p. 400), that the muscles, even at rest, are in a slightly extended condition, and they act in this way on the bones like elastic cords. A saving of power is thus effected, because the muscles are always slightly taut and not on the slack, and they are thus ready to exert a pull the instant an active contraction begins. It is also evident, that when one set of antagonist muscles (like the flexors of the arm) acts, they exert a pull on the opposite set (the extensors), which becomes greater and greater up to the end of the contraction of the flexors. Elastic power is thus stored up in the extensors, which comes into play when the flexors relax. The elasticity of the extensors is sufficient to keep the limb extended with almost no muscular effort. The same antagonistic play of elastic and contractile forces is seen in such a muscle as the orbicularis oris, by which, when at rest, the opening of the mouth is kept symmetrical.

The power of a muscle is in proportion to its cross-sectional area and the extent of its movements. The latter (termed the *lift*) is usually in proportion to the length of the muscle. A long thin muscle like the sartorius has a large lift but small power, while the peroneus longus, about the same length, but with more numerous fibres, has greater power but a smaller lift.

4. **Mechanism of the Body in Locomotion.**—The movements of the body as a whole assume various forms, such as walking, running, leaping, swimming, etc.

It is not within the scope of this work to do more than briefly allude to some general facts. Although many of the movements were investigated by Borelli, about the year 1680, the brothers Weber were the first to adopt rigorous and precise methods. Recently, the whole subject has been re-investigated by Marey, who has devised many ingenious forms of apparatus on the principle of the registration of transmitted movements. His arrangement consists of a slipper or shoe, having a thick sole, in which there is an air chamber, *a*, communicating with a recording tambour by the tube, *b*. With each pressure of the sole of the foot against the ground, the air is compressed in this chamber, and this pressure, transmitted to the recording tambour, is registered on a cylinder carried by the operator, as seen in Fig. 449. In addition, a small tambour, fitted for transmitting vertical oscillations, is placed on the top of the head. Three tambours record the movements, one for each foot, and one for the vertical oscillations of the whole body. The operator also is provided with a bag containing air, by the compression of which the three recording levers can be brought against the cylinder when the movements of the body become tolerably uniform.

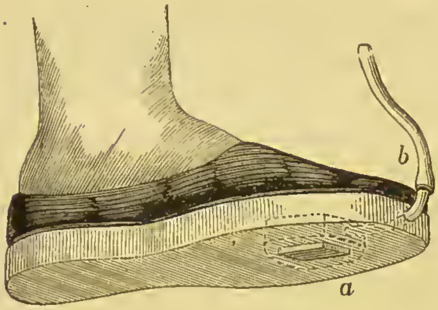

FIG. 448.—Marey's apparatus for transmitting movements from the sole of the foot.

FIG. 449.—Marey's apparatus for recording movement in locomotion.

An example of a tracing thus obtained is shown in Fig. 450. Marey has also devised a kind of notation which shows at a glance the rhythm, the time of the duration of the pressure, the foot exerting this pressure, and also the length of time during which the body is suspended. An example showing the mode of this notation is given in Fig. 451. This is the same curve as in Fig. 450, obtained in running. The lines 1 and 2 form a *staff*, "on which will be written this simple music, consisting only of two notes, which we will call right foot, left foot. From the commencement of the ascending part of one step-curve belonging to the right foot, let us drop upon the staff a perpendicular, *a*; this line will indicate the commencement of the pressure of the right foot. A perpendicular, *b*, let fall from the end of the curve, will determine where the pressure of this foot ends. Between these two points, let us trace a broad white line; it will express by its length the duration of the pressure of the right foot."[1] A similar construction is made for the left foot. Between the pressure of the two feet there is found to be "*silence*" in the rhythm, that is, the expression of the instant "*when the body is suspended above the ground* in running."

FIG. 450.—Tracings obtained from a man in the act of running. *a*, vertical oscillations of the body; *b*, impact and rise of the right foot; *c*, impact and rise of the left foot. When the foot presses on the ground the curve descends, it remains straight so long as the sole touches the ground, and it ascends as the sole leaves the ground. The upper horizontal part of the curve represents the time the foot remains in the air.

By means of this notation, two of the chief modes of progression are represented in Fig. 452.

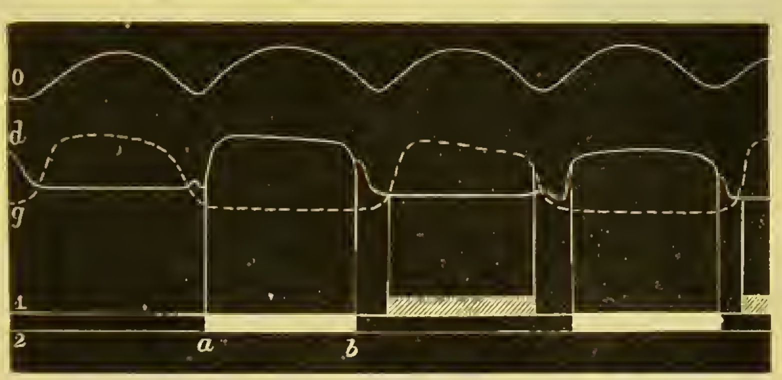

FIG. 451.—Marey's Notation of Rhythm in different modes of progression. Running.

Walking.—In walking, the body never entirely quits the ground. This is shown by the upper tracing in Fig. 452. The forces which act

FIG. 452.—Notation of walking (upper line) and running (lower line). (Marey.)

on the body in ordinary walking may be studied with the aid of Fig. 453. Let G represent the centre of gravity of the body; two forces

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[1] *Marey's Animal Mechanism*, p. 133.

act on it: (1) the one, shown by the line, G J, representing the direction of gravity; the other (2) produced by extending the limb G J′, causing the centre of gravity to move in the direction G F. The latter may be resolved into two, the one vertical, G V, tending to carry the centre of gravity upwards, causing the *vertical* oscillation in walking; the other, *horizontal*, G H, which determines progression. The two limbs represent two sides of a triangle, the hypotenuse of which is formed by the posterior extended limb, the perpendicular, G J, by the limb which supports the body, and the short side, J′ J, represents the length of the step.

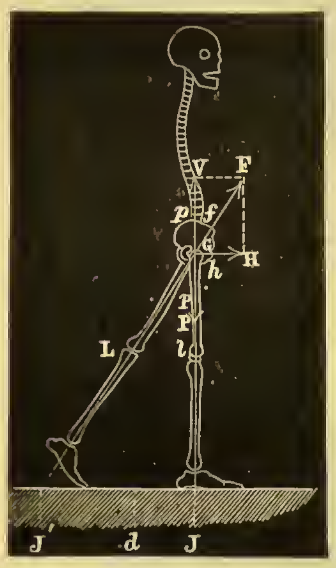

Fig. 453.—Forces which act in walking. (Weber.)

At the beginning of the step, one of the limbs, the *supporting leg*, is placed below the centre of gravity (*p p l*, Fig. 453); and the other, the *oscillating or swinging limb* (G J′, Fig. 453) is placed behind. In passing through the complete step, according to Weber, the limbs assume the successive positions shown in Fig. 455.

The advance of the hinder leg itself is not, in ordinary circumstances, as shown by Weber, a muscular action, but consists of the fall or swing of the leg forwards, through the arc of a circle, in a manner similar to the oscillation of a pendulum. It has recently, however, been demonstrated by Marey and others that frequently, and more especially during fatigue, muscular action is necessary. The supporting leg leaves the ground gradually, touching it at last only with the ball of the great toe, and when it leaves the ground it is completely extended, but it passes from the vertical to the inclined position in such a manner that the pelvis does not describe a curve, but moves horizontally. The hip joint flexes slightly, so that the extended leg becomes too short as it were, and then it assumes the position of the swinging leg. At the end of the pendulum-like swing, the extensors come into play so as to lengthen the leg, the foot is applied to the ground, and the swinging leg becomes a supporting leg (Fig. 455). When one leg pushes against the ground, the other is in a state of rest, and when the supporting leg is stretched or extended as much as possible, so that there is danger of the body falling forwards, the other leg swings forward, and, taking the place of the supporting leg, prevents the threatened fall. Thus the centre of gravity of the body is moved forwards. As regards the leg, at one moment its lower end is fixed and its upper end moves forward, and the next moment both its point of suspension at the upper end and its lower end are moving forwards. In this way, in walking, there is a constant forward movement of the centre of gravity. In quick walking, the advancing leg reaches the ground when only half an oscillation has been performed, but in very slow walking, the limb performs nearly a whole oscillation. The velocity of the advance of the limb is consequently regulated by its length, or by the distance of its centre of gravity from the point of rotation, that is, about 500 mm. for a limb of the ordinary length of 850 mm. According to E. Weber, the rapidity of the swing of living and dead legs is the same, showing that the swing is that of a pendulum due to gravity. Increased speed is attained in walking by depression of the centre of gravity of the trunk, greater flexion of the limbs, a more forcible thrust of the hind limb against the ground, longer steps, and by allowing the supporting limb to remain a shorter time in contact with the ground. Lateral movements of the body are

FIG. 454.—Tracings of the impact and the rise of the two feet in ordinary walking. *o*, oscillations of the head; *d*, movement of right foot; *g*, movement of left foot.

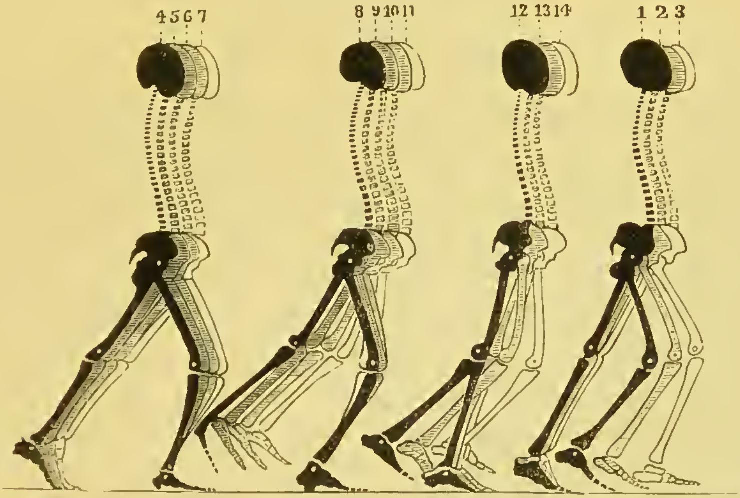

FIG. 455.—Diagram showing the successive positions of the two limbs during walking. (Weber.) The positions follow in the order of the numbers.

determined by the supporting leg acting on one side of the centre of gravity, but they are balanced by an opposite swing of the arms. Thus, when the left leg gives a greater speed to the left half of the trunk, the right arm swings forward, and brings the centre of gravity again into the mesial plane.

Running.—In running, the hinder leg is raised before the advancing one reaches the ground, so that there is a short time during which the body is not supported by the limbs, as shown in Fig. 452. The trunk is more inclined forwards, the limbs are more bent, the steps longer, and succeed each other more rapidly, and the vertical oscillations are greater than in walking. Thus, the length of the step in running is to that in walking as 2 : 1, and the time as 2 : 3; so that a person may run three times as fast as he can walk.

These movements are illustrated by the following notation, in which R = right leg, L = left leg, S = supporting, and O = oscillating positions of the limbs:—

$$\text{Slow Walking, } \begin{cases} \text{R—S O S S S O S S, etc.} \\ \text{L—S S S O S S S O, etc.} \end{cases}$$

$$\text{Quick Walking, } \begin{cases} \text{R—S O S O S O, etc.} \\ \text{L—O S O S O S, etc.} \end{cases}$$

$$\text{Running, } \begin{cases} \text{R—S O O O S O O O, etc.} \\ \text{L—O O S O O O S O, etc.} \end{cases}$$

$$\text{Jumping, } \begin{cases} \text{R—S O S O, etc.} \\ \text{L—S O S O, etc.} \end{cases}$$

The *time relations* of various kinds of movements have been determined by Marey with the aid of photography. He took a series of practically instantaneous pictures of a man walking, running, or jumping (the time of exposure of the plate being about ·001 sec.) with a revolving camera. Each picture of course represents a phase of movement at a particular moment of time. In this way, certain postures are observed which usually escape detection, and when the series of pictures on a band of paper is placed in a wheel of life, or zoetrope, and the instrument is rotated, the figures are seen to move in a natural manner. This method has also been carried out with great completeness by Muybridge. Marey has also photographed bright shining spots on certain parts of the moving figure of a man clothed in black (such as head, chest, pelvis, thigh, leg, foot), and has thus got the curves of movement of these parts. These investigations, although curious and interesting, have not added much to what has been previously ascertained by other methods by the Webers and by Marey himself.

It is impossible to ascertain with great accuracy the force of a particular muscle or group of muscles in a living man. By means of Regnier's dynamometer, it has been found that the force exerted by the muscles of the back amounts, in most adults, to from 400 to 600 lbs.,[1]

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[1] 1 lb. = ·4536 kilog.

and in very powerful adults to 700 or 800 lbs. lifted a few inches. The muscles of the leg exert a power equal to about 400 lbs.

The age, stature, and weight of individuals modify greatly the amount of muscular exertion of which they are capable. The average height of men in Great Britain is about 69 inches, and of women 63½ to 64 inches.[1] With this stature, men weigh from 140 to 160 lbs., women, 110 to 120. The full stature and strength of the male is reached about the age of 25. At 15 years of age, lads, 5 feet 4 inches in height, may lift from 200 to 280 lbs.; at 20, when 5 feet 8 inches in height, the lift is from 350 to 415 lbs.; and at 25, the stature being 5 feet 9 inches, it may reach as much as from 400 to 450 lbs. (Allen Thomson.) The following table gives a comparison between the working power of man and certain animals :—

	Mean Weight.	Work in 8 hours.	Work per Second and per Kilogramme of Weight.
	Kilograms.	Kilogrammetres.	Kilogrammetres.
Man, - - -	70	316,800	0·157
Ox, - - -	280	1,382,400	0·172
Horse, - - -	280	2,102,400	0·261

The horse excels all other domestic animals in working power. Thus, according to Redtenbacher, the amount of work per kilogramme of body-weight per hour is as follows for various animals in kilog.-metres :—horse, 940; mule, 800; ass, 640; ox, 620; and man, 560.

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[1] 1 inch = 25·4 mm.

SECTION XV.

REPRODUCTION.

Chap. I.—GENERAL STATEMENT.

Living organisms possess the power of reproducing their kind. The process by which they do so may be either asexual or sexual. A third mode of reproduction, termed spontaneous generation, that is, the origin of living beings *de novo*, without parents, is possible.

1. **Spontaneous Generation.**—It is beyond the province of this work to enter upon the vexed question of the possibility of the origination of life from dead matter, without the existence of parentage. Such a mode of production of living things is sometimes termed *abiogenesis* or *heterogenesis*. In the opinion of the author, no instance of life originating *de novo* has been proved. There can be no doubt that the rigid exclusion of the living germs in air from boiled infusions of organic matter does prevent the occurrence of life in these infusions. Nor can there be any doubt that in water and in air there are innumerable living particles or germs, which, when they fall into a fluid having organic matter in solution, multiply therein, and so excite fermentive or putrefactive changes (see Vol. I. p. 188). The admission of these facts, however, does not invalidate the possibility of abiogenesis occurring in certain conditions, and it is unphilosophical to assert the impossibility of its occurrence now or in some past time. The intimate relations known to exist between physical, chemical, and vital phenomena, depending on the laws of the conservation and transmutation of energy, and the theory of evolutional development, indicate the probability of abiogenesis, and it is one of the problems of biological science to ascertain the conditions in which this may occur.

2. **Asexual Generation.**—This mode of reproduction, which includes generation by budding, by fission, or by endogenous formation, has been already referred to in treating of cells (Vol I. p. 296). A variety of it constitutes *parthenogenesis*, by which we understand the production of offspring, unlike their parents, which may take place without, in connection with each individual birth, a union of male and female elements. This is often associated with the law of *alternate*

generations, and it is illustrated by the development of various forms of *Medusæ*, *Tænia*, and of *Aphides*. Here one sexual congress is sufficient, not for one, but for several generations of beings, some of whom may have certain characters unlike those of their immediately antecedent parent.

The most striking example of true parthenogenesis is seen in bees. Here we find a female with fully developed sexual organs, the *queen bee*, numerous females with imperfectly developed sexual organs, the *workers* or *neuters*, and the male bees, or *drones*. During the flight of the virgin queen in hiving, copulation occurs with a drone, and the sperm-sac is filled with fecundating fluid. The queen then, in the hive, deposits an egg in the large cell of a certain part of the comb, and she admits a small amount of spermatic fluid into contact with the egg. Into other smaller cells she drops an egg without any spermatic fluid. The unimpregnated eggs develop into drones (males), and the impregnated eggs become worker bees. If the queen bee is not impregnated, or if all the fluid in the sperm-sac has been exhausted, then she can breed drones only. By feeding a worker with a special kind of food, she grows in size, her sexual organs reach full development, and she becomes a queen bee, fit for the production of offspring.

3. **Sexual Generation.**—In the higher animals, reproduction essentially is the result of the blending of two elements—a female element or *ovum*, and a male, or *spermatozoid*. These are differentiated parts of the body of the parents, and by their union activities are initiated which result in the development of a new being. They may be produced in the same individual, as in many mollusca, a condition termed *hermaphroditism ;* but in the higher animals, they are specially differentiated products supplied by different individuals.

As a rule, sexual union takes place only between animals of the same species, but it may occur between individuals of the same genus but of different species. When this is fruitful, a being termed a *hybrid* is the result. Such may be formed by the rabbit and hare, lion and tiger, dog and wolf, and ass and horse. The animals show characters more or less common to both parents. They are usually barren, and the generative organs are imperfectly developed. The wild goat and the domestic goat, and the hare and rabbit produce hybrids capable of breeding indefinitely. Rarely, a mule-mare may be impregnated by a mule-horse, but if abortion does not occur, the offspring is weak and sterile, and usually soon perishes.

CHAP. II.—THE STRUCTURE OF THE SEXUAL ORGANS.

(*a*) **The Male Organs.**—The *testis* or testicle, shown in Fig. 79, p. 215, Vol. I., is a complicated tubular gland enclosed in a strong fibrous covering. This covering, the *tunica albuginea*, develops, above and behind, a mass of tissue, pushed into the testicle, and termed the *corpus Highmorianum* or *mediastinum testis.* From this numerous septa radiate outwards to the *tunica albuginea,* thus dividing the testis into a number of pyramidal lobules, the bases of which are directed to the *tunica albuginea,* while their apices point to the *corpus Highmorianum.* The *tunica albuginea,* composed of strong connective tissue, has on its upper surface a single layer of epithelial cells. Below the outermost layer, the connective tissue is looser and contains vessels, and it is known as the *tunica vasculosa.* The *corpus Highmorianum,* also formed of connective tissue, encloses a network of fine anastomosing canals, the *rete testis* or *rete vasculosum Halleri.* The septa consist of connective tissue. Among the fibres we find flat or roundish connective tissue cells, pigment cells, and fat cells.

The *tubuli seminiferi,* or small tubes of the testis, are composed of three portions : (1) they begin as *tubuli contorti* ; these pass into (2) the *tubuli recti* ; and these run into (3) the *rete testis.* The *tubuli contorti* are small convoluted tubes, 140 μ in diameter, originating in a manner not thoroughly understood beneath the *tunica vasculosa*—probably in a fine network or in blind-ends—and running on towards the *corpus Highmorianum.* Uniting with each other to some extent at acute angles, the *tubuli contorti* pass into the *tubuli recti.* These are narrower tubes, about 20 to 25 μ in diameter ; they pass into the *corpus* and form the *rete testis,* the canals of which are 24 to 180 μ in diameter. The wall of the *tubulus contortus* shows, from without inwards (1) a layer of connective tissue, mixed with numerous cells ; (2) a delicate *membrana propria,* and (3) a layer of epithelial cells, the appearances of which vary according to the state of functional activity of the testis. Two conditions are usually observed : (1) a state of rest, in which the epithelial cells form several layers, and (2) a state of activity, in which there is a great increase of nuclei, and in which also the spermatozoids are found in different states of development. (See Fig. 80, p. 216, Vol I.) The mode of formation of the spermatozoids has already been discussed (p. 216, Vol. I.). It may be briefly summarized. The head of the spermatozoid corresponds to the nucleus of a cell. The epithelial elements in a seminiferous tubule are of two kinds : (1) roundish cells, not directly concerned in the formation of spermatozoids (Fig. 83, A *c*, C 4, p. 218, Vol. I.)—and hence termed *indifferent cells*—and (2) the true *seminal germ cells* (*Spermatogonia*). In a state of rest, the latter are polygonal elements resting on a *membrana propria,* but when they become active, they rise into peculiar elongated bodies, club-shaped at the upper end; and the nuclei, by subdivision, form several nuclei, one of which remains at the base, while the others are found in the club-shaped end. The cell is at this stage termed a *spermatogemma* (Fig. 83, B 2, p. 218, Vol. I.). The club-shaped end now grows outwards, into finger-shaped processes, each of which contains a nucleus, and each nucleus forms the head of a spermatozoid. The cell is now termed a *spermatoblast* (Fig. 83, A *b*, C 3, p. 218, Vol. I.). Finally, these processes separate from the basal part of the cell and from each other, becoming *spermatozoa.*

The *tubuli recti*, and the canals of the *rete testis*, have a delicate *membrana propria*, on which a single layer of cylindrical cells rests.

