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AN AMERICAN TEXT-BOOK

OF

PHYSIOLOGY

BY

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PREFACE TO THE SECOND EDITION.

Advantage has been taken of the necessity of issuing a second edition of the American Text-Book of Physiology to alter somewhat its general arrangement. The book has proved to be successful, and for the most part has met only with kindly and encouraging criticisms from those who have made use of it. Many teachers, however, have suggested that the size of the book, when issued in a single volume, has constituted to some extent an inconvenience when regarded from the standpoint of a student's text-book that may be needed daily for consultation in the lecture-room or the laboratory. It has been thought best, therefore, to issue the present edition in two volumes, with the hope that the book may thereby be made more serviceable to those for whose aid it was especially written.

This change in the appearance of the book has necessitated also some alteration in the arrangement of the sections, the part upon the Physiology of Nerve and Muscle being transferred to the second volume, so as to bring it into its natural relations with the Physiology of the Central Nervous System.

The actual amount of material in the book remains substantially the same as in the first edition, although, naturally, very many changes have been made. Even in the short time that has elapsed since the appearance of the first edition there has been much progress in physiology, as the result of the constant activity of experimenters in this and the related sciences in all parts of the world, and an effort has been made by the various contributors to keep pace with this progress. Statements and theories that have been shown to be wrong or improbable have been eliminated, and the new facts discovered and the newer points of view have been incorporated so far as possible. Such changes are found scattered throughout the book.

The only distinctly new matter that can be referred to specifically is found in the section upon the Central Nervous System, and in a short section upon the modern ideas and nomenclature of physical chemistry, with reference especially to the processes of osmosis and diffusion. The section dealing with the Central Nervous System has been recast in large part, with the intention of making it more suitable to the actual needs of medical students; while a brief presentation of some of the elementary conceptions of physical chemistry seems to be necessary at the present time, owing to the large part that these views are taking in current discussions in physiological and medical literature.

The index has been revised thoroughly and considerably amplified, a table of contents has been added to each volume, and numerous new figures have been introduced.

August, 1900.

PREFACE.

The collaboration of several teachers in the preparation of an elementary text-book of physiology is unusual, the almost invariable rule heretofore having been for a single author to write the entire book. It does not seem desirable to attempt a discussion of the relative merits and demerits of the two plans, since the method of collaboration is untried in the teaching of physiology, and there is therefore no basis for a satisfactory comparison. It is a fact, however, that many teachers of physiology in this country have not been altogether satisfied with the text-books at their disposal. Some of the more successful older books have not kept pace with the rapid changes in modern physiology, while few, if any, of the newer books have been uniformly satisfactory in their treatment of all parts of this many-sided science. Indeed, the literature of experimental physiology is so great that it would seem to be almost impossible for any one teacher to keep thoroughly informed on all topics. This fact undoubtedly accounts for some of the defects of our present text-books, and it is hoped that one of the advantages derived from the collaboration method is that, owing to the less voluminous literature to be consulted, each author has been enabled to base his elementary account upon a comprehensive knowledge of the part of the subject assigned to him. Those who are acquainted with the difficulty of making a satisfactory elementary presentation of the complex and oftentimes unsettled questions of physiology must agree that authoritative statements and generalizations, such as are frequently necessary in text-books if they are to leave any impression at all upon the student, are usually trustworthy in proportion to the fulness of information possessed by the writer.

Perhaps the most important advantage which may be expected to follow the use of the collaboration method is that the student gains thereby the point of view of a number of teachers. In a measure he reaps the same benefit as would be obtained by following courses of instruction under different teachers. The different standpoints assumed, and the differences in emphasis laid upon the various lines of procedure, chemical, physical, and anatomical, should give the student a better insight into the methods of the science as it exists to-day. A similar advantage may be expected to follow the inevitable overlapping of the topics assigned to the various contributors, since this has led in many cases to a treatment of the same subject by several writers, who have approached the matter under discussion from slightly varying standpoints, and in a few instances have arrived at slightly different conclusions. In this last respect the book reflects more faithfully perhaps than if written by a single author the legitimate differences of opinion which are held by physiologists at present with regard to certain questions, and in so far it fulfils more perfectly its object of presenting in an unprejudiced way the existing state of our knowledge. It is hoped, therefore, that the diversity in method of treatment, which at first sight might seem to be disadvantageous, will prove to