The arteries of the testis are branches of the internal spermatic artery. They pass partly from the *corpus Highmorianum* and partly from the *tunica vasculosa* into the septa, and end in a capillary network surrounding the *tubuli contorti.* From the capillaries the veins originate, and they follow the course of the arteries. The lymphatics form a plexus below the *tunica albuginea*, and lymph spaces pass from these to surround the *tubuli contorti.* Nothing is known of the mode of termination of the nerves.

The *spermatozoids* have already been described (p. 218, Vol. I.).

The *tubuli recti* and the canals in the *rete testis* belong to the discharging structures of the testis, but the larger structures concerned in conveying the semen from the testis are the *epididymis*, the *vas deferens*, the *vesiculæ seminales* and the *ejaculatory duct.* From the upper end of the *rete testis*, 7 to 15 *vasa efferentia testis* proceed, and each becoming convoluted, a number of cone-shaped bodies are formed, the bases of which are directed outwards. The confluence of these *coni vasculosi* produces the head of the epididymis (*globus major*), and by their anastomoses, one duct is formed, the *vas epididymis*, which, in complex coils, constitutes the body and tail of the epididymis, and it finally issues from its smaller end (*globus minor*), to become the *vas deferens.* The *vasa efferentia*, in their first portion, consist of a layer of cylindrical ciliated epithelium, resting on a *membrana propria.* Outside of this we find several layers of smooth muscle. The coils of the *vas epididymis*, held together by loose connective tissue, show the same structure. The circular layer of muscle attains considerable thickness. The *vas deferens* shows non-ciliated cylindrical epithelium, resting on a *membrana propria.* Beyond this there is a circular muscular layer, and still more externally

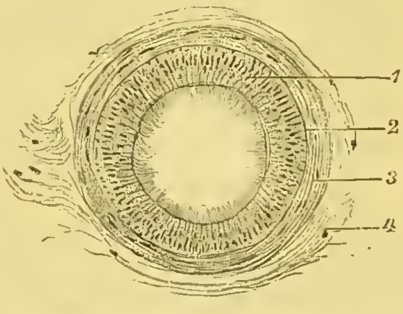

FIG. 456.—Transverse section of the *vas epididymis* of man. × 80 d. 1, stratified cylindrical epithelium, with long cilia; 2, *membrana propria*; 3, circular layer of muscle; 4, loose connective tissue. (Method No. 133, Appendix.)

a longitudinal layer of smooth muscle. The end of the *vas deferens* shows swellings or *ampullæ*, in which are found small tubular mucous glands, the cells showing pigment granules. The structure of the *vesiculæ seminales* and of the *ductus ejaculatorius* shows the same elements as in the *vas deferens*. The *paradidymis*, or *organ of Giraldès*, in the spermatic cord, and the *vas aberrans Halleri*, which is a vestige of the embryonal kidney, show the same structure. Both consist of a small canal clothed with cubical ciliated epithelium, surrounded by a mass of vascular connective tissue. The *hydatid of Morgagni* is a minute lobule having a stem or handle composed of connective tissue and covered with cylindrical ciliated epithelium. The stem contains a small canal, also lined with ciliated cells. It is regarded by some as the homologue of the ovary, and it has been termed the *ovarium masculinum*. Another hydatid-like body, without a stem, is sometimes found. It is a vesicle, lined with cubical cells, and full of fluid.

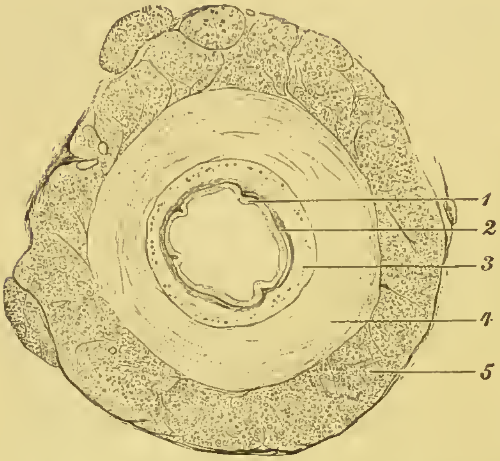

FIG. 457.—Transverse section of the first portion of the *vas deferens* of man. × 20 d. 1, cylindrical epithelium; 2, *membrana propria*; 3, sub-mucous coat, with longitudinally arranged muscular bundles cut transversely; 4, circular muscular layer; 5, longitudinal muscular layer. (Method No. 134, Appendix.)

2. The *prostate gland* consists of glandular substance and of smooth muscle. The gland substance is composed of from 30 to 50 acinous glands, with very small acini. The glands open by two large, and a number of small, ducts into the urethra. The cells in the gland are short and cylindrical in form. Transitional epithelium occurs in the prostatic part of the urethra. In old persons, the vesicles are often full of small concretions, as large as 7 mm. in diameter. Non-striated muscle exists in large amount, running between the small acini. Near the ducts, the muscle forms a strong circular layer, and bundles are also found on the surface of the prostate, which merge externally into bundles of striated muscle, belonging to the *transversus perinæi* muscle. The prostate is richly supplied with vessels. Nothing is known about nerve terminations in this gland.

3. The *glands of Cowper* are acinous, with large vesicles, lined by a single layer of cylindrical epithelium. Their ducts show two or three layers of cubical cells.

4. The *penis* consists of three cylindrical bodies—the two *corpora cavernosa penis* and the *corpus cavernosum urethræ* being surrounded by fascia and skin. The *corpus cavernosum penis* is formed of a *tunica albuginea* and of a spongy tissue. The *tunica* is a firm membrane, 1 mm. in thickness, composed of connective tissue with numerous elastic fibres, more especially on its external surface, where an inner circular and an outer longitudinal layer are found. The spongy substance are formed of bands of connective tissue, containing much muscular tissue, and bands cross and anastomose in all directions, forming a very complex network, the meshes of which are lined by a single layer of flat endothelial cells. These meshes are filled with venous blood. The walls of the arteries are very thick. The capillaries form a superficial and delicate network below the *tunica albuginea*, and a deeper network, lying on the superficial stratum of the spongy tissue. This plexus, usually termed the deep cortical network, communicates with the venous spaces in the spongy tissue. The helicine arteries are small branches lying in the connective tissue septa, and they form curled twigs, often terminating in blind ends. The veins originate partly in the deep cortical network, partly from the spaces of the spongy tissue, and pass through the *tunica albuginea;* they end in the *vena dorsalis.* The *corpus cavernosum urethræ* is formed of two parts, a central part surrounding the urethra, consisting almost entirely of a dense network of veins developed in the submucous coat of the urethra, and a peripheral part resembling in structure the *corpus cavernosum penis.* It differs in the arteries not terminating directly in venous spaces. The *glans penis* is formed of veins, much convoluted, and bound together by connective tissue. It also contains small arteries and capillaries.

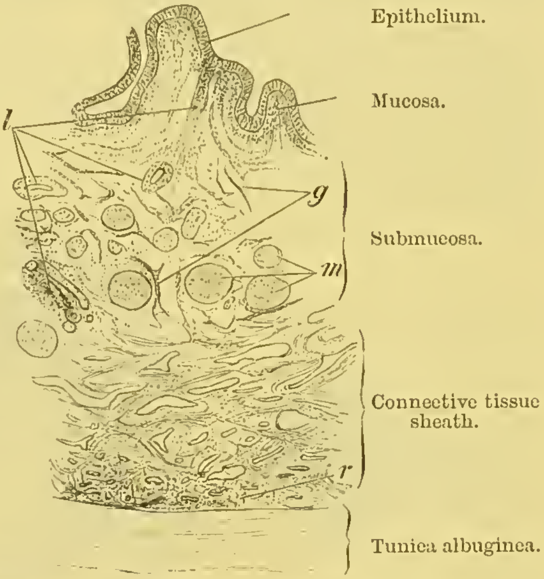

FIG. 458.—Section of *pars cavernosa urethræ* of man. × 20 d. *l*, the glands of Littre; *g*, blood-vessels; *m*, section of longitudinal muscular layers; *r*, network of vessels. (Method No. 135, Appendix.)

(*b*) The Female Organs.

1. The *ovaries* consist of a stroma of connective tissue in strata, and of glandular substance. Externally we find a strong fibrous coat, the *tunica albuginea*, formed of bundles of connective tissue intersecting in all directions. Next we find the cortical substance (Fig. 87, p. 220, Vol. I.), in which the proper gland substance exists, and, most internally, we have the medullary substance in which there are numerous coiled vessels and smooth muscular fibres. The minute structure of the ovary and of the Graafian vesicles has already been described in Vol. I. p. 220, *et seq.* See also Fig. 459.

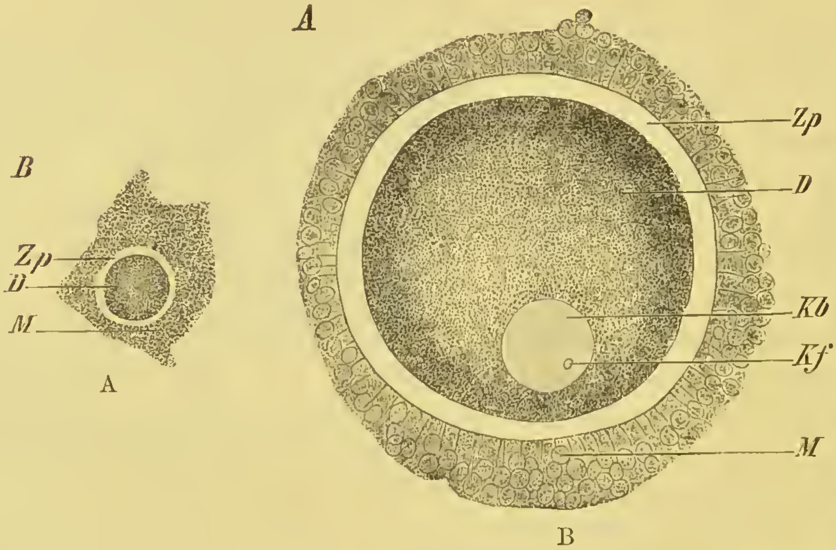

FIG. 459.—Ovum from the Graafian vesicle of a cow. A, × 50 d ; B, × 240 d. *M*, cells of the *tunica granulosa; Zp*, *zona pellucida ; D*, yolk ; *Kb*, germinal vesicle ; *Kf*, germinal spot. (Method No. 136, Appendix.)

When the Graafian vesicle has attained its full maturity, it bursts on the side next the surface of the ovary, and the ovum, surrounded by cells from the *discus proligerus* and *tunica granulosa*, escapes into the Fallopian tube. The empty vesicle then becomes a *corpus luteum.* If the ovum has not been impregnated, the *corpus luteum* disappears in a few weeks, but if pregnancy occurs, a true *corpus luteum* is formed, attaining a diameter of 10 mm., and remaining for years in the ovary. A true *corpus luteum* is formed of a fibrous membrane formed by proliferation of the cells of the *membrana granulosa*, and this surrounds a cavity filled with blood, derived from the rupture of vessels in its neighbourhood. Later, young connective tissue is developed from some of the cells of the clot, the cells of the *membrana granulosa* proliferate, and the clot itself becomes yellow, the hæmoglobin of the disintegrating blood corpuscles decomposing, with the formation of hæmatoidin crystals (Figs. 52, 53, p. 129, Vol. I.).

The arteries of the ovary, which are branches of the internal spermatic artery, enter the hilum, divide in the medulla, and there pursue a very tortuous course. Thence they run into the cortical substance, forming networks. The veins form a dense plexus near the hilum. Numerous lymphatics are also found, and nerves ramify among the larger vesicles.

2. The épоophoron, or *parovarium*, and the *paroophoron*, are the remains of embryonic structures. The former, found in the broad ligament, near the hilum of the ovary, consists of small tortuous canals, ending in cul-de-sacs, lined with ciliated cylindrical epithelium. The épоophoron is a relic of the sexual portion of the Wolffian body. The paroophoron, also found in the broad ligament, is formed of small canals, lined with cylindrical cells, and it is a relic of the urinary portion of the Wolffian body.

3. The *Fallopian tube* is formed of three membranes: (1) internally, a mucous membrane; (2) in the middle, a muscular layer; and (3) externally, a serous membrane. The mucous membrane is thrown into a series of longitudinal folds, so that a transverse section of the tube is star-shaped. The folds are largest at the upper ends of the tubes, where they constitute the so-called fimbriated extremities. The thick mucous membrane consists (*a*) of a single layer of ciliated epithelium; (*b*) of a *membrana propria*; (*c*) of a thin *muscularis mucosæ*, the smooth muscular fibres running longitudinally; and (*d*) of a *submucosa*, formed of a thin layer of fibrillar connective tissue. The muscular coat is composed of an inner and thicker circular layer of fibres, and of an outer and thinner longitudinal layer. The serous coat is formed of the peritoneum. Blood-vessels form a rich and narrow-meshed plexus in the mucous membrane. The veins run in the direction of the folds of mucous membrane.

4. The wall of the uterus has a mucous membrane, muscular tissue, and a serous covering. The mucous membrane, 1·5 to 2 mm. in thickness, has a single layer of cylindrical ciliated epithelium. The *membrana propria* is formed of delicate connective tissue, bound by a homogeneous cement substance, and among the fibres there are numerous leucocytes. We also find numerous simple or bifurcated tubular glands, having a *membrana propria*, on which there is a single layer of cylindrical cells, bearing short cilia. The muscular coat is composed of bundles of smooth muscular fibre interwoven in a most intricate manner. Three strata may be distinguished, but these are not clearly

defined; an *inner*, the *stratum sub-mucosum*, having the fibres running length-ways; a *middle*, the strongest, in which circularly-placed fibres preponderate, containing wide veins, and hence called the *stratum vasculare*; and an *outer*, containing fibres running both longitudinally and circularly, and termed the *stratum supravasculare.* In the *cervix uteri*, the mucous membrane is thicker and has ciliated epithelium in its upper two thirds. Papillæ covered with stratified pavement epithelium are also found. In addition to isolated tubular glands, we also meet with short mucous glands, which, becoming filled and swollen with secretion, constitute the *cysts* or *glands of Naboth.* The muscular tissue of the *cervix* shows inner and outer longitudinal layers on each side of a middle circular layer. Blood-vessels are very abundant, especially in the *stratum vasculare.* Capillary networks surround the glands in the mucous membrane, and a plexus of lymphatics is also found in the membrane. From these lymphatics, branches run into the muscular tissue and anastomose with another network in the subserous coat. Nerve filaments are found in the muscular layers, but their relation to the mucous membrane is unknown.

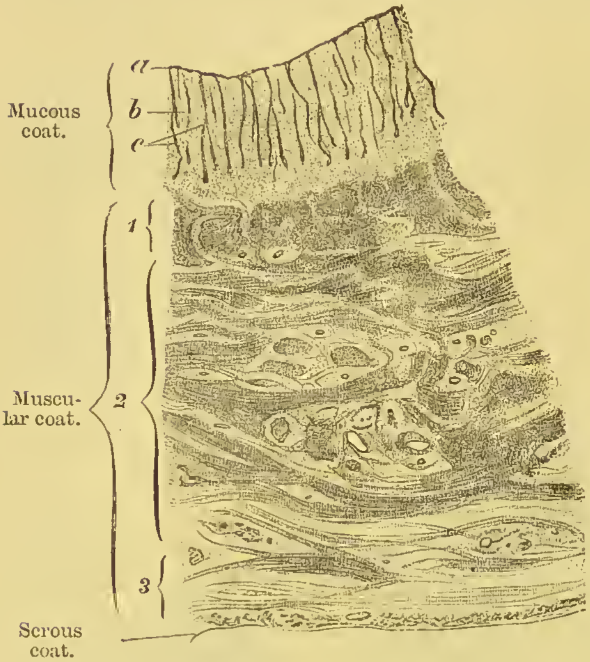

FIG. 460.—Transverse section through middle of uterus of a girl, fifteen years of age. × 10 d. *a*, epithelium; *b*, *membrana propria*; *c*, glands. 1, *stratum submucosum*; 2, *stratum vasculare*; 3, *stratum supravasculare.* (Method No. 137, Appendix.)

During menstruation, the mucous membrane becomes thicker, reaching up to 6 mm., from an increase in the interstitial or cement matter, and from the presence of leucocytes; the glands also increase in length, and the blood-vessels are distended. The epithelium is shed in small patches. In the pregnant state, not only does the mucous membrane become thicker, but there is an enormous thickening of the muscular layers (p. 434, Vol. I.).

5. The *vagina* is formed of a mucous membrane, a muscular coat, and a fibrous coat. The mucous membrane shows: (1) a layer of stratified

squamous epithelium; (2) papillæ having a *membrana propria* of delicate connective tissue with a few elastic fibres. Numerous leucocytes are present, either so abundant as to form nodular masses, or wandering between the epithelial cells; (3) a submucous coat of loose connective tissue and strong elastic fibres. No glands exist. There are an inner circular and an outer longitudinal layer of smooth muscle. The outer fibrous layer is composed of firm connective tissue, mixed with much elastic tissue. Capillary networks abound in the mucous and submucous coats, and between the bundles of muscular fibres we find a dense network of wide veins. The nerves, which are numerous in the outer fibrous layer, show numerous small ganglia.

6. In the neighbourhood of the *clitoris*, and of the opening of the urethra, there are numerous mucous glands, ·5 to 3 mm. in length, and on the *labia minora* there are sebaceous glands, ·2 to 2 mm. in length, but no hair follicles. The structure of the clitoris resembles that of the penis; on the *glans clitoridis* there are tactile end-bulbs. The *glands of Bartholin* resemble Cowper's glands (p. 738) in structure. The structure of the *labia minora* is that of the skin. The secretion of the vagina contains flat epithelium cells, leucocytes, and frequently an infusorium known as *Trichomonas vaginalis.*

CHAP. III.—CERTAIN PHENOMENA CONNECTED WITH THE REPRODUCTIVE FUNCTION.

1. **The Phenomena of Menstruation.**—From the age of about fifteen to that of forty-six years, an ovum escapes from the ovary of the healthy human female at intervals of twenty-eight days. This occurrence is coincident with various changes in the uterus and pelvic organs, which cause both local and general symptoms. The local conditions are (1) a somewhat increased size of the uterus, probably from the increased afflux of blood; (2) thickening of the mucous membrane; (3) portions of mucous membrane may become detached; and (4) capillaries are ruptured so as to produce a discharge of blood, mixed with mucus, termed the *menses* or *menstrual fluid.* This discharge continues for a period of from three to five days; sometimes copious, but more frequently scanty, at the commencement, it reaches a maximum in amount, and then slowly passes away. From 120 to 200 grms. of blood are lost. The source of the hæmorrhage is rupture of vessels in the mucous membrane of the uterus. During the menstrual period the blood pressure in the generative organs is enormously increased. Parts of the

epithelium are detached in very small patches. The blood is mixed with a large amount of mucus. Frequently a woman suffers at the menstrual period from a sense of fulness in the pelvic region, weariness, pains in the back and limbs, sickness, vomiting, and other constitutional affections. Menstruation rarely occurs during pregnancy or lactation. Although there is, in a healthy state, an intimate connection between ovulation and menstruation, the latter, or some phenomenon very similar to it, may possibly occur without the former. Sexual desire is independent of menstruation, but immediately after it there is a great susceptibility to impregnation.

2. **Puberty in the Female.**—The age of puberty marks the capability for procreation. In temperate climates, it occurs usually at the age of fifteen or sixteen years, and in the tropical climates of the east as early as the age of eleven or twelve. The term of fecundity in healthy individuals is about thirty years, but there are many exceptions to this rule. At puberty, changes occur not only in the generative organs but in other parts of the body, giving to the female form the characteristic appearances of womanhood. Puberty occurs sooner in small than in large animals. Thus it happens in the guinea-pig, rabbit, rat, and in birds during the first year; in the cat and dog in the second year; in the horse, ox, and lion in the third year; in the larger monkeys in the fourth year; in the camel in the fifth year, and in the elephant between the twentieth and thirtieth year. Phenomena similar to those of menstruation occur in many animals, and the condition is known as *the rut.* Cows and sheep rut twice, the cat, bitch, and pig two or three times, and the rabbit and guinea-pig eight or twelve times, in the course of the year. The condition lasts in the mare and cow from two to four days, and in the pig and bitch from six to ten days. During rutting, the females have a peculiar smell by which the males are attracted from even long distances. The females then show great excitement, and it is only during rutting that coition is permitted.

3. **The Change of Life, or Climacteric Period.**—At the age of about forty-five, the menses cease. The change occurs gradually, the amount of fluid becoming less at each successive period; but in some women, there may be intervals of many weeks, or even months, between the last few menstrual periods. A series of bodily changes, the reverse of those occurring at puberty, supervene after the cessation of menstruation.

4. **The Passage of the Ovum to the Uterus.**—When an ovum escapes from a Graafian vesicle, it is received into a space formed by the fimbriated extremity of the Fallopian tube grasping the ovary. The

dilated end of the tube is applied to the ovary by a reflex influence exciting the muscular fibres of the dilated end of the tube. In some rare cases, the ovum may drop into the peritoneal cavity, and if fecundation occur in these circumstances, extra-uterine pregnancy will be the result. The ovum is carried along the tube by ciliary movement, and by the peristaltic contractions of its muscular walls. The length of time the ovum requires to pass onwards into the uterus varies from three to five days. It was the discovery of Bischoff that ova come to ripeness in the ovaries alternately, that is to say, a Graafian vesicle in one ovary becomes mature, and discharges its ovum, and at the next period a similar occurrence takes place in the other ovary. It is doubtful if this alternation invariably occurs. In the human being, as a rule only one ovum escapes at a time, but sometimes two, and much more rarely three. The ovaries of the cow and the mare give off usually one, sometimes two ova, of the goat one to four, and of the pig, cat, and bitch, as many as ten in one rutting period.

5. **Coition.**—In fishes, the male sprinkles the spermatic fluid over the spawn of the female, and there is no congress of the sexes in any sense. In many amphibians and reptiles, the male clings to the back of the female, and sheds the semen over the ova as they pass from the cloaca or uro-genital aperture. In birds and mammals, the fecundating matter must be introduced by a special organ, the penis, into the generative passage of the female. The penis becomes rigid owing to an increased afflux of blood to the cavities of the *corpora cavernosa penis*, due to the action of nervous filaments which cause a dilatation of arteries of the organ. Goltz has found that a nervous centre connected with erection exists in the lumbar region of the spinal cord. Tactile or psychical influences excite this centre, which acts through the sacral nerves and hypogastric plexus. The *nervi erigentes* originate from the two first sacral nerves. The centre may be influenced reflexly or by impressions transmitted from the brain when it is excited by voluptuous imaginations. Probably also the centre may be excited by the circulation through it of venous blood. In diseases of the spinal cord (such as *tabes dorsalis*) the activity of the centre is destroyed. In the female, during coition, there are phenomena of a similar kind affecting the clitoris, the vaginal walls, the uterus, and possibly the Fallopian tubes. Coitus results in the ejaculation of semen by a reflex mechanism excited by contact and friction. The semen accumulates in the *vesiculæ seminales*; by contractions of these vesicles and of their efferent canals the fluid passes into the urethra, from which it is expelled by rhythmical contractions of the muscular fibres surrounding the bulbous part of the urethra. At the

same moment, it is mixed with the secretion of the prostate and of Cowper's glands. It has been supposed that, in the female, a discharge also occurs from Bartholin's glands.

6. **Fecundation.**—The essential nature of fecundation has already been fully discussed (p. 223, Vol. I. *et seq.*).

7. **Fecundity.**—The general law appears to be that the larger the animal is and the longer the duration of its life, the less is its fecundity. Thus, according to Leuckart, the human female may produce one child per annum; the elephant, one young one every three or four years; the horse and camel, one every two years; the cow and deer, one yearly; the sheep and goat, one or two yearly; the cat, three to six twice yearly; the dog, four to ten twice yearly; the pig, six to twelve twice yearly; the hare, two to five twice or thrice yearly; the rabbit, four to seven five or eight times yearly; and the mouse, four to ten four to six times yearly (Munk).

CHAP. IV.—THE DEVELOPMENT OF THE EMBRYO.

The earlier stages of the development of the embryo have already been described (Chap. II. p. 214, and Chap. IV. p. 244, Vol. I.).[1] We shall now take up the subject at the stage of division of the yolk (Fig. 461, and Fig. 111, p. 234, Vol. I.). If the segmentation involves the whole of the yolk, it is termed *holoblastic*, as occurs in mammals, batrachians, lower crustaceans, worms, etc., but if it involves a portion only of the yolk, leaving the remainder for the nutrition of the embryo during the earliest stages, it is called *meroblastic*, as in birds, amphibians, upper crustacea, insects, and cepalopods. The ovum of the human being is holoblastic. By segmentation, a large number of spherical bodies are formed, constituting the mulberry mass or *morula*, the ovum increasing in size during the process. Segmentation occurs while the ovum is

FIG. 461.—Yolk elements of egg of common fowl. A, yellow yolk; B, white yolk. (Balfour.)

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[1] The student should read these chapters in connection with the subject now under discussion.

passing down the Fallopian tube, and it is over by the third or fifth day. The centre of the morula soon shows a certain amount of fluid, probably derived by imbibition from the fluids around it, and the fluid presses the primitive cells towards the periphery, against the *zona pellucida*, forming a single layer of flattened hexagonal cells. This sac-like structure, lined with cells, is termed the *blastodermic vesicle* (Fig. 120, p. 251, Vol. I.). Some of the smaller cells of segmentation collect at one pole of the vesicle, the *blastopore*, there forming an elevation, in which a depression appears, the convexity being directed inwards. Here the cells form a double layer, the outermost cells being the larger. This is the situation of the *area embryonalis*, in which the embryo is to be formed. The cells next the *zona* constitute the *ectoderm* or *epiblast*, and the inner, which occupy an area more limited in extent, form the *endoderm* or *hypoblast*. The embryonal spot appears in the human ovum, and in that of pachyderms, ruminants, and dogs, on the tenth or twelfth day, and in the rabbit on the fifth day. The hypoblastic cells increase rapidly, and form a layer of cells lining the epiblast, more especially near the embryonal spot. The hypoblastic cells are small, translucent, slightly granular bodies, while those of the epiblast are large, more cylindrical, and more strongly granular. In the embryonal spot the epiblastic cells rapidly proliferate so as to form here a prominence. Next, an intermediate layer of cells appears, developed from the epiblast. This is the *mesoblast* (see Figs. 113, p. 245, and 114, p. 246, Vol. I.). From these layers all the tissues of the embryo are derived, as described at p. 251, Vol. I. See also Figs. 117 and 118, p. 249, Vol. I., in which it will be seen that the blastodermic vesicle becomes infolded, so as to form a cup-shaped body, or rather as if one cup were placed within another, the lips being contin-

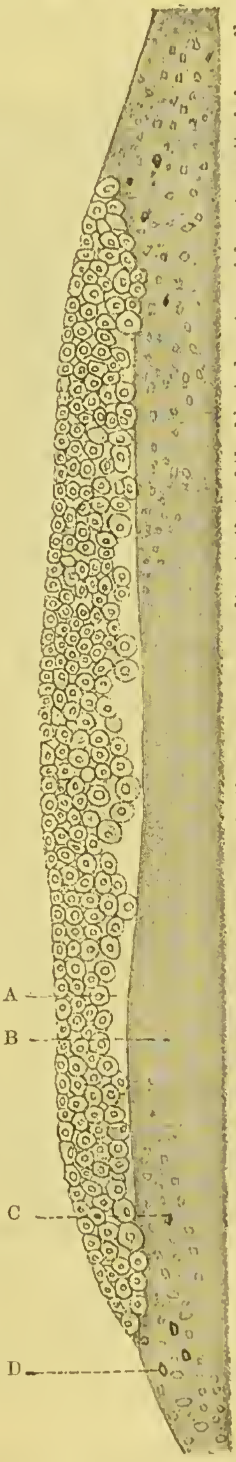

Fig. 462.—Section through the germinal membrane of a hen's egg, in the stage corresponding to that of the blastodermic vesicle. A, cavity below cells; B, yolk; CD, nuclei in yolk. (Rauber.)

uous. The cup shows two layers, an outer epiblastic and an inner hypoblastic, and the space between the two represents the remains of the original cavity of segmentation. The cavity of the infolded portion is the primitive intestine, and its opening is the primitive mouth or *blastopore*. At this stage the embryo is termed a *gastrula*.

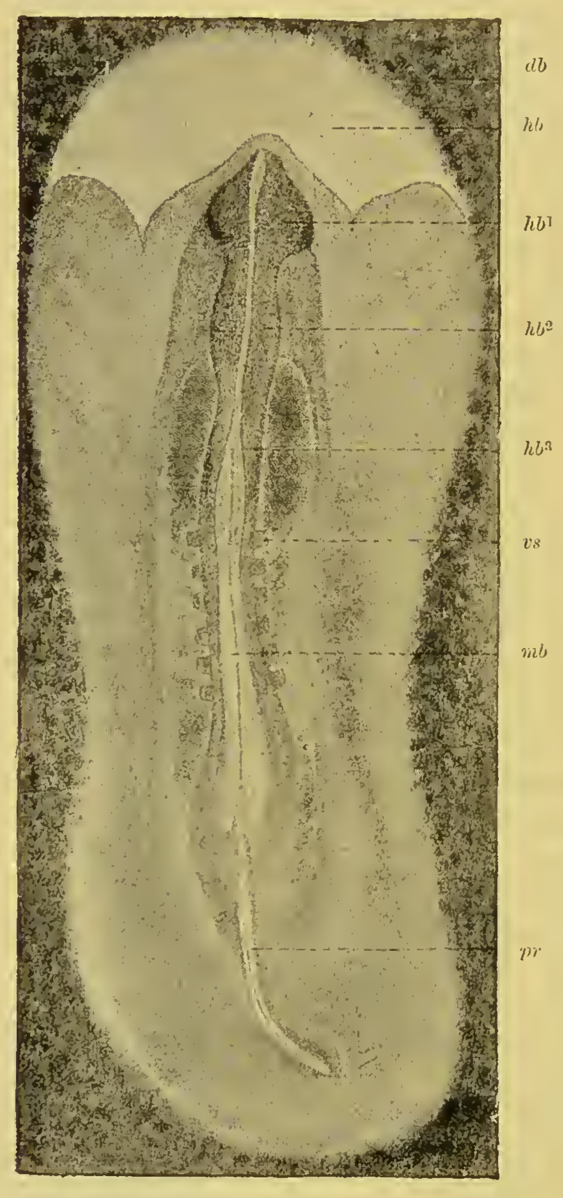

Fig. 463.—Chick at end of twenty-three hours. *db*, germinal area (*area opaca*); *hb*, portion of area pellucida. The development of the nervous system is seen. hb^1, first cerebral vesicle; hb^2, second cerebral vesicle; hb^3, third cerebral vesicle; *mb*, posterior end of medullary groove open; *vs*, six primitive segments. The posterior end shows the primitive streak and the primitive groove, *pr*. (M. Duval.)

At the embryonal spot proliferation goes on rapidly, more especially near the periphery, so that the centre, known as the *area pellucida*, is clearer than the darker peripheral zone, the *area opaca*. This is seen in the rabbit about the seventh or eighth day. In the centre of the *area pellucida*, now somewhat oval in form, appears an elongated portion marked off from the rest and constricted in the middle. This is the *primitive trace*, and in the centre of it, and running longitudinally, we see first a line, the *primitive streak*, and, later, this line shows a furrow or groove, the *primitive groove*. The lips of the groove constitute the *dorsal ridges* or *medullary folds*; the folds enclose plates known as the *medullary plates*, and they coalesce so as to form the *neural canal*. (See Fig. 116, p. 248, Vol. I.). From the neural canal there are developed the cerebro-spinal axis and the terminal organs of sense, the lumen of the tube becoming the central canal of the cord, the aqueduct of Sylvius, and the ventricles of the brain. From the medullary plates the epidermis, epidermic formations, the glands, the salivary glands, and the mucous and serous glands of the nasal and oral cavities are formed.

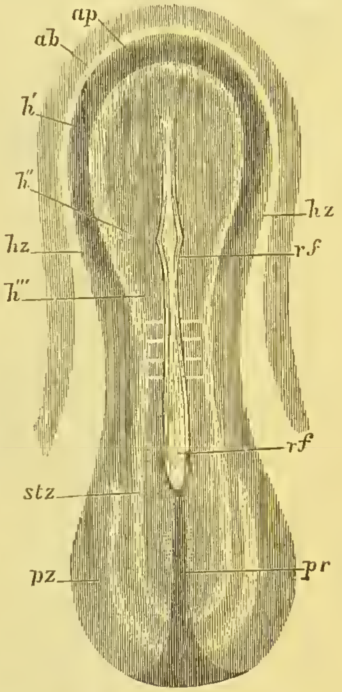

Fig. 464.—Embryo rabbit of about nine days, from the dorsal side. × 22 d. *ap*, *area pellucida; rf*, medullary groove; *h'*, medullary plate in the region of the future fore-brain; *h''*, medullary plate in the region of the future mid-brain; *ab*, optic vesicle; *h'''*, hind brain; *stz*, vertebral zone; *pz*, lateral zone; *hz*, heart. (Von Kölliker.)

By growth and differentiation of cells of the mesoderm, a rod-like structure of cartilage, the *chorda dorsalis*, appears below the neural canal. Each half of the mesoderm then divides into two longitudinal plates. The plate next the *chorda dorsalis* is termed the *primitive vertebral plate*, and the external plate is called the *lateral plate*. The *primitive vertebral plate* divides transversely, so as to form a number of cubical bodies (Fig. 245, *v w*, p. 479, and Fig. 464), the *primitive vertebræ*, from which originate the parts of the vertebræ, exclusive of their bodies and the muscles and ligaments of the vertebral column. Each primitive vertebra differentiates into a dorsal plate, from which the muscles are developed, and an original vertebra. The latter surround the *chorda dorsalis*, and become the vertebral arches, while the *chorda* forms the bodies, and the remains of it are represented by the intervertebral discs. The body of each vertebra really consists of the adjacent halves of two primitive vertebræ, because each primitive vertebra splits by a transverse division in its centre. From the *lateral plates* are developed, by horizontal cleavage, two plates, an outer, termed the *parietal layer of the*

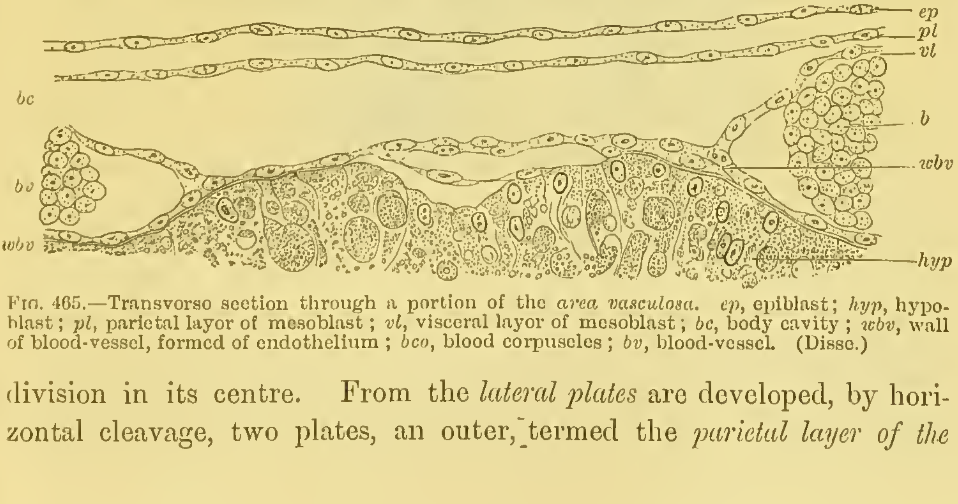

Fig. 465.—Transverse section through a portion of the *area vasculosa*. *ep*, epiblast; *hyp*, hypoblast; *pl*, parietal layer of mesoblast; *vl*, visceral layer of mesoblast; *bc*, body cavity; *wbv*, wall of blood-vessel, formed of endothelium; *bco*, blood corpuscles; *bv*, blood-vessel. (Disse.)

mesoblast, which unites with the epiblast, and an inner, termed the *visceral layer of the mesoblast*, which unites with the hypoblast. Near the vertebral plates a cavity remains between the parietal and visceral layers of the mesoblast, which is the first arrangement of the *pleuro-peritoneal cavity* (see Fig. 116, p. 248, Vol. I.). Later in development, the parietal and visceral layers of the mesoblast separate so as to form the true *body cavity*, the parietal layer forming the walls of the body, except the vertebræ, and the visceral plate forming the intestinal

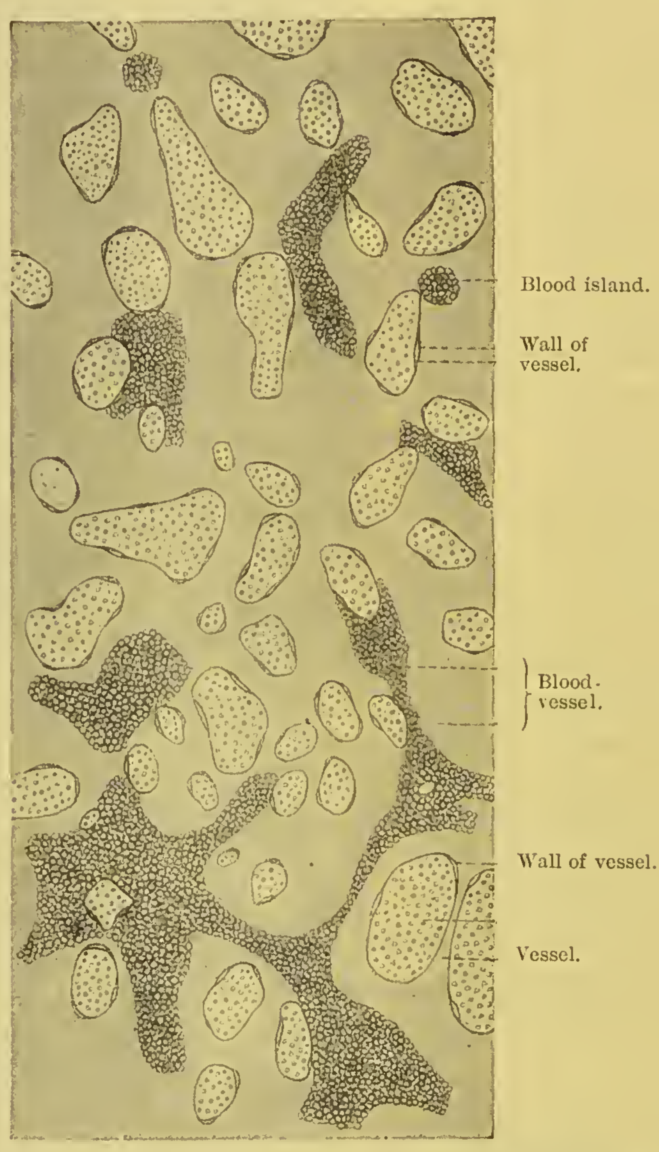

FIG. 466.—Development of vessels and corpuscles in embryo of common fowl (twelfth hour). The dark parts are masses of embryonic blood corpuscles. (Dissc.)

tube, except the epithelium. The term *middle plate* is given to portions of the embryo where there is a confluence between the visceral and parietal layers of the mesoblast, before they separate to form the body cavity, and in the space between the middle plate, the vertebral plate, and the epiblast, there appear the *Wolffian bodies*, which represent the primitive condition of the urinary and sexual organs.

The mesoderm is also the layer from which the vessels are developed. Even before the appearance of the primitive vertebræ, vessels appear as cellular cords, which become hollow by vacuolation, and blood corpuscles are formed from certain of the cells of the spaces (Figs. 465 and 466). From the visceral layer of the mesoblast the heart appears as a short straight rod; this soon becomes hollow so as to form a tube, and the tube twists like the letter *S* and begins to beat. From the upper or anterior half of the cardiac tube two aortæ spring, which run forwards and then backwards, and unite to form a single short vessel. From this arise two *primitive aortæ*, which run backwards on each side of the *chorda dorsalis*. Each aorta gives off four or five little arteries, the *omphalo-mesenteric*

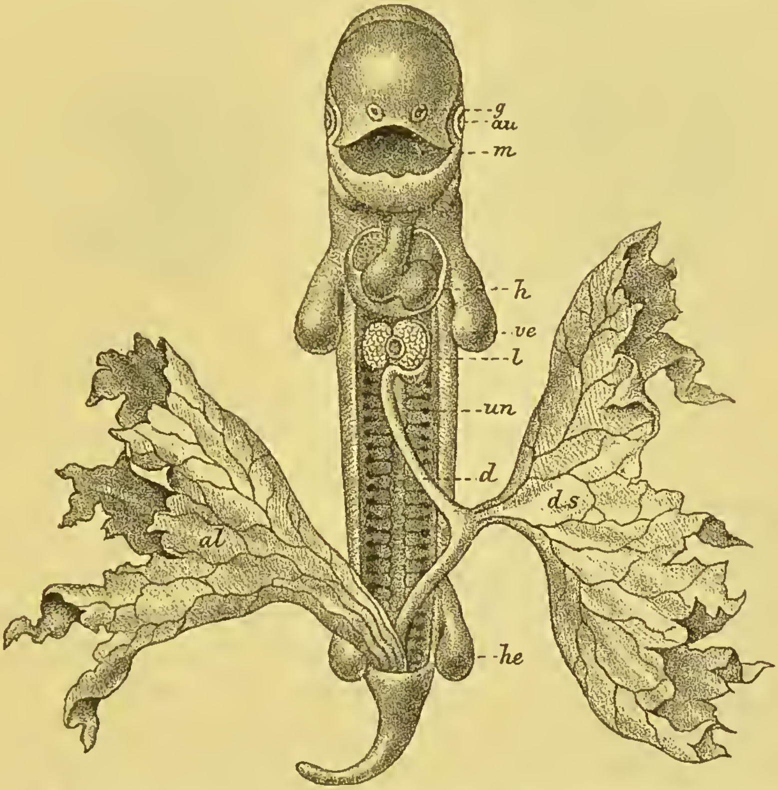

FIG. 467.—Embryo of dog, twenty-fifth day. × 5 d. Seen from the front. *d*, intestinal tube; *ds*, yolk bag; *al*, allantois; *un*, Wolffian body; *l*, primitive liver surrounding the lumen of the omphalo-mesentric vein; *ve*, anterior, *he*, posterior extremity; *h*, heart; *m*, mouth; *au*, eyes; *g*, nasal openings. (Bischoff.)

arteries, which run outwards beyond the germinal area, to form a network in the *area vasculosa.* From these capillaries a vein originates which, running round the edge of the *area vasculosa*, ultimately forms two veins, the *omphalo-mesenteric veins.* These pass to the left lower or posterior part of the heart, receiving branches from the posterior part of the embryo.

In the hypoblast, and soon after the first appearance of the vascular system, a groove appears, the *intestinal furrow*, which ultimately forms a tube by the coalescence of its lips. The muscular wall of the tube, the connective tissue, and the vessels, come from the visceral layer of the mesoblast, while the epithelium and the glands in the intestine are derived from the hypoblast. The intestinal tube is at first closed anteriorly and posteriorly, but a small opening exists about the middle. This is the opening of the *vitelline duct*, which communicates with the vitellus or yolk bag. At this stage the embryo is lying face downwards on the yolk bag, and both the cavity of the body and the cavity of the intestine are open inferiorly (Fig. 467).

CHAP. V.—THE CONNECTION OF THE MOTHER AND THE FŒTUS.

To understand the intimate relation that is established between the mother and the offspring for respiratory and nutritional purposes, it is necessary to consider (1) certain developments in connection with the fœtus, and (2) certain developments in the uterus of the mother. In some animals, such as the fish, the amount of yolk is sufficient for the nourishment of the embryo until it can feed itself, and it respires directly by the gases in the water. Such an embryo, at an early period, shows the appearance seen in Fig. 468, where the yolk bag is seen to communicate with the intestinal canal, and in which no other vesicles or membranes are necessary. In amphibians and reptiles the yolk bag is drawn into the body cavity at a very early period, and the embryo is nourished largely by the albuminous matter in which the egg is embedded. In birds the arrangement is much the same as in mammals, but a sufficient store of nourishment is contained in the yolk and white of the egg, and the chick breathes by gaseous interchanges taking place through the porous shell of the egg. It is necessary therefore in the bird to bring the blood of the chick into close relation with the external air for respiratory purposes, and at the same time to bring it into relation with

FIG. 468. — Fish with umbilical vesicle underneath.

the nutritious matter stored up in the egg. The mammal, however, has only a very small amount of nutritious matter in the egg, and the fœtus has to be brought at a very early period into such close relation to the mother that the blood of the fœtus receives from the blood of the mother nutritious matter, while at the same time the fœtus also respires by the mother's blood.

At each border of the embryonal area, a portion of the mesoblast, clothed with the epiblast, rises into a fold, the *amniotic fold*, and these folds coalesce over the back of the embryo, while they grow downwards in a sac-like form, so as to enclose the embryo on all sides in a sac termed the *amnion.* The outer layer of the fold, sometimes termed the *false amnion*, coalesces with the *zona pellucida*, now much thickened, and the two form the *chorion.* The space between the inner layer and the surface of the embryo, termed the *cavity of the amnion*, contains the *waters* or *amniotic fluid.* The inner layer also ultimately coalesces with the chorion. The fluid, probably a transudate from the embryo's blood, contains 2 to 3 per cent. of solids.

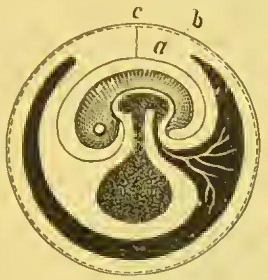

FIG. 469.—Diagram to show embryonal sacs. *a*, cavity of amnion; *b*, *zona pellucida*; *c*, layer of amnion. Pear-shaped body is the umbilical vesicle. The body with vessels is the allantois. (Dalton.)

FIG. 470.—Diagram to show embryonal sacs in bird's egg. *a*, umbilical vesicle; *b*, amnion; *c*, allantois, with vessels, extending all round on inner surface of shell. (Dalton.)

After some time, the duct of the umbilical vesicle, the *vitelline* duct, becomes narrower and longer, so that the vesicle is further moved from the embryo, as in Fig. 471. From the posterior portion of the intestine a vesicle develops, termed the *allantois*, lined by epithelium from the intestine, while its wall is formed from the visceral layer of the mesoblast. The allantois, when it has developed to its normal size, communicates with the intestine by a duct called the *urachus.* It contains the *allantoic fluid*, in which there exist about 4 per cent of solids, in which urea, allantoin, albumin, and salts have been found. It may be regarded as embryonal urine.

FIG. 471.—Diagram of embryo, showing the umbilical vesicle.

The surface of the *chorion*, which is formed, as stated above, by the confluence of the *zona pellucida* with the amnion, becomes covered with villi, and the blood-vessels of the embryo, ramifying on the allantois, form loops in the villi of the chorion. During these changes, the umbilical vesicle has become smaller and smaller, and by the time the vessels of the chorion have reached the villi, by which, as will be seen presently, the blood of the fœtus is brought near the mother's blood, the umbilical vesicle has almost disappeared. The relations of the embryonal vesicles is well shown in Fig. 472.

As the ventral laminæ of the wall of the embryo grow, they gradually approach and ultimately coalesce, leaving only a passage at the umbilicus, for the duct or neck of the allantois. In the abdominal cavity, a portion of the allantois, or rather of its duct or neck, becomes constricted at the inner opening of the umbilicus, and the deeper portion becomes the urinary bladder (Fig. 472).

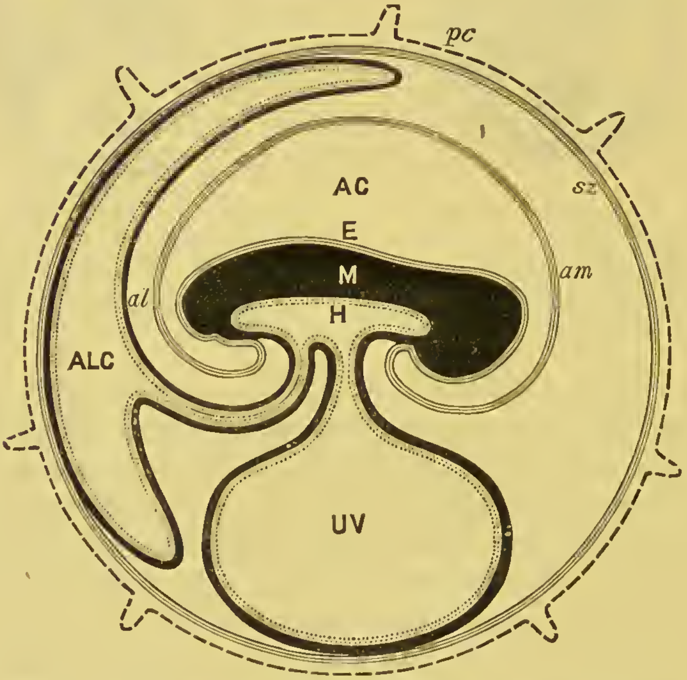

Fig. 472.—Diagram of the embryonal vesicles. *pc*, *zona pellucida*, with villi; *sz*, serous layer; *am*, amnion; AC, cavity of amnion; UV, umbilical vesicle; *al*, allantois; ALC, cavity of the allantois; E, outer layer of embryo, epiblast; M, middle layer, mesoblast; H, alimentary canal. (Sir William Turner.)

The developmental processes above described are completed by the end of the third or beginning of the fourth week of intra-uterine life, and from this time the growth of special organs goes on with greater rapidity, because the fœtus is henceforth more amply supplied with nutritious matters from the blood of the mother.

We shall next consider the changes that occur in the uterus to fit it for the reception of the ovum. The mucous membrane becomes thickened by the proliferation of epithelium, the uterine glands become larger, and their secretion becomes much more copious. The surface of the mucous membrane also becomes villous or shaggy in appearance, and it now constitutes a membrane termed the *decidua*. The part lining the uterus generally is termed the *decidua vera*, the portion near the fundus of the uterus in which the ovum is embedded is the *decidua reflexa* (so called because it covers, or is reflected over the ovum), and the portion to which the allantois and the villi of the chorion are to be attached is the *decidua serotina*. As the ovum increases in size, the *decidua reflexa* comes into contact with the *decidua vera*, and from the action of pressure the vessels and glands of the *decidua reflexa* become atrophied. The *decidua vera* also becomes atrophied, so that by the end of the sixth month both *deciduæ* form only a thin membrane. During the earliest stages of pregnancy, the *decidua vera* is about 10 mm. in thickness, but by the end of the fifth or sixth month it is only 1 to 2 mm. The uterine glands become enlarged, and their openings have thick roundish-shaped mouths. We then find the *decidua* has two layers; an outer layer rich in epithelial cells, and a deeper layer, spongy in character. By the middle of the period of gestation, the spongy part has developed enormously, so that spaces of considerable size are formed. Between the uterine glands we find large globular

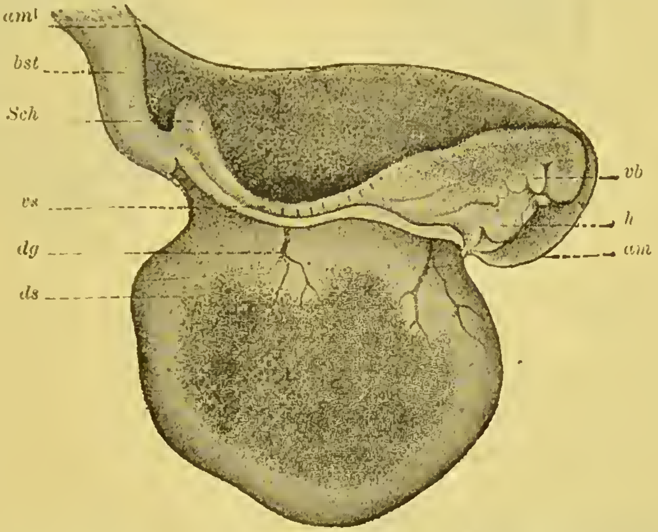

Fig. 473.—Human embryo with the umbilical vesicle and the amnion (the fifteenth or eighteenth day). *am* and am^1, amnion; *bst*, position of anus; *Sch*, caudal end; *vs*, primitive vertebrae; *dg*, blood-vessels on umbilical sac, *ds*; *h*, heart; *vb*, visceral arches. (Coste and His.)

cells, 30 to 40 μ in diameter, termed the *decidual cells* of Friedländer. The position of the *deciduæ* is shown diagrammatically in Fig. 474.

As already shown, the vessels of the allantois, which are continuous with those of the intestinal canal, from which the allantois grows, pass out into the villi of the chorion. The omphalo-mesenteric vessels are now useless, as all the yolk has been absorbed. The neck of the allantois elongates and it contains two arteries, now called the *umbilical arteries.* These supply vessels to the allantois which, as already stated, form capillary loops in the villi of the chorion. The villi of the chorion are formed partly from the wall of the allantois which is rich in vessels, and partly from the serous covering of the ovum, or *zona pellucida.* The serous covering consists of epithelial cells, which proliferate so as to form a layer of considerable thickness. Each villus contains a capillary network and one or more small veins. The villi of the chorion are now pushed, or rather they grow, into the uterine mucous membrane in such a way as to bring the blood of the fœtus into close relation to the blood of the mother.

Fig. 474.—Diagram of uterus showing the *deciduæ.* (Dalton.)

Fig. 475.—Diagram showing the villi of the chorion opposite the allantois. (Dalton.)

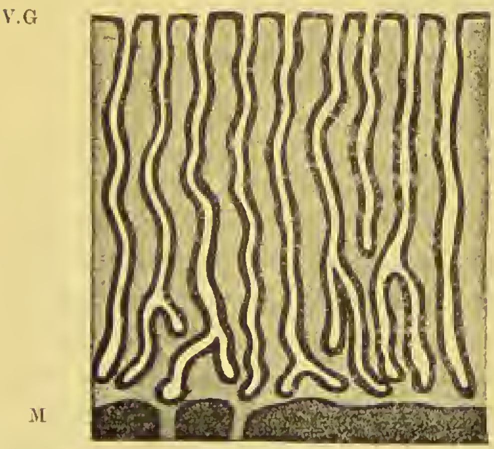

Fig. 476.—Diagram showing a section through the mucous membrane of the uterus in the unimpregnated state. V.G., uterine glands; M, muscular layer. (Kundrat and Engelmann.)

Along with the formation of the *deciduæ*, the wall of the uterus becomes enormously thickened by development of muscular tissue, and the large venous sinuses, described at p. 758, increase in size, so as to form a cavernous-like tissue, supplied with blood by the branches of the uterine arteries. At the same time, the uterine glands become much longer. The appearance of the mucous membrane of the uterus in the unimpregnated state is shown diagrammatically in Fig. 476, and the changes produced during pregnancy are depicted in Fig. 477.

In monotremes and marsupials, no firm connection is established between the mother and offspring, the ova remaining loosely in the uterus. In these, no chorion exists, and, of course, no placenta. Hence they may be called *achoriata* or *aplacentaria*. Other mammals have a placenta. In the solidungulæ (horse and ass), in the pachyderms (except the elephant), in the camel, and in the whale (cetacea), the villi of the chorion are scattered all over the ovum, and hence they have a diffuse placenta. The small villi of the chorion, 1 to 2 mm. in length, pass into depressions in the uterine mucous membrane between the mouths of the uterine glands. In the pig, villi occur only in the middle of the ovum. In ruminants, the villi occur only at certain places, so that many small placentæ or cotyledons are formed. The cotyledons correspond to hypertrophied portions of the uterine mucous membrane. When the villi are withdrawn from the depressions in the cotyledons of the mucous membrane, no bleeding takes place, and the cotyledonary enlargements are serviceable for future pregnancies. In the human being, however, as also in monkeys, carnivora, rodents, and in the elephant, the villi are so irregular in form, and so intimately related to the venous sinuses in the uterine wall, that they cannot be drawn out like the finger out of a glove; but the walls of the uterine sinuses are torn, bleeding occurs, and portions of the uterine part of the placenta, as well as the fœtal part, come away after the birth of the offspring. In man, monkeys, rodents, and in the elephant, the placenta is disc-shaped, the chorion becoming attached to the uterine mucous membrane only at one end of the ovum; in carnivora, on the other hand, the chorion surrounds the ovum like a band, so that the placenta is zonular.

As already shown, the part of the decidua entering into the formation of the placenta is the *decidua serotina*. It constitutes the maternal portion. The fœtal portion is the part of the chorion, termed the *chorion frondosum*, which comes into contact with, and sends its villi into, the depressions or crypts of the *decidua serotina*. The two together, *chorion frondosum* and *decidua serotina*, form the *placenta*. If a section be made through the wall of the uterus and the attachment of the chorion to this part, we may see the structure demonstrated in Fig. 477. The relation of the *decidua serotina* to the other two *deciduæ* is illustrated by Fig. 474.

The villi of the chorion are formed of connective tissue, and they are covered by an epithelial layer derived from the *decidua serotina* (Fig. 478).

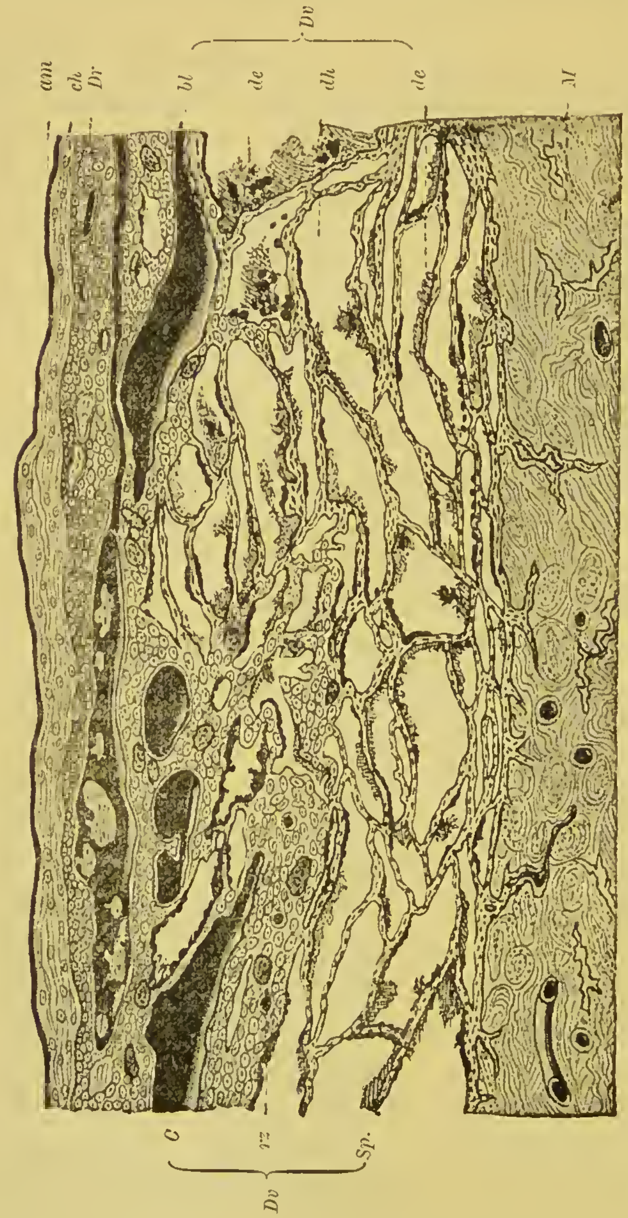

FIG. 477.—Section through the attachment of the placenta to the uterus at the sixth month of pregnancy. *M*, muscular structure of uterus; *Dv*, *decidua vera*; *C*, compact, and *Sp*, spongy, portions of decidua; *Dr*, *decidua reflexa*; *ch*, chorion; *am*, amnion; *bl*, blood-vessels in the compact layer; *dh*, spaces formed by enlarged glands; *de*, glandular epithelium; *rz*, giant cells in the compact tissue. (Leopold.)

As already explained, these villi are pushed into the cotyledons which contain large vascular spaces, formed by a dilatation of the maternal blood-vessels of the *decidua serotina*. The villi perforate the walls of these spaces, and the irregularly-shaped villous ends float in the maternal blood, being separated from it by the epithelial layer already referred to. The maternal blood is brought to the vascular spaces by spirally-

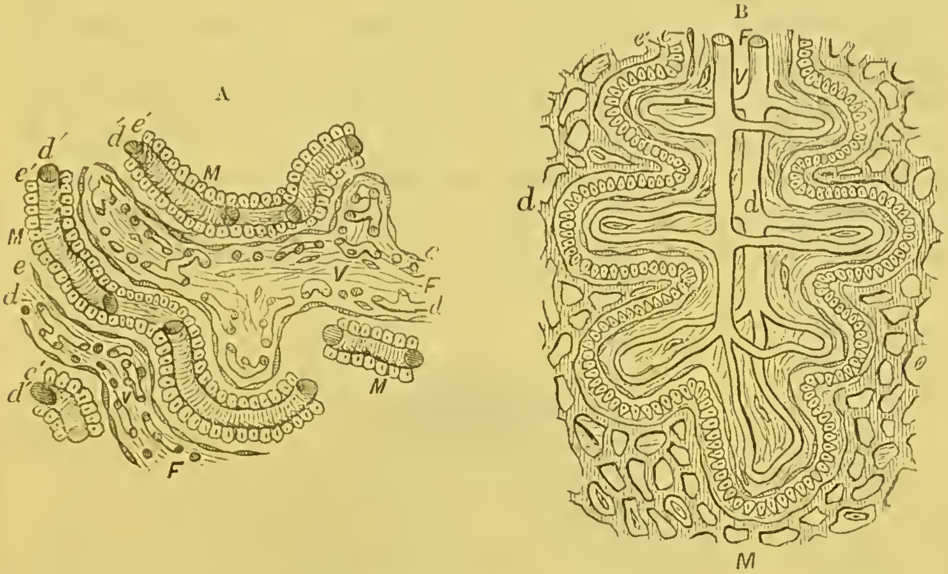

Fig. 478.—Diagrammatic view of the minute structure of the placenta. A, of a cat; and B, of a cow. *F*, fœtal, *M*, maternal parts of placenta; *c*, epithelium of chorion; *c′*, epithelium of maternal placenta; *d*, fœtal blood-vessels; *d′*, maternal blood-vessels; *v*, villus. The layer, *e′*, represents the maternal cells derived from the *decidua serotina*. (Sir William Turner.)

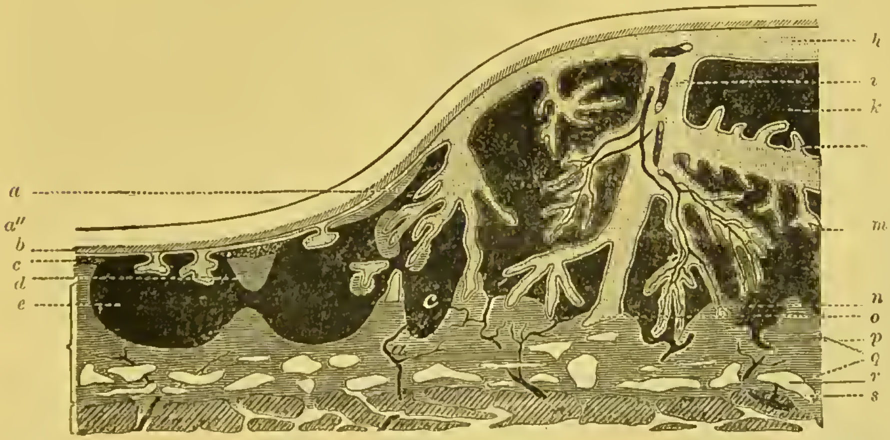

Fig. 479.—Semi-diagrammatic view of the relations of the placenta and uterus in the middle of the fifth month. *a′*, portion of decidua serotina; *a″*, amnion; *b*, chorion; *c′*, decidua reflexa; *d*, portion of decidua serotina; *e*, uterine sinus (all the portion in black); *f*, decidua serotina with glands; *g*, muscular coat; *h*, villi of chorion; *i*, vessels in villi of chorion; *k*, uterine sinus; *l*, *m*, *n*, *o*, ends of villi of chorion; *p*, *q*, decidua serotina; *r*, *s*, sections of glands. The chorionic portion, with irregularly shaped villi has a dotted surface; the space of the uterine sinus is black; the serotina is represented by a shading of horizontal lines; and the reflexa, *c*, is shown by faint white dots. Observe *a*, one of the curling uterine arteries, opening into *c*, the uterine sinus. These arteries in the serotina are represented black. (After Leopold and O. Hertwig.)

coiled vessels, which do not break up into capillaries, but open into the spaces. The fœtal blood is brought to the capillaries in the villi of the chorion, so that the latter resemble the gills of a fish immersed in water, the water being here represented by the maternal blood. There is diffusion, both as regards nutritive matters and gases, between the bloods of the two beings, mother and offspring, through the thin membranes separating them. The fœtal blood in the vessels of the chorion is richer in carbonic acid and poorer in oxygen than the blood of the mother, and it gets rid of carbonic acid and receives oxygen. At the same time, the high pressure in the maternal vessels favours the transudation of albuminous, fatty, saccharine, and saline matters into the placental tissues, and these matters will be imbibed by the fœtal vessels. The arrangement is shown in Fig. 478 and also in Fig. 479.

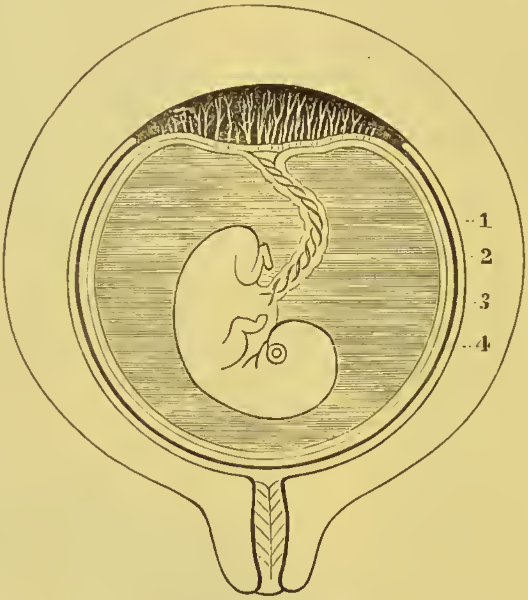

Fig. 480.—Diagram showing the fœtus *in utero*. 1, wall of uterus; 2, *decidua vera;* 3, 4, sac of amnion, filled with fluid. (Dalton.)

The position of the fœtus and of the placenta in the uterus is shown diagrammatically in Fig. 480. The dark disc-shaped mass at the fundus is the placenta.

The Fœtal Circulation (Fig. 481).—The embryonic heart consists of a pulsating *sinus venosus* and of a pulsating *bulbus arteriosus*, each communicating with the ventricle. A septum is developed both in the ventricle and in the *sinus venosus*, dividing both into a right and left half, but the right auricle communicates with the left by an opening, the *foramen ovale.* The aorta and pulmonary artery are next formed, but a wide branch exists between these, the *ductus Botalli*, or *ductus arteriosus.* In the mature fœtus, the fluid brought from the placenta by the umbilical vein is partly conveyed at once to the *vena cava ascendens* by means of the *ductus venosus*, and partly flows through two trunks that unite with the portal vein, returning the blood from the intestines into the substance of the liver, thence to be returned to the *vena cava* by the hepatic vein. Having thus been transmitted through the placenta and liver, the blood that enters the *vena cava* is purely arterial in its character, but, being mixed in the vessels with the venous blood returned from the trunk and lower extremities, it loses this character in some degree by the time that it reaches the heart. In the right auricle, which it then enters, it would also be mixed with the venous blood, which is brought down from the head and upper extremities by the descending cava, were it not that a provision exists to impede (if it does not entirely prevent) any further admixture. This consists in the arrangement of the Eustachian valve, which directs the *arterial* current (that flows upwards through the ascending cava) into the *left* side of the heart, through the foramen ovale, an opening in the septum between the auricles, whilst it directs the *venous* current (that is being returned by the superior vena cava) into the *right* ventricle. When the ventricles contract, the arterial blood contained in the left is propelled into the ascending aorta, and supplies the branches that proceed to the head and upper extremities before it undergoes any further admixture, whilst the venous blood contained in the right ventricle is forced into the pulmonary artery, and thence through the *ductus arteriosus*—branching off from the pulmonary artery before it passes to the two lungs—into the descending aorta, mingling with the arterial

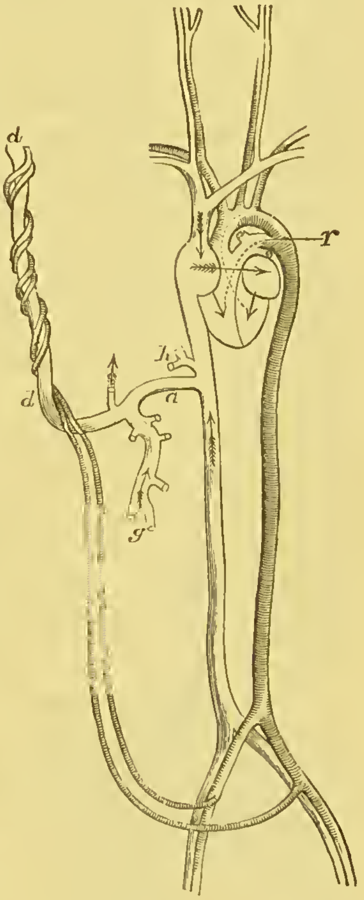

Fig. 481.—Diagram of the fœtal circulation. *d d*, umbilical vein, with two umbilical arteries coiled round it; *a*, *ductus venosus* : *h*, vessels to liver; *g*, vessels from alimentary canal; *r*, *ductus arteriosus.*

currents which that vessel previously conveyed, and thus supplying the trunk and lower extremities with a mixed fluid. A portion of this is conveyed by the umbilical arteries to the placenta, in which it undergoes the renovating influence of the maternal blood, and from which it is returned in a state of purity. In consequence of this arrangement, the head and upper extremities are supplied with pure blood returning from the placenta, whilst the rest of the body receives blood which is partly venous. This is probably the explanation of the fact, that the head and upper extremities are most developed, and, from their weight, occupy the inferior position in the uterus. At birth, the course of the circulation undergoes changes. As soon as the lungs are distended by the first inspiration, a portion of the blood of the pulmonary artery is diverted into them and undergoes æration, and, as this portion increases with the full activity of the lungs, the ductus arteriosus gradually shrinks, and its cavity finally becomes obliterated. At the same time, the *foramen ovale* is closed by a valvular fold, and thus the direct communication between the two auricles is cut off. When these changes have been accomplished, the circulation, which was before carried on upon the plan of that of the higher reptiles, becomes that of the complete warm-blooded animal, all the blood which has been returned in a venous state to the right side of the heart being transmitted through the lungs before it can reach the left side or be propelled from its arterial trunks. After birth, the umbilical arteries shrink and close up, and become the lateral ligaments of the bladder, while portions remain as the superior vesical arteries. The umbilical vein becomes the *ligamentum teres.* The *ductus venosus* also shrinks, and finally is closed. The *foramen ovale* is also closed, and the *ductus arteriosus* shrivels and becomes the *ligamentum arteriosum.*

CHAP. VI.—CONCLUDING PHENOMENA OF REPRODUCTION AND LACTATION.

1. The Phenomena of Pregnancy.—In the human being the term of pregnancy is from 275 to 280 days (or ten lunar months) from the time of fecundation. During that time, the uterus increases in size, its wall becomes enormously thickened, and the organ rises gradually from the pelvis into the abdominal cavity. Coincident with these changes, the mammary glands increase in size, the areolæ round the nipples become darker in colour, not unfrequently pigment may be deposited in unusual quantity in the skin, the female may become full and plethoric, more especially during the later months, and there are many constitutional effects varying in different individuals. Munk gives in weeks the time of gestation of the following animals—elephant, 90; giraffe, 63; horse, 48; cow, 40; sheep and goat, 20 to 22; pig, 17; dog, 9; cat, 8; and rabbit, 5 weeks.

2. **The Phenomena of Parturition**—It has been conjectured that the exciting cause of parturition is fatty degeneration of the decidual cells. We must also suppose that the uterine nerves are irritated so as to bring about clonic spasms of the muscular coat of the uterus. Under the strong pressure of the contracting muscular walls of the uterus, the most prominent part of its contents is forced into the canal of the cervix, and opens the mouth of the uterus widely, so that uterus and vagina are now one cavity. The membranes then rupture and the amniotic fluid escapes. The fœtus is expelled by the contractile force of the uterine walls, aided by the abdominal and other muscles. It is soon followed by expulsion of the placenta. When the latter separates, in the human female, the uterine vessels are torn across, and there is a loss of blood. The hæmorrhage, which comes chiefly from the large placental sinuses, is soon arrested in a healthy state, by the powerful contractions of the uterus. The whole placenta, maternal and fœtal, separates and is extruded. The inner surface of the uterus, opposite the attachment of the placenta, may be covered with shreds of decidual membrane and clots of blood, both of which are ultimately removed in a discharge, termed the *lochia,* which passes for several days. After parturition, the muscular walls of the uterus atrophy by fatty degeneration, and the mucous membrane resumes its normal state. When several fœtuses are developed, each is expelled with its own placenta.

There is a reflex centre in the lumbar region of the spinal cord, connected with the rhythmic contractions of the uterus during parturition.

In a healthy woman, not supplying her offspring with milk, ovulation and menstruation usually commence about six weeks after the accouchement. If lactation is persevered in, as a rule, menstruation does not occur until after a period of ten or twelve months.

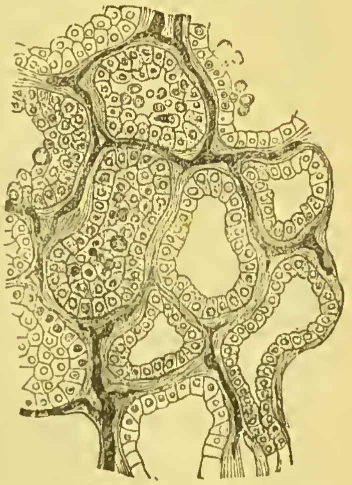

Fig. 482.—Vesicles from the mammary gland of a woman during suckling, showing acini, some filled with milk, and also the capillaries.

3. **Lactation.**—The *mammary gland,* during pregnancy and suckling, consists of from 15 to 20 acinous glands, bound together by loose connective

tissue, so as to form a gland-like organ. Each gland has its own duct opening on the *nipple*, and a little before it opens on the nipple each duct shows a small fusiform enlargement, the *milk sac*. The milk sacs with the globular vesicles of the gland show an arborescent appearance in section. Each acinus is lined by cylindrical epithelium resting on a *membrana propria* (Fig. 483). The size of the epithelial cells varies. They are short in full acini, and cubical or even cylindrical in empty ones. Outside the *membrana propria* we find connective tissue interspersed with leucocytes and connective tissue cells.

After lactation has ceased, the connective tissue between the lobules increases in quantity, and the small lobules gradually disappear. In children of both sexes the mammary glands consist of connective tissue enclosing minute glandular ducts, having bulbous ends, but true vesicles are wanting. In even the adult man the gland may have this structure.

FIG. 483.—Transverse section of mammary gland of a pregnant rabbit. × 240 d. *f*, fat in cells; *m*, *membrana propria*. (Method No. 138, Appendix.)

The skin of the nipple and the areola is strongly pigmented, and has granules of pigment in the deeper layer of cells of the epidermis. The papillæ are long in this region. Smooth muscular fibres form a ring round the orifices of the ducts, and some run to the summit of the nipple. In the skin of the areola round the nipple, in pregnant and suckling women, we may find accessory milk glands, the *glands of Montgomery*.

The blood-vessels break into a network of capillaries surrounding the acini, and lymphatics are numerous in the gland itself and also in the areola. The nerves supplying the gland are probably distributed to the vessels and to the smooth muscular fibres.

FIG. 484.—Thick section through the mammary gland of a woman, two years after parturition. × 50 d. 1, coarser, 2, finer, duct; 3, lobules of gland separated by connective tissue. (Method No. 139, Appendix.)

The mammary glands are two in number in man, monkeys, elephant, and sloth; two to four in ruminants and pachyderms; ten in rodents and carnivors, and eight to twenty-two in pigs (Munk).

Milk, when examined with the microscope, is a clear fluid, in which we find drops of fat or oil, 2 to 5 μ in diameter. These are the *milk globules* suspended in the fluid. From the fact that the globules do not coalesce, it is supposed that each globule is surrounded by a thin caseinous envelope. Sometimes also we see in milk larger globules even enclosing cells that may be leucocytes (Fig. 485).

The milk secreted before, and for a few days after parturition, shows peculiar characters. We find *colostrum corpuscles*, large cells full of coloured or colourless fatty particles.

The milk globules are formed in the epithelial cells of the gland, and it has been ascertained that the cells do not perish when the secretion escapes. The fatty particles are pushed to the lumen of the gland and escape from the cell, and the latter may again form fresh particles.

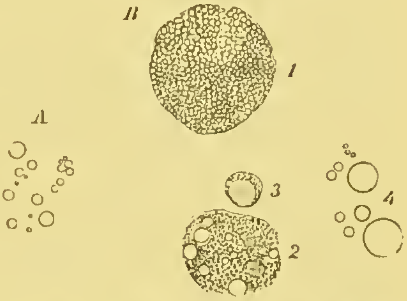

FIG. 485.—*A*, milk globules from woman's milk. × 560 d. *B*, elements of colostrum from a pregnant woman. × 560 d. 1, cell containing small fatty globules; 2, cell containing coloured fatty globules; 3, leucocyte; 4, milk globules. (Method No. 140, Appendix.)

A woman secretes from 1 to 1·3 litre of milk *per diem*. A cow may secrete as much as 24 litres, that is 25 kilogs. in the same time. This amount represents about 3 kilogs. of solids. The weight of the mammary gland of the cow is about 5 kilogs. with 24 per cent. of solids, so that the gland, in favourable circumstances, will secrete 2·5 times its own weight in twenty-four hours. Sheep and goats secrete 1 to 1·5 litre daily (Munk).

Milk is of a whitish colour, opaque to light, and odourless. It has a sweet taste. The specific gravity is from 1025 to 1034. When fresh, the milk of woman, of the cow, and of the goat is neutral or weakly alkaline, and that of carnivors may be slightly acid. When allowed to stand, fatty globules float to the top, constituting a layer of cream. On prolonged exposure to air, milk first becomes neutral, then acid, and the acidity increases until a point is reached when coagulation takes place, the milk separating into a fluid, the *milk serum* or *whey*, and a clot, formed of casein. The amount of water fluctuates from 82 to 90 per cent., and the solids from 10 to 18 per cent. About 2 to 5 per cent. of the solids consist of albuminous substances, chiefly casein, an alkali-albumin kept in solution by the alkaline salts present in milk. When the salts are neutralized by an acid, the casein coagulates; hence it does not coagulate merely on heating. In addition to casein we have a small amount of albumin coagulable by heat. It is remarkable that casein can be separated from milk, and from the soluble albumin, by pressing it through porous earthen cylinders (Munk). The casein, as already stated, forms a thin envelope round each globule of fat, and if it is destroyed by mechanical movement (as in churning), the caseinous envelope is ruptured and the drops of oil run together to form *butter.* By removing *cream,* the milk left, *skimmed milk,* is poorer in fat, and if water is then added, the milk acquires a bluish colour.[1] When milk is diluted with 70 times its volume of water, it becomes transparent. Skimmed milk has a higher specific gravity than fresh milk, because the fatty particles of cream are lighter than water.

The fats of milk contain olein, palmitin, stearin, caproin and butyrin. Human milk contains twice as much olein as palmitin and stearin, but they are about equal in cow's milk. In cow's milk, olein constitutes $\frac{2}{5}$ths, palmitin $\frac{1}{3}$rd, stearin $\frac{1}{6}$th, and butyrin and caproin $\frac{1}{14}$th of the total fat (Lebedeff). Butter consists of the fat of milk. Butter-milk contains 9 to 10 per cent. of solids, including all the casein, milk-sugar, and about 1 per cent. of fats. Centrifugalized milk contains almost no fat—only ·2 per cent., so that it is milk minus fat.

Milk contains 4 to 6 per cent. of milk-sugar. This changes into lactic acid by fermentation when milk sours. The casein precipitated carries fatty particles with it, so that cheese consists of fat and casein. By the action of hydrochloric or sulphuric acids it is changed into lactose or galactose, a sugar capable of alcoholic fermentation. The addition of yeast to milk may also first produce lactic acid, which, in turn, produces lactose from milk-sugar, and this may then undergo the alcoholic fermentation. Koumis is thus obtained. It contains 10 per cent. of solids; 2 to 3 per cent. of alcohol, 2 per cent of fat, 2 per cent. of sugar, 1 per cent. of lactic acid, 1 to 2 per cent. of casein, and 1 volume per cent. of carbonic acid.

The salts of milk average ·6 per cent. and they consist chiefly of phosphate of lime, with chloride of calcium, phosphate of magnesium, and traces of iron. The ash of milk is very similar to that of blood corpuscles. Milk also contains 7·6 per cent. of carbonic acid and traces of oxygen and nitrogen.

The following tables show many interesting facts regarding the composition of milk, and the figures should be compared with those in Table III.[2]

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[1] Tatlock gives the average composition of skimmed milk as follows:—(1) *By repose and skimming*—fat, 1; casein, 3·44; milk-sugar, 5·14; ash, ·75, and water, 89·67. (2) *By separator*—fat, ·20; casein, 3·40; milk-sugar, 5·01; ash, ·75, and water, 90·64.

[2] Robert R. Tatlock, *The Produce of the Dairy*, 1888.

Table I.—*Ash of Cow's Milk.*

	Per cent.
Potash,	20·00
Soda,	3·67
Lime,	24·56
Magnesia,	4·35
Phosphoric acid,	32·07
Sulphuric acid,	·69
Chlorine,	14·66
	100·00

Table II.—*Composition of Various Milks.*

	Cow.	Ewe.	Goat.	Mare.	Ass.	Sow.	Bitch.	Human.
Butter fat, ...	3·53	11·28	5·80	2·50	1·55	6·60	9·72	3·10
Casein (curd), ...	3·34	8·83	4·20	2·70	1·70	12·89	11·70	2·45
Milk-sugar, ...	4·75	3·58	4·94	5·50	5·80	·50	3·00	6·70
Mineral matter (ash)	·75	1·09	1·00	·50	·50	3·01	1·35	·30
Water, ...	87·63	75·22	84·06	88·80	90·45	77·00	74·23	87·45
	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00
Specific gravity,	1031·7	1039·3	1032·7	1031·0	1033·0	1044·0	1036·0	1033·5

Woman's milk is distinguished from cow's milk by containing less saline matter, less fat, and by the nature of the casein. The casein of cow's milk forms large masses when coagulated : that of woman's forms very fine flakes. The casein of woman's milk is more readily acted on by the gastric juice. The casein of mare's milk resembles that of human milk. It is, therefore, not a matter of indifference to the child to have the milk of the cow instead of the milk of its mother.

The quality of the milk changes during lactation, which lasts in women and in the cow about ten months, and in the sheep and goat four months. In women, the percentage of casein and fat increases to the end of the second month, but the sugar diminishes even in the first month. During the fifth and seventh months, the fat also diminishes, and the casein diminishes between the ninth and tenth months. The salts increase for the first five months; then they diminish.

The quantity of solids is increased by a good diet, especially if it be rich in albuminous matter. Thus, with a poor diet, the solids in the milk of women during the siege of Paris were 11·7 per cent.; but, at a later period, with a rich diet, they rose to 14 per cent. The increase affected all the constituents. The same results have been found with animals. It is curious that a large increase of fat in the food tends to diminish the fat in milk, while the carbohydrates have no influence. The last portions of milk drawn from a gland are richer in fat than the first portions. Two days after weaning, the solids decrease by $\frac{1}{3}$rd, the casein by $\frac{5}{6}$ths, and the milk sugar by $\frac{1}{4}$th.

Table III.—*Composition of some Condensed Milks.*

	Swiss.	Swiss (pure).	Alpine (pure).	English.	Anglo-Swiss.	Italian.	Scandinavian.
Butter fat,...	9·76	11·37	11·15	8·30	11·73	10·45	9·50
Casein, ...	10·20	11·48	11·29	11·84	15·17	14·84	15·36
Milk-sugar,	51·02	13·37	13·14	50·79	16·24	49·90	15·63
Cane-sugar,		None.	None.		29·46		32·14
Ash, ...	2·32	2·38	2·07	2·00	2·30	2·12	2·43
Water, ...	26·70	61·40	62·35	27·07	25·10	22·69	24·94
	100·00	100·00	100·00	100·00	100·00	100·00	100·00

DEATH.

Death is the cessation of all vital phenomena, without the capability of resuscitation. During the whole of the lifetime of an individual, there is death in one sense occurring here and there throughout the body. Each tissue is developed, grows to maturity, performs its functions, decays, and dies. Probably no tissue lasts throughout the whole of the somatic life. Thus the cells of the blood are continually changed. Again hairs, nails, feathers, and teeth have each a certain period of existence, at the termination of which they die and separate from the rest of the body. At last, however, a time comes when the general death of the body takes place. This is what we usually term *death*. It results from failure either of the action of the heart, of the lungs, of the brain, or from death of the blood, as in cases of severe septic poisoning. Death beginning at the heart (*fainting*) is termed *syncope*, at the brain, *coma*, and at the lungs, *asphyxia*. When the action of the heart becomes weaker and weaker until it ceases to beat, either from feebleness of its walls, or from poisoning by carbonic acid or want of oxygen, in consequence of a state of asphyxia, death is said to occur by *asthenia*. After *somatic* death, the tissues may live for a short time, but they gradually die one by one. Muscular irritability disappears, and the muscles stiffen from coagulation of their substance. This state, the "stiffness of death," is called *cadaveric rigidity*. After a time, the rigidity passes off, the muscles and other tissues become soft, and the body, now the prey of putrefactive organisms and subjected to the physical and chemical agencies of nature, is resolved into the elements of which it was at first composed.

APPENDIX.

Regarding Reagents, see Vol. I. p. 260; Modes of Isolation, Vol. I. p. 265; Modes of Fixing, Vol. I. p. 266; Hardening, Vol. I. p. 268; Decalcification, Vol. I. p. 268; and Staining, Vol. I. p. 270.

SPECIAL METHODS OF MAKING HISTOLOGICAL PREPARATIONS.

1. Blood-Vessels of the Stomach and Intestine, Method No. 1, Fig. 2, p. 33. Portions of the stomach and intestines, injected from the abdominal aorta, are fixed in Müller's fluid and hardened in alcohols of increasing strength. Portions about 1 mm. in thickness may be preserved in dammar, after having been passed through spirit of turpentine.

2. Mucous Glands of the Lips, Method No. 2, Fig. 10, p. 38. Cut from mucous membrane of the lower lip of a human subject small portions 1 cm. in breadth, fix in 50 c.cm. of Kleinenberg's sulpho-picric acid, and after twenty-four hours harden in 50 c.cm. of strong alcohol. Cut sections after three days. Stain with hæmatoxylin. Mount in dammar.

3. Tooth, Method No. 3, Fig. 11, p. 40. Cut sections, transverse and longitudinal, about 2 mm. thick, and treat as directed for bone. See Vol. I. p. 497, Method No. 52. Decalcify as described under Method No. 54, Vol. I. p. 498.

4. Tooth, Method No. 4, Fig. 12, p. 41. See Method No. 3, above.

5. Tooth, Method No. 5, Fig. 13, p. 41. See Method No. 3, above.

6. Odontoblasts, Method No. 6, Fig. 14, p. 42. Remove the teeth from the gums of a newly-born child, break them into small pieces, and place in 60 c.cm. of Müller's fluid. After six days remove the pulp with fine forceps, and examine a portion of the upper surface. Stain with picrocarmine and mount in glycerine.

7. Development of Tooth, Method No. 7, Fig. 16, p. 43. Obtain the jaws of embryo pigs or sheep. In embryo pigs 6 cm. in length, teeth may be found in the first stage, Fig. 16, p. 43, and in an embryo 10 to 11 cm., the second stage may be noticed, Fig. 17, p. 43. For the later stages, examine the jaws of very young kittens or whelps. Place the head in 100 c.cm. of Kleinenberg's sulpho-picric acid for twenty-four hours, then harden in 80 to 100 c.cm. of 90 per cent. alcohol for six to eight days. Next decalcify for five days in 100 c.cm. of distilled water to which 2 c.cm. of nitric acid have been added. Harden further in alcohol for six days. Stain small portions in borax-carmine, immerse in absolute alcohol for several days, and then cut into sections. Mount in dammar. Notice that the enamel organ has not separated from the papilla.

8. Development of Tooth, Method No. 8, Fig. 17, p. 43. See Method No. 7, above.

9. Development of Tooth, Method No. 9, Fig. 18, p. 43. See Method No. 7, above.

10. The Tongue and its Papillæ, Method No. 10, Fig. 19, p. 46. Remove from upper surface of human tongue portions 2 cm. in breadth, place in 100 to 200 c.cm. of Müller's fluid; change this fluid repeatedly; at end of fourteen days wash the bits of tissue, harden in strong alcohols. For the *papillæ fungiformes*, select membrane from the tip of the tongue; for the *p. filiformes*, from the middle of the tongue; and for the *p. circumvallatæ*, from near the root. Stain with hæmatoxylin. Mount in dammar. For preparations shown in Figs. 22 and 23, p. 48, fix and harden the mucous membrane in absolute alcohol. Search for mucous and serous glands near the root. The rabbit's tongue shows the muscular structure well.

11. The Tongue, Method No. 11, Fig. 20, p. 46. See Method No. 10, above.

12. The Tongue, Method No. 12, Fig. 21, p. 47. See Method No. 10, above.

13. The Tonsils, Method No. 13, Fig. 22. p. 48. The tonsils from the human subject do not show their structure satisfactorily, and those of the cat and rabbit are more suitable. They constitute in these animals small oval bodies, 5 mm. in length, on the lateral side of the lower jaw. Fix in 60 c.cm. of Kleinenberg's sulpho-picric acid, and harden in 50 c.cm. of strong alcohols. Stain with hæmatoxylin, or with eosin and hæmatoxylin. Mount in dammar or glycerine.

14. Salivary Glands, Method No. 14, Fig. 23, p. 48. See Method 10, above.

15. Salivary Glands, Method No. 15, Fig. 24, p. 50. Obtain from a human cadaver small portions (·5 to 1 cm. in breadth) of the parotid, submaxillary, and sublingual glands, place in 30 c.cm. of absolute alcohol and change it in from five to twenty hours. Stain in mass with borax-carmine, and make thin sections. Stain other unstained sections in hæmatoxylin for two or three minutes, and lastly stain with eosin. Mount in dammar. The ducts and semilunes become red. The *membrana propria* of the sublingual and the mucous cells of the submaxillary become red. Distinguish carefully the semilunes from the *m. propria*, the latter having a homogeneous appearance while the former are granular. In a borax-carmine preparation the mucous cells are clear. With hæmatoxylin they are sometimes colourless and sometimes of different shades of blue. The reticulum in the cell becomes blue. Bisected acini are most suitable for study; tangential sections are difficult to understand.

16. Parotid Gland, Method No. 16, Fig. 25, p. 51. See Method No. 15, above.

17. Submaxillary Gland, Method No. 17, Fig. 26, p. 51. See Method No. 15, above.

18. Œsophagus, Method No. 18, Fig. 31, p. 65. Fix small pieces in Müller's fluid (human, 2 cm. broad, or bits from cat or rabbit 2 cm. in length). At end of fourteen days place in 50 c.cm. of strong alcohol, colour with hæmatoxylin, and mount in dammar. See also Fig. 35, p. 72.

19. Stomach, Method No. 19, Fig. 36, p. 72. Place portions of stomach (2 to 5 cm. broad) for two to five days in 100 to 150 c.cm. of ·5 per cent. chromic acid, frequently renewed. Then in 60 c.cm of alcohols of increasing strength. Mount thick unstained sections in dammar.

20. Glands of Stomach, Method No. 20, Fig. 37, p. 73. From the fundus of the stomach of a newly-killed rabbit cut a portion 2 cm. in breadth, strip off the muscular coat, and teaze a bit of mucous membrane, ·5 to 1 mm. in thickness, in a ·75 per cent. solution of common salt. The glands are thus readily demonstrated; stain with picrocarmine, and mount in dilute glycerine.

21. Glands of Stomach, Method No. 21, Fig. 38, p. 74. Best studied from the stomach of a dog or cat which has received little food for twenty-four hours. The stomach of the rabbit is not so suitable on account of the small size of the principal cells. Small portions of the mucous membrane are placed in 10 c.cm. of absolute alcohol, and the alcohol is changed in half an hour. Human stomach shows the glands well. Sections may be cut and stained. (1) For *glands of the fundus*, stain vertical sections with eosin and mount in dammar. Look at the bottom of the gland for the best demonstration of the cells. Very thin sections stained with hæmatoxylin and eosin are useful. Notice the narrow lumen of the glands in transverse sections. (2) The *glands of the pylorus* are best seen when stained with hæmatoxylin and mounted in dammar. The lumen of the pyloric gland is wider. To see the epithelium on the surface of the mucous membrane of the stomach, place small portions in 30 c.cm. of Ranvier's alcohol for five hours. Then stain with picrocarmine and mount in dilute glycerine. See Fig. 35, p. 72, and Fig. 40, p. 76.

22. Glands of the Stomach, Method No. 22, Fig. 39, p. 74. See Method No. 21, above.

23. Glands of Intestine, Method No. 23, Fig. 43, p. 76. This method applies both to small and to large intestine. Cut out a small bit of mucous membrane and place it, with the mucous surface upwards, in a drop of ·75 per cent. solution of NaCl. Teaze off a small bit of mucous membrane, transfer to another slide, and examine in salt solution. Look for the cylindrical epithelium and the goblet cells.

24. Glands of Intestine and Brunner's Glands, Method No. 24, Fig. 44, p. 77. Remove from duodenum of a cat about one hour after death, place for three to six days in 100 c.cm. of a ·5 per cent. solution of chromic acid. Sections may then be stained with hæmatoxylin and mounted in dammar or glycerine.

25. Small Intestines, Method No. 25, Fig. 45, p. 78. Place small portions, 2 to 4 cm. in length, of intestine of a young dog or kitten in 100 to 200 c.cm. of Müller's fluid. Change fluid frequently. At end of two to four weeks wash in water, and harden in alcohols of gradually increasing strengths. Cut sections transversely to axis of intestine. Stain with hæmatoxylin and mount in dammar. In dealing with human intestine, it is a good method to stretch and pin small portions, with the mucous surface uppermost, on bits of cork, and to place these in the hardening fluids.

26. Peyer's Glands, Method No. 26, Figure 46, p. 78. These can be seen with the naked eye bulging from the mucous membrane. Cut out small portions and treat by Method No. 25. They are readily found in lower part of ileum of the cat. Rinse the membrane thoroughly with Müller's fluid. Masses of lymphatic tissue are found in the *appendix vermiformes* of the rabbit. Fix in 1 per cent. chromic acid, and harden in alcohols of increasing strength. Hardening in Müller's fluid is better adapted for showing the germ centres than hardening in alcohol.

27. Blood-Vessels of the Stomach and Intestine, Method No. 27, Fig. 47, p. 80. Inject vessels of stomach and intestines from the descending aorta, fix portions in Müller's fluid, and harden in alcohols of increasing strengths. Cut sections. Mount in dammar, after passing through spirits of turpentine and oil of cloves or oil of lavender. The muscular layer may be peeled off to make the section thinner.

28. Auerbach's Plexus and Meissner's Plexus, Method No. 28, Fig. 48, p. 81. The intestines of the rabbit and guinea-pig are more serviceable than those of the cat for displaying these plexuses. Prepare 200 c.cm. of dilute acetic acid by add-

ing 25 drops of strong acetic acid to 200 c.cm. of distilled water. Cut out a bit of intestine, 10 to 30 cm. in length, tie up the lower end so as to make a bag, fill the bag with the dilute acetic acid, tie up the upper end, and immerse the whole in the acid. At the end of one hour change the fluid. In twenty-four hours, wash with water, cut open the bag, and remove a small strip of intestine 1 cm. in length. From this piece strip off the mucous from the muscular coat. (*a*) *Auerbach's.*—Float out on a watch glass, placed on a bit of black paper, and on the dark back ground the white knots of Auerbach's plexus are easily seen with the naked eye. Wash thoroughly with water, immerse for eight to sixteen hours in 5 to 10 c.cm. of a 1 per cent. of osmic acid, in the dark. Wash and mount in dilute glycerine. Fresh preparations taken from acetic acid are more beautiful than those prepared by the osmic acid method. (*b*) *Meissner's.*—Scrape off with a scalpel the epithelium from the *muscularis mucosæ*, place a small bit of the membrane, thus denuded, on a slide in a drop of acetic acid and examine.

29. MEISSNER'S PLEXUS, Method No. 29, Fig. 49, p. 82. See Method No. 28, above.

30. PERITONEUM, Method No. 30, Fig. 50, p. 82. Kill a rabbit, open the abdomen, and push below the great omentum a cork plate 2 cm. broad, fix a bit of the membrane on this with bristles or small pins, cut off the membrane round the top of the plate, and place in 20 to 30 c.cm. of a 1 per cent. sol. of nitrate of silver. At end of thirty minutes the solution becomes milky in appearance, wash with distilled water, and place the membrane in a shallow vessel containing 100 c.cm. of distilled water, exposed to the sunlight. In a few minutes the membrane becomes brown. Transfer to 70 per cent. alcohol; at end of thirty minutes, cut off small bits, 5 to 10 mm. broad, stain with hæmatoxylin and mount in dammar, or still better, in glycerine. The fine network of fibres in the mesentery may be seen by spreading it out and staining with picrocarmine.

31. LIVER OF FROG, Method No. 31, Fig. 51, p. 106. Place a frog's liver in 150 c.cm. of Müller's fluid for three weeks, wash for one hour under the water tap, and then harden, in the dark, in 100 c.cm. of alcohols of increasing strengths. Cut thin sections. Stain in logwood and mount in dammar. Bile capillaries are seen with high powers as sparkling points, not to be confounded with the vacuoles in the liver cells.

32. LIVER OF MAMMALS, Method No. 32, Fig. 52, p. 106. To see the *hepatic cells*, examine a little liver substance scraped off with a scalpel and broken up with needles in a drop of ·75 per cent. of common salt. Notice the large number of coloured corpuscles and leucocytes usually present. To demonstrate *lobules*, place small portions of pig's liver, 2 cm. broad, in 30 to 50 c.cm. of absolute alcohol. The lobular structure soon becomes apparent. At end of forty-eight hours, cut sections and stain with hæmatoxylin. Human liver is well adapted for showing *hepatic cells* and *bile ducts*. Place small pieces, 2 cm. broad, for four weeks in 200 c.cm. of Müller's fluid, and then transfer to alcohols of increasing strengths for a few days. Stain with hæmatoxylin and mount in dammar. To demonstrate *interlobular connective tissue*, shake a few thin sections of human liver, stained with eosin and hæmatoxylin in distilled water in a test tube. The hepatic cells are thus washed out, and the interlobular connective tissue becomes apparent.

33. HEPATIC CELLS, Method No. 33, Fig. 58, p. 109. See Method No. 32, above.

34. HEPATIC CELLS, Method No. 34, Fig. 59, p. 109. See Method No. 32, above.

35. HUMAN LIVER, Method No. 35, Fig. 60, p. 109. See Method No. 32, above.

36. Blood-Vessels of the Liver, Method No. 36, Fig. 61, p. 110. (*a*) Place a portion, 2 cm. broad, of liver of a rabbit killed with chloroform in 50 c.cm. of absolute alcohol. Do this quickly so as not to allow much bleeding. After two days a natural injection may be seen on the upper surface. Cut sections parallel to upper surface and mount in dammar. (*b*) It is not very difficult to artificially inject the liver. Inject Prussian blue either along the portal vein or by the vena cava, Immerse the liver in 500 c.cm. of Müller's fluid. In six days place portions which appear to be well injected, 2 cm. broad, for two or three weeks, in 150 c.cm. of Müller's fluid. Then harden in alcohols of increasing strengths. Mount tolerably thick sections in dammar.

37. Blood-Vessels of the Liver, Method No. 37, Fig. 62, p. 110. See Method No. 36, above.

38. Blood-Vessels of the Liver, Method No. 38, Fig. 63, p. 111. See Method No. 36, above.

39. Intralobular Connective Tissue, Method No. 39, Fig. 64, p. 112. See Method No. 32, above.

40. Pancreas, Method No. 40, Fig. 66, p. 123. Treat as described for salivary glands in Method No. 15. The granular appearance of the cells next the lumen of the gland cannot be seen in preparations mounted in dammar, but are best sought for in a solution (·75 per cent.) of common salt.

41. Lymphatics and Lymphatic Glands, Method No. 41, Fig. 72, p. 150. (*a*) *Lymphatic vessels.*—Select for examination the lymphatics of the inguinal region, the lumina of which are wide, and prepare them according to the methods suitable for blood-vessels. See Method 57. (*b*) *Small lymphatic channels.*—Inject the tissue with Prussian blue by a hypodermic syringe. It is a coarse method, not to be much depended on. (*c*) *Lymphatic glands.*—Remove several from the mesentery of a kitten. Fix and harden in 30 c.cm. of absolute alcohol and cut sections at end of twenty-four hours. Stain lightly with hæmatoxylin and eosin. Shake a number of sections in a test tube with water for three or five minutes. Mount in dammar or glycerine.

42. Lymphatic Gland, Method No. 42, Fig. 73, p. 151. See Method No. 41, above, *c*.

43. Thymus, Method No. 43, Fig. 74, p. 158. Place the thymus of a young animal for four weeks in Müller's fluid, then in alcohols of increasing strengths, cut, stain with hæmatoxylin, and mount in dammar. Avoid mistaking transverse sections of vessels for the corpuscles of Hassall.

44. Spleen, Method No. 44, Fig. 75, p. 159. (*a*) *Elements of the spleen.*—Examine a little scraping from a fresh spleen in a drop of salt solution. Observe the coloured and colourless corpuscles, fibres, and endothelial cells of vessels (especially in human spleen). In the latter we may also find cells containing corpuscles (Fig. 77, p. 159), and multinuclear cells. (*b*) *Sections of entire spleen.* Place a human spleen in 1,000 c.cm., or a cat's spleen in 250 c.cm., of Müller's fluid. At end of two weeks (cat), or five weeks (human), wash the spleen at the water tap, cut it into portions 2 cm. in breadth, and harden these in alcohols of increasing strengths. Observe the Malpighian bodies with the naked eye. Cut sections and stain with hæmatoxylin, not deeply, and mount in dammar or glycerine. To see the trabeculæ well, place the sections already stained with hæmatoxylin for half a minute in eosin. The trabeculæ are thus stained by the eosin. (*c*) *Adenoid tissue of spleen.*—Place a few sections stained with hæmatoxylin and eosin in a test tube with water,

and shake violently for a few minutes. Many of the leucocytes are thus washed out and the retiform tissue becomes apparent. (*d*) *Karyokinetic changes in spleen.*—Small portions of spleen removed from the animal immediately after death are fixed in chromo-osmium-acetic acid (p. 268, Vol. I.), hardened in alcohol, and fine sections are stained with saffranin. Mount in dammar. Use very high powers as the karyokinetic appearances are very small.

45. Elements of Spleen, Method No. 45, Fig. 77, p. 159. See Method No. 44, above, *a*.

46. Adenoid Tissue of Spleen, Method No. 46, Fig, 78, p. 160. See Method No. 44, above, *c*.

47. Karyokinetic Division in Spleen, Method No. 47, Fig. 79, p. 160. See Method No. 44, above, *d*.

48. Spleen, Method No, 48, Fig. 80, p. 161. See Method No. 44, above.

49. Thyroid Body, Method No. 49, Fig. 81, p. 162. Remove from the neck the thyroid body along with the œsophagus and the tongue, and immerse the organs for two to six weeks in 200 to 400 c.cm. of Müller's fluid, wash the part thoroughly under the water tap for an hour, and then place in 200 c.cm. of alcohol. At end of eight days cut transverse and longitudinal sections through the trachea and the thyroid body, stain for five minutes in hæmatoxylin, and mount in dammar.

50. Supra-renal Body, Method No. 50, Fig. 82, p. 162. Place the entire body of a small human fœtus in 200 c.cm. of ·1 per cent. of chromic acid; then, after immersion for four or five days, harden it in 150 c.cm. of alcohols of increasing strengths. Mount sections in glycerine. (*a*) To see the finer structure, teaze small portions in a drop of salt solution. (*b*) For fine sections, place small portions of fresh organ (1 to 2 cm. broad) in 100 c.cm. of Kleinenberg's picric acid, for twenty-four hours, then harden in alcohol, stain with hæmatoxylin, and mount in dammar.

51. Supra-renal Body, Method No. 51, Fig. 83, p. 163. See Method No. 50, *b*.

52. Bone Marrow, Method No. 52, Fig. 84, p. 164. See Method No. 56, p. 498, Vol. I.

53. Blood Corpuscles, Method No. 53, Fig. 86, p. 166. (*a*) Prick the finger with a clean needle, and place a drop of blood on a clean slide, and cover with a cover glass. Observe normal appearance of blood. (*b*) Observe effect of water by placing a drop at margin of cover glass. (*c*) Observe effect of a drop of weak acetic acid. (*d*) Magenta solution. (*e*) Drop of tannic acid solution. (*f*) Strong salt solution. (*g*) Strong solution of sugar. (*h*) Study colourless blood corpuscle as to amœboid movement, (α) immediately under cover glass, (β) on hot stage (p. 167), or (γ) with putty cell (Fig. 88, p. 166). (*i*) Measure the diameter of a blood corpuscle. (*k*) Count the corpuscles by method described at p. 185. (*l*) Estimate the amount of hæmoglobin by method described at p. 183. (*m*) Study diapedesis in mesentery of frog, after a subcutaneous injection of a very weak solution of curare. (See Fig. 89. p. 166.)

53 *a*. Embryonic Vessels, Method No. 53 *a*, Fig. 92, p. 172. Kill with chloroform a rabbit about seven days old, open the abdomen, remove the mesentery and place it in 80 c.cm. of a saturated solution of picric acid. At end of an hour, cut out small bits of mesentery about 1 cm. square and place them on dry slides. Stretch out with needles. Place a drop of hæmatoxylin on the preparation, and allow it to remain for a few minutes. Then pour the hæmatoxylin off and lay the slide in a flat dish. Then gently raise the bit of membrane from the slide and place it for

five minutes in a watch glass containing a solution of eosin. Wash with water, and mount in glycerine, or in dammar, passing the section in the latter case through absolute alcohol and oil of cloves. The eosin tints the blood corpuscles a brilliant red.

54. PITUITARY BODY, Method No. 54, Fig. 93, p. 177. See Method No. 49.

55. EARTHY MATTER IN PINEAL BODY, Method No. 55, Fig. 94, p. 178. Teaze a bit of pineal body in a drop of salt solution. To make the granules clearer add a drop of weak hydrochloric acid.

56. HEART AND GREAT BLOOD-VESSELS, Method No. 56, Fig. 102, p. 201. Cut out a papillary muscle from a heart, a bit of aorta 2 cm. broad, and a bit of brachial artery 1 to 2 cm. long, along with a bit of a renal vein 1 cm. long, and suspend the parts by a thread in 40 c.cm. of absolute alcohol. Sections may be cut in from twenty-four to forty-eight hours. Stain with hæmatoxylin, and mount in dammar. Transverse sections are unsatisfactory, and longitudinal sections show the muscular coats best.

57. SMALL BLOOD-VESSELS AND CAPILLARIES, Method No. 57, Fig. 137, p. 253. Dissect off a portion of pia mater from the base of a human brain, and place for three or four days in 50 c.cm. of Müller's fluid. Wash thoroughly under water tap and then harden in 40 c.cm. of absolute alcohol. Place in a watch glass and look for (*a*) minute vessels and (*b*) larger vessels. Stain a group of small vessels in hæmatoxylin and mount in dammar. To see the larger vessel, select a longitudinal strip of vessel, stain with hæmatoxylin, and mount in dammar. Capillaries are also readily found in teazed pia mater. Elastic fenestrated membranes are easily got by teazing the basilar artery in a drop of a 35 per cent. solution of caustic potash.

58. LARGE VESSELS, Method No. 58, Fig. 138, p. 253. See Method No. 56 above.

59. LARGE VESSELS, Method No. 59, Fig. 139, p. 254. See Method No. 56, above.

60. ENDOTHELIUM OF VESSELS, Method No. 60, Fig. 140, p. 254. Pith a newly-born kitten, inject descending aorta with 50 c.cm. o ·5 per cent. solution of nitrate of silver (25 c.cm. of a 1 per cent. solution + 25 c.cm. of distilled water), and then tie the aorta. At end of half an hour, cut open the aorta and large vessels, and expose inner surface to sunlight in 20 c.cm. of distilled water, until a brown tinge appears. Teaze off the adventitia with forceps and examine the tunica interna in a drop of glycerine. The cement substance uniting the endothelial cells is then seen with occasionally darker transverse lines, indicating the cement uniting the muscular fibres of the tunica media. Mount in glycerine. (See Fig. 142, p. 256.)

61. VEIN, Method No. 61, Fig. 141, p. 255. See Method No. 56, above.

62. BRONCHUS, Method No. 62, Fig. 178, p. 300. Remove the larynx, trachea, and lungs from a kitten. Inject absolute alcohol into the trachea until the lungs are filled, ligature the trachea, and place the parts for two to eight days in 150 c.cm. of 90 per cent. alcohol. Cut out a piece of lung, 1 c.cm. broad, containing a small bronchus, remove the adherent lung substance with scissors, make fine transverse sections, stain with hæmatoxylin, and mount in dammar.

63. EPITHELIUM OF LUNG, Method No. 63, Fig. 179, p. 301. Use a kitten newly killed. Remove trachea and lungs, and inject into trachea a dilute solution of nitrate of silver (50 c.cm. of a 1 per cent. solution in 200 c.cm. of distilled water). Ligature the trachea and immerse the whole in the remainder of the solution of nitrate of silver not used. Keep in the dark for twenty-four hours. Then rinse the lungs in distilled water and transfer to 150 c.cm. of alcohols of increasing strengths. Keep in the dark as much as possible. The reduction of the silver may be noticed

even in one hour. Expose the lungs to sunlight for a few minutes, and they acquire a brown colour. Cut sections with a very sharp knife, and as the lung tissue is still soft, it will be found to be impossible to make fine sections. Place the sections for ten to sixty minutes in 5 to 20 c.cm. of water to which a grain or two of common salt has been added. Do not stain such sections. Mount unstained in dammar. Examine first with low powers, and when the cubical cells can be seen, examine these with high powers, so as to make out the points indicated at p. 301.

64. Alveoli of Lung, Method No. 64, Fig. 180, p. 302. See Method No. 63, above. To see the elastic fibres, cut off a small portion, 1 cm. square, from the surface of a fresh lung, spread out with needles on a dry slide, cover with a cover glass, and allow a drop of a weak solution of caustic potash to pass below the cover glass. The potash brings the elastic fibres into view.

65. Injected Lung, Method No. 65, Fig. 181, p. 303, see p. 273, Vol. I.

66. Skin, Method No. 66, Fig. 199, p. 379. Remove a bit of fresh skin from the under surface of the fingers, or from the palm of the hand, or from the sole of the foot (1 to 2 cm. in breadth), taking some of the subcutaneous tissue along with it, and place the pieces in 30 c.cm. of absolute alcohol. To prevent curling up of the pieces, pin them down on cork plates. Change the alcohol in twenty-four hours. Stain in mass in 30 c.cm. of borax-carmine. Then transfer into 30 c.cm. of 90 per cent. alcohol, and finally into absolute alcohol. Cut sections and mount in dammar. Thick sections are most suitable for showing sweat glands.

67. Nail, Method No. 67, Fig. 200, p. 381. Fix the terminal phalanx of the finger of a young child (an infant two to four weeks old) in 100 to 200 c.cm. of Müller's fluid, harden in 100 c.cm. of alcohols of increasing strengths, decalcify, harden again in alcohol, cut sections, stain with hæmatoxylin, and mount in dammar.

68. Elements of Nail, Method No. 68, Fig. 201, p. 381. Heat a small bit of nail in a test tube with 5 c.cm. of concentrated caustic potash solution until the fluid bubbles. Then transfer the bit of nail, in a drop of potash solution, to a slide, and scrape its upper surface. Examine the scrapings with a high power.

69. Hairs, Method No. 69, Fig. 202, p. 382. Fix small pieces (2 to 3 cm. in breadth) of the scalp in 200 c.cm. of Müller's fluid, and then harden in 100 c.cm. of alcohols of increasing strengths. Make sections so as to expose the entire length of the hair follicle. Mount uncoloured thick sections in glycerine. Cut a few sections so as to show transverse sections of hairs. Stain with carmine and hæmatoxylin, or, still better, first with hæmatoxylin and then with picrocarmine. Mount in dammar.

70. Hair, Method No. 70, Fig. 203, p. 383. Examine a hair in a drop of salt solution. The cuticle of the human hair is very delicate, and shows striations indistinctly. Such striations are well seen in wool. To see the elements of a hair, place a portion, 1 to 2 cm. in length, on a slide in a drop of pure sulphuric acid, and lay a cover glass on it. Press the cover glass with the point of a needle and fibres may be seen detaching from the cortex. Warm the slide gently, and on again pressing with the needle fine elements are seen, like those depicted in the figure. To see the hair follicles, macerate a bit of human skin bearing hairs (a lip bearing a moustache) in acetic acid (1 c.cm. of acid to 100 c.cm. of distilled water). After two days, hairs along with their sheaths may be pulled out, and are to be examined in a drop of distilled water. The cells of Henle's sheath may separate so as to simulate a fenestrated membrane.

71. Hair, Method No. 71, Fig. 204, p. 383. See Method No. 70 above.

72. Development of Hairs, Method No. 72, Fig. 205, p. 384. Remove portions (2 cm. in breadth) of the skin of the forehead of a fœtus of five or six months, stretch on cork, and fix for fourteen days in 100 to 200 c.cm. of Müller's fluid. Then harden in 100 c.cm. of alcohol. Stain with borax-carmine, cut sections perpendicular to the surface, and mount in dammar.

73. Hair, Method No. 73, Fig, 206, p. 384. Cut sagittal sections of the eyelid of a fœtus, and treat as described in Method No. 69.

74. Sebaceous Glands, Method No. 74, Fig. 207, p. 385. Fix and harden the alæ of the nose of a fœtus, in 20 to 30 c.cm. of absolute alcohol. Cut sections, stain with carmine and hæmatoxylin, and mount in dammar.

75. Blood-Vessels of the Skin, Method No. 75, Fig. 208, p. 387. Inject the hand of a child with Berlin blue through the ulnar artery, fix in 1 to 2 litres of Müller's fluid. In twenty-four hours cut out portions (2 to 3 cm. broad) of the skin of the palmar surface, and place these, for two to four weeks, in 100 to 200 c.cm. of Müller's fluid, and then in alcohols of increasing strengths. Cut thick sections, and mount in dammar.

76. Uriniferous Tubule, Method No. 76, Fig. 210, p. 394. The kidney of a very young animal (a newly born kitten) is best adapted for the purpose. The kidney is halved : one half (*a*) is used for investigation while fresh, and the other (*b*) is placed in 30 c.cm. of pure hydrochloric acid.

(*a*) Small bits, the size of a pea, are teazed in a drop of salt solution, and with a low power one can see the red glomeruli and the coiled and straight tubes. The convoluted tubes are darkly granular, and the straight tubes are clear. High powers show the nuclei of the cells in the tubules.

(*b*) At the end of nine hours, small bits of kidney are removed from the solution of hydrochloric acid, placed in a test tube, and well shaken with distilled water. Allow the tube to rest undisturbed for twelve hours, and then carefully pour off the water from the sediment. Examine a little of the sediment with a low power, and numerous minute canals will be found. Isolate any portion considered worthy of preservation, and place in a drop of glycerine, to which a little picrocarmine has been added.

77. Cortex and Medulla of Kidney, Method No. 77, Fig. 212, p. 395. Fix the kidney of a kitten in 200 to 300 c.cm. of Müller's fluid, and harden in 100 c.cm. of alcohols of gradually increasing strength. Examine thick transverse and longitudinal sections, unstained, in glycerine, with low powers. Prepare thin sections through (*a*) the apices of the papillæ; (*b*) the bases of the papillæ, and (*c*) the cortex. Stain with hæmatoxylin, and mount in dammar.

78. Cortex of Kidney, Method No. 78, Fig. 213, p. 395. See Method No. 77, above.

79. Isolated Renal Cells, Method No. 79, Fig. 216, p. 396. See Method No, 77, above.

80. Medulla of Kidney, Method No. 80, Fig. 218, p. 396. See method No. 77, above.

81. Injected Kidney, Method No. 81, Fig. 219, p. 397. Inject a kidney, fix in 300 c.cm. of Müller's fluid, and harden in 150 c.cm. of alcohol of increasing strengths. The *Stellulæ Verheynii* may be seen with the naked eye.

82. Pelvis of Kidney and Ureter, Method No. 82, Fig. 225, p. 430. Fix portions of the pelvis, 1 mm. square, and of the ureter, 1 to 2 cm. in length, in 100 c.cm. of

Müller's fluid, and at end of fourteen days transfer to 100 c.cm. of absolute alcohol. Cut sections, stain with hæmatoxylin, and mount in dammar.

83. Bladder and Urethra, Method No. 83, Fig. 226, p. 430. See Method No. 82, above. Also, cut a small portion of mucous membrane of bladder, 1 cm. square, and place it in 30 c.cm. of Ranvier's alcohol. Then teaze out a portion, stain with picrocarmine, and mount in acidulated glycerine. (*a*) To demonstrate the *female urethra* remove a portion 2 cm. in length, together with the adhering anterior wall of the vagina, fix in 100 to 200 c.cm. of Müller's fluid, and harden, after two or three weeks, in 100 c.cm. of alcohols of increasing strength. Stain transverse sections with hæmatoxylin, and mount in dammar. (*b*) For *male urethra*, portions of the pars prostatica, pars membranacea, pars cavernosa, and fossa navicularis, are to be treated as detailed under (*a*).

84. Nerves, Method No. 84, Fig. 231, p. 450. See Methods 30, 31, 32, 33, 34, and 35, p. 493, Vol. I. To obtain such a preparation as is shown in Fig. 231, place a bit of sciatic nerve for six days in solution of chromic acid, wash under water tap for two hours, and then harden in alcohols of increasing strengths. Make thin sections, stain with picrocarmine, and mount in glycerine.

85. Spinal Cord, Method No. 85, Fig. 252, p. 489. It is important, in the first place, to obtain the organ in as fresh a condition as possible, and in the second place it should be cut into short lengths. If the whole cord is to be immersed in the preserving fluid, make transverse cuts at different levels, so as to allow the fluid to reach the interior. Always use considerable quantities of fluid, and change it frequently. I. Weigert's Method. Remove portions of fresh cord, 2 cm. long, from (1) the cervical region, (2) the thoracic region, and (3) the lumbar region, and suspend them in 200 to 300 c.cm. of Müller's fluid. At the end of six weeks (during which time the fluid is to be changed two or three times), transfer the pieces (*without previous washing in water*) into 150 c.cm. of 70 per cent. alcohol, and on the following day into 90 per cent. alcohol. Keep the preparation in the dark, and change the alcohol twice during the first eight days. Then place portions of the cord in 30 c.cm. of a saturated solution of neutral acetate of copper added to 30 c.cm of distilled water. After remaining in this solution for three days, they are transferred to 60 c.cm. of 90 per cent. alcohol, and sections may be cut on the following day. The sections are placed in 10 c.cm. of Weigert's hæmatoxylin, in which they become black. After two hours, the black sections are lifted out of the watch glass, and placed in 30 c.cm. of distilled water. The sections become partially decolorized in about half an hour, the grey matter becoming yellow, while the white matter has a deep blue tint. Again placed in a fresh quantity of 30 c.cm. of distilled water, the sections are left there for one hour. Transfer to a watch glass into 90 per cent. alcohol, and one minute afterwards into absolute alcohol. Half a minute later, place the sections in a small watch glass containing xylol (not oil of lavender or oil of cloves). A section is lifted out of the xylol with a spatula and placed on a slide, the superfluous xylol is poured off, and a drop of Canada balsam (not dammar) diluted with xylol is placed over it. This process brings out the nerve fibrils with great distinctness.

II. Coloration of Axis Cylinders and Cells. Fix portions of cord in Müller's fluid, and harden in alcohol, as detailed under *Weigert's Method.* The cells are more easily coloured if the preparation has remained for a long time in alcohol. Transverse sections are stained by immersion for two or three days in 10 c.cm. of picrocarmine. Mount in dammar. If the staining has succeeded, the grey matter is stained of a rose-colour, the nerve cells and axis cylinders red, and the white substance of Schwann yellow. Instead of picrocarmine, the sections may be placed in 10 c.cm. of strong carmine solution.

86. Spinal Cord, Method No. 86, Fig. 253, p. 490. See Method No. 85, II.

87. Neuroglia, Method No. 87, Fig. 254, p. 491. Thin sections of white matter of the cord are stained for twenty-four hours in 5 c.cm. of saffranin, the excess of stain removed by immersion for a few minutes in absolute alcohol, and preserved in dammar.

88. Brain, Method No. 88, Fig. 255, p. 492. Employ the procedure detailed in Method No. 85. To show the finest fibrils, the sections should remain for twenty-four hours in hæmatoxylin; but to display those between the pyramidal cells of the cortex immersion for two hours is sufficient.

89. Brain Cells, Method No. 89, Fig. 256, p. 492. Place portions, 2 to 3 cm. in breadth, of the cerebral cortex, or of the cerebellum, in 40 c.cm. of absolute alcohol. Change the alcohol frequently, and at end of three or five days cut vertical sections, stain with hæmatoxylin or eosin, and mount in glycerine. The brain cortex may also be hardened in Müller's fluid and alcohol as detailed in Method No. 85, II.

90. Corpuscula Amylacea, etc., Method No. 90, Fig. 257, p. 492. Open the brain of an adult and scrape a little matter from the surface of the *thalami optici* in the 3rd ventricle. Break up the matter with needles in a drop of salt solution. The corpuscles have a bluish-green colour, and show stratification. Mixed up with these we find the structures depicted in Fig. 257. Examine a bit of choroid plexus and observe the blood-vessels and epithelium.

91. Cerebellum, Method No. 91, Fig. 258, p. 493. See Method No. 88, above.

92, 93, 94. Taste Organ, Methods Nos. 92, 93, 94, Figs. on p. 571. After hardening, cut vertical sections of the circumvallate papillæ of any animal or the papilla foliata of a rabbit. The taste buds may also be acted on by osmic acid. Cut off a horizontal bit of the papilla foliata with as little underlying muscle as possible, spread out the bit on a cork, and pin it down with hog's bristles. Expose the piece on the cork for one hour to the vapour of osmic acid. Then cut in thin sections, colour slightly with hæmatoxylin, and mount in dammar. The nerves may be demonstrated by the action of chloride of gold. Place a circumvallate papilla for ten minutes in the filtered juice of a lemon, and then place it for one hour, in the dark, in 5 c.cm. of a 1 per cent. solution of chloride of gold. Wash thoroughly with distilled water, and then allow it to lie for one or two hours in 20 c.cm. of distilled water to which 3 drops of acetic acid have been added. Expose the papilla in distilled water to the action of light until the gold has been reduced. Then harden the papilla, in the dark, in 30 c.cm. of strong alcohol, cut in thin sections, and mount in dammar. The nerve fibres appear of a dark red colour, and the taste goblets are of a dark violet. The papilla foliata of the rabbit is not suitable for this process.

95. Olfactory Organ, Method No. 95, Fig. 294, p. 574. Divide a young rabbit's head in the mesial line. The olfactory mucous membrane is easily recognized by its brown colour. A small portion, 5 mm. broad, is cut out and placed in 20 c.cm. of Ranvier's alcohol. At the end of five to seven hours it is transferred to 20 c.cm. of picrocarmine, and on the following day it is placed in 10 c.cm. of distilled water. Ten minutes afterwards, the portion of membrane is *dashed* on a slide into a drop of dilute glycerine. Avoid breaking it up with a needle. Place the cover glass over it, and, on examining with a high power, the olfactory cells may be seen. For the examination of the regio respiratoria, remove small portions of mucous membrane, 5 to 10 mm. broad, from lower half of the septum narium,

and harden in 20 c.cm. of absolute alcohol. Stain with hæmatoxylin and mount in dammar. Preparations showing the respiratory region in vertical section may be obtained from the human subject. Cut thick sections and mount in glycerine.

96, 97, 98. Regio Olfactoria, Methods Nos. 96, 97, 98, Figs. on pp. 575-6. Tear off small portions, 3 to 6 mm. broad, of the brown olfactory mucous membrane, from the upper portion of the septum of a rabbit, and place them for three hours in 20 c.cm. of Ranvier's alcohol; then transfer to 3 c.cm. of a 2 per cent. solution of osmic acid added to 3 c.cm. of water, and allow them to remain in this solution for twenty-four hours in the dark. Then place for half an hour in 20 c.cm. of distilled water, and harden in 30 c.cm. of strong alcohol. Cut sections, stain with hæmatoxylin, and mount in dammar. To see the *glands of Bowman* examine thick sections.

99 to 105. Eyeball, Methods Nos. 99 to 105, pp. 581 to 585. Remove a fresh eyeball from the orbit, with a small bit of optic nerve attached, clean away the fatty and muscular tissue attached to it, and with a sharp razor make a transverse incision into the eyeball, about 10 mm. in length, and in the equatorial region. Place the eye in 150 c.cm. of a ·05 per cent. solution of chromic acid. At the end of twelve to twenty hours, complete with scissors the transverse division of the eyeball into an anterior and a posterior half. Change the fluid. In twenty hours wash the portion thoroughly and harden in 100 c.cm. of alcohols of increasing strength. (*a*) Remove the lens carefully from the anterior portion and lay it aside for sections,. Next cut a quadrant out of the anterior portion, containing the ciliary region and the iris. Cut sections, stain with hæmatoxylin, and mount in dammar, or glycerine. (*b*) Cut out a bit of cornea, 5 to 10 mm. broad, and cut sections to show structure of cornea, p. 583. The laminated structure is best seen in unstained sections, mounted in dilute glycerine. (*c*) Cut a small portion, 5 to 10 mm. broad, from posterior half of eye, so as to include the three coats—sclerotic, choroid, and retina. Stain with hæmatoxylin and mount in dammar. This preparation shows the sclerotic and the choroid. The retina will probably become detached. (*d*) Cut out a portion round the entrance of the optic nerve, including all the coats, and make sections parallel with the optic nerve, cutting from within outwards, that is, dividing the retina first. Stain with carmine and hæmatoxylin and mount in dammar (Fig. 316, p. 592).

100 and 100*a*. See p. 783.

106 to 110. Eyeball, Methods Nos. 106 to 110, pp. 587 to 591. A fresh eyeball is removed, incised at the equator, and placed in 100 to 200 c.cm. of Müller's fluid; at end of twenty-four hours, divide it into an anterior and a posterior half. Change fluid every four or five days, and in three weeks wash both parts thoroughly under the water tap. Cut out a small portion, 8 mm. in breadth, including all the layers, and use it for teazing. (*a*) *Choroid.*—Sections of Choroid, in dilute glycerine, sometimes show vessels, sometimes the capillaries of the chorio-capillaris, sometimes ramified pigment cells and elastic fibres. We may stain any suitable portions with hæmatoxylin and mount in dammar. (*b*) *Retina.*—Teaze a small bit of retina in a drop of Müller's fluid. The human retina shows large cones, but in the retina of most of the common animals they are small. Unless the retina be obtained in a very fresh state the external portions of the cones cannot be found, as they quickly break up into transverse plates. The cones are best studied in the eyes of fishes. (*c*) The remaining portions of the eyeball are transferred from water to 80 c.cm. of alcohols of increasing strengths. After complete hardening, remove the iris, make meridional sections, stain with hæmatoxylin, and mount in dammar. (*d*) Remove a portion of retina, 1 cm. in length, from the region of the *ora serrata*, make

meridional sections, stain with hæmatoxylin, and mount in dammar. (*e*) Treat in a similar way a portion of retina from the fundus of the eye. Müller's fibres are seen in sections perpendicular to the surface. (*f*) Among the lower animals, the quadrumina alone have a yellow macula and a *fovea centralis*. In the eye of the cat, sheep, and probably of most mammals (excluding man and the monkeys), we find a spot not coloured yellow, but showing a structure similar to that of the macula. This is called the *area centralis*. Make meridional sections through the macula and fovea of a human eye. It is very difficult to make a section through the delicate fovea. Do not detach the retina but cut it along with the choroid.

107. Retinal Elements, Method No. 107, Fig. 308, p. 587. Take an eyeball from an animal just killed. Divide the eye at the equator, remove the vitreous humour very carefully, and teaze out on a slide minute bits of retina in vitreous humour. Place a very thin cover glass over the preparation, supporting it on two sides by thin bits of paper, so as not to press on the retinal elements. Thus minute rods and cones may be seen, especially surface forms, as if they were seen in transverse section. Examine the pigment epithelium for the hexagonal cells. These may often be obtained by scraping a little from the choroidal surface, after removal of the retina.

108. Retinal Elements, Method No. 108, Fig. 309, p. 588. The eye of a small animal (frog, triton, fish, etc.) is convenient. Place the unopened eye in a 1 per cent. solution of osmic acid. After twenty-four hours, cut it across at the equator and macerate it for two or three days in distilled water. Cut out a small bit of retina, 2 mm. broad, and teaze it in a drop of water. Stain under the cover glass with picrocarmine and mount in dilute glycerine.

100. Lacunæ and Canals in Cornea, Method No. 100, Fig. 300, p. 581. Examine the eye of an ox, as fresh as possible. Scrape off some of the epithelium in front of the cornea, and then wash the anterior surface with a jet of water. Divide the eyeball into an anterior and posterior segment by a transverse incision in front of the attachment of the muscles, and place the anterior half, containing the cornea, on the epithelial surface. Remove the ciliary processes, lens, and iris, so that only the anterior part of the sclerotic and the cornea remain. Place these in 40 c.cm. of a 1 per cent solution of nitrate of silver; keep in the dark for three to five hours, and then, in 50 c.cm. of distilled water, expose to sunlight. Then harden in 50 c.cm. of alcohols of increasing strengths, and cut sections parallel to the surface, and especially from the posterior part, where the lacunæ and canals are largest. Stain with hæmatoxylin and mount in dammar. The forms are *negative*, that is to say, the lacunæ and canals are white and the ground is brown or brownish-yellow. The hæmatoxylin brings out the nuclei of the corneal cells. To obtain *positive* forms, in which the lacunæ and canals are black on a light ground, take the cornea, treated as already described, out of the 1 per cent. solution of nitrate of silver, and place it, for five minutes, in 100 c.cm. of distilled water into which 3 grammes of chloride of sodium have been dissolved, then transfer into 50 c.cm. of distilled water, and expose to sunlight for reduction. This method is sometimes unsuccessful, and the next is more certain.

100*a*. Lacunæ and Canals in Cornea, Method No. 100, Fig. 581, p. 300. Filter the juice of a lemon through a bit of flannel. Kill a frog, remove the cornea, and place it for about one minute in the lemon juice. Then transfer it to 5 c.cm. of distilled water, and after a few minutes into 10 c.cm. of a 1 per cent. solution of choride of gold. Leave it in the gold solution for fifteen minutes in the dark. Place it in 10 c.cm. of distilled water, wash it gently, and then expose it to daylight in 50 c.cm. of distilled water and two drops of acetic acid. In forty-eight hours, the reduction is complete. Place the cornea in 10 c.cm. of 70 per cent. alcohol and leave it in the dark. Next day draw off fine lamellæ and mount in dammar.

111. See No. 99*d*.

112 and 113. Lens, Methods No. 112 and 113, Fig. 317, p. 593. Place a lens removed from a fresh eye in 50 c.cm. of Ranvier's alcohol. After two hours, puncture the anterior and posterior surface with a needle and draw off the capsule. A muddy fluid sometimes oozes from the lens on puncturing it. Shake the alcohol and let the lens lie in it for forty-eight hours. The lens then separates into disc-shaped portions. A stripe of a disc is teazed in a drop of salt solution. Stain fibres with picrocarmine and mount in acidulated glycerine.

114. Transverse Section of Lens, Method No. 114, Fig. 318, p. 594. Place a lens on a bit of cotton wool in 50 c.cm. of a ·05 per cent. solution of chromic acid. In forty-eight hours, split up the lens into disks, transfer these to 30 c.cm. of 70 per cent. alcohol. Next day, transfer to 30 c.cm. of 90 per cent. alcohol. In twenty-four hours, cut sections in various directions. If the fibres have been cut transversely, a number of polygonal forms are seen.

115. Lens Capsule and Epithelium, Method No. 115, Fig. 318, p. 594. Fix an eyeball in 100 to 200 c.cm. of Müller's fluid. (*a*) *Surface preparations.*—Open eye in three days, take out lens, draw off, with forceps, a bit of anterior layer of capsule, place it for five minutes in a weak solution of hæmatoxylin, and mount in dammar. The capsule appears faintly blue, and the epithelium covering it is seen. The posterior portion of the lens does not show epithelium. (*b*) *Sections of capsule and epithelium.*—Leave the eye for fourteen days in Müller's fluid, remove lens, wash it for one hour under the water tap, and harden in 50 c.cm. of absolute alcohol. Cut meridional sections through anterior surface and also through equator, stain with hæmatoxylin, and mount in dammar.

115*a*. Vessels of Eye, Method No. 115*a*, Fig. 320, p. 596. Open fresh eye and one can readily see the *arteria centralis retinæ*. To see the vessels of the choroid, place the eyeball on a small glass funnel inserted into a small bottle and, beginning at the equator, dissect off the sclerotic with scissors and forceps, from behind the *ora serrata* as far back as the entrance of the optic nerve. Avoid tearing the choroid. Next, with a camel-hair pencil dipped in water, gently work as if endeavouring to remove the choroid, and minute vessels will be readily seen. This is all that can be done with the uninjected eyeball. If the eyeball has been injected, fix it in Müller's fluid, harden it in alcohol, and then portions of injected ciliary processes and of iris may be removed. Mount these in dammar.

116. Nerves and Vessels of Cornea, Method No. 116, Fig. 322, p. 597. These may sometimes be seen in the fresh cornea of an ox by examining a section in a drop of vitreous humour. Examine near the junction of the cornea with the sclerotic. The vessels often contain corpuscles.

116. Nerves of Cornea, Method No. 116, Fig. 322, p. 597. Treat with chloride of gold as above described. After hardening, cut surface sections, so as to see epithelium, and also vertical sections. Mount in dammar.

117. Eyelid, Method No. 117, Fig. 323, p. 598. Fix the eyelid of a child in about 100 c.cm. of a 5 per cent. solution of chromic acid for one to three days, wash thoroughly at the water tap, and then harden in 50 c.cm. of alcohols of increasing strengths. Stain in hæmatoxylin, and mount in dammar.

118. LACHRYMAL GLAND, Method No. 118, Fig. 326, p. 601. This is easily obtained from the human eye. In the rabbit it is very small, like a bit of muscle, and apt to be confounded with Harder's gland, a body situated in the mesial angle of the eye. Treat as described under Method No. 15, for parotid gland.

119, 120, 121, 122. TACTILE ORGANS, Method Nos. 119, 120, 121, 122, Figs. 367, 368, 369, 371, pp. 648, 649. Prepare the solution of chloride of gold (p. 273, 8, Vol. I.) and the filtered juice of a lemon. Remove from the palmar surface of a human finger (as soon after amputation as possible) small portions of skin, 5 mm. square and 1 mm. in thickness, immerse them for five minutes in the lemon juice, and then place for one hour in the solution of chloride of gold, and in the dark. Wash in distilled water and then place the portions in 10 c.cm. of distilled water to which a few drops of acetic (or formic) acid have been added. Expose to daylight. In forty-eight hours the bits of epidermis will have a dark violet colour. Harden in 30 c.cm. of absolute alcohol. In eight days cut sections and mount these in dammar. Examine with high powers for simple tactile cells, intra-epithelial nerve fibres, Langerhan's cells, and Wagner's corpuscles.

123. VATERIAN OR PACINIAN CORPUSCLES, Method No. 123, Fig. 374, p. 651. These are readily obtained from the mesentery of a kitten, appearing as small oval translucent spots to the naked eye. Examine in the fresh condition in a drop of salt solution. Take great care not to rupture the corpuscle by pressure on the cover glass. Allow a few drops of a 1 per cent. solution of osmic acid to pass below the cover glass, and after the corpuscle has been slightly blackened, draw off the acid and replace by dilute glycerine.

124 to 130. EAR, Method Nos. 124 to 130, Figs. 389 to 396, pp. 663 to 668. First study the macroscopical structure of the ear so as to be thoroughly familiar with all the parts. (1) *Otoliths.*—With a small chisel remove the wall of the tympanum from the upper margin of the oval to the lower margin of the round window. Keep the preparation under water and we readily notice in it whitish stains in the saccule and in the utricle. Lift out the saccule and utricle and spread them out in a drop of *dilute* glycerine. Otoliths are present in great numbers. (Fig. 389, p. 663.) (2) *Ampullæ.*—On lifting the sacs, the ampullæ of the semicircular canals often adhere to them. These may be stained with picrocarmine and mounted in glycerine.

125 to 130. EAR COCHLEA, Method Nos. 125 to 130, Figs. 390 to 396, pp. 664 to 668. Bear in mind that the base of the cochlea lies in the wall of the inner auditory passage, and that its apex is directed forwards so that its axis is transverse to the longitudinal axis of the petrous portion of the temporal bone. Remove the bone in front of and around the fenestra rotunda, open the apex of the cochlea, and place the preparation in 20 c.cm. of a ·5 per cent. solution of osmic acid (5 c.cm. of a 2 per cent. solution of osmic acid to 15 c.cm. of distilled water). In twenty-four hours, place the preparation in 200 c.cm. of Müller's fluid. In from three to twenty days, break up the cochlea and examine it under water. We perceive the *lamina spiralis ossea* and *lamina spiralis membranacea* as a delicate membrane or fold attached to the axis of the cochlea. Break off with fine forceps a small portion of the *lamina spiralis ossea*, and lift it with a needle into a drop of dilute glycerine. Turn the vestibular portion of the lamina upwards, and break off with a needle the thick axial part. Examine with a low power. The auditory teeth are readily seen. Raise and depress the tube of the microscope so as to bring parts successively into view. Thus the head plates of the rods of Corti, and the meshes of the *membrana reticularis* may be seen. Stain with picrocarmine and preserve dilute glycerine.

129, 130. EAR, COCHLEA, Method Nos. 129, 130, Figs. 395, 396, pp. 667, 668. To make sections through the bony and membraneous cochlea. The cochleas of the guinea-pig and of the bat are serviceable because they are not embedded in bone. If the human cochlea is to be investigated, obtain the ear of a child, and chisel out the labyrinth as carefully as possible. This is not very difficult, as the loose bony tissue surrounding the bony labyrinth may be removed with even a penknife. Make one or two minute openings into the cochlea to admit the preservative fluids. Place the cochlea in 15 c.cm. of distilled water + 5 c.cm. of a 2 per cent. solution of osmic acid. After twenty-four hours, wash it thoroughly under the water tap, and harden in 60 c.cm. of alcohols of increasing strengths. After hardening, the cochlea is decalcified in the following mixture: 1 c.cm. of a 1 per cent. solution of chloride of palladium + 10 c.cm. of hydrochloric acid + 1,000 c.cm. of distilled water. The cochlea is placed in 100 c.cm of this fluid, and the fluid is frequently changed. After complete decalcification harden again in alcohol, and cut sections so that each section contains a portion of the axis of the cochlea. Stain with picrocarmine and mount in dammar.

To prepare the *concha*, place portions in 200 to 300 c.cm. of Müller's fluid, in six weeks wash under water tap, and then harden in 100 c.cm. of alcohols of increasing strengths. Stain with hæmatoxylin and mount in dammar.

131, 132. CERUMINOUS GLANDS, Method Nos. 131, 132, Figs. 397, 398, p. 669. Obtain from the external meatus small portions about 1 centimetre square, and place these in 30 c.cm. of absolute alcohol. Cut sections in the course of a day or two. Stain with hæmatoxylin. The ear of an infant shows the glands very distinctly.

133, 134, 135. VAS DEFERENS, and URETHRA, Method Nos. 133, 134, 135, Figs. 456, 457, 458, pp. 737, 738, 739. Place portions of these organs, 1 to 2 cm. in length, in 200 c.cm. of Müller's fluid, for fourteen days. Then wash thoroughly under the water tap, and finally harden in 60 c.cm. of alcohols of increasing strengths. Stain with hæmatoxylin and mount in dammar.

For TESTIS, see Method 3, Vol. I. p. 487; TUBULI SEMINIFERI, Method 4, Vol. I. p. 487; SPERMATOBLASTS, Method No. 5, Vol. I. p. 488; ELEMENTS OF TESTIS, Method No. 6, Vol. I. p. 487.

136. OVARY AND OVA, Method No. 136, Fig. 459, p. 740. See Methods No. 7 and 10, Vol. I. p. 488. For the FALLOPIAN TUBE, fix portions 1 to 2 cm. long in 100 c.cm. of Müller's fluid, and then harden for fourteen days in 60 c.cm. of alcohols of increasing strengths. Stain sections with hæmatoxylin and mount in dammar.

137. UTERUS, Method No. 137, Fig. 460, p. 742. The human uterus is not very suitable. That of a cat is more serviceable. To be prepared in usual manner by fixing in Müller's fluid and hardening in alcohol.

138. MAMMARY GLAND, Method No. 138, Fig. 483, p. 764. Fix and harden the nipple and a part (3 to 4 cm. broad) of the gland in 60 to 100 c.cm. of absolute alcohol. Cut sections perpendicularly through the nipple and stain with hæmatoxylin. Mount in dammar.

139. MAMMARY GLAND, Method No. 139, Fig. 484, p. 764. Place portions of the gland (3 to 5 mm. broad) from a pregnant or suckling animal in 5 c.cm. of chromo-osmium-acetic acid, and two days thereafter place them in 30 c.cm. of absolute alcohol. Cut sections in ten days. Stain very thin sections with saffranin, and mount in dammar.

140. MILK, Method No. 140, Fig. 485, p. 765. Examine a drop of fresh milk, either alone, or after the addition of a drop of salt solution. Observe the action of acetic acid, ether, and pressure of the cover glass. To see the COLOSTRUM, examine a drop from the breast of a pregnant woman shortly before parturition. The nuclei of the colostrum corpuscles may be seen after the addition of a drop of picrocarmine.

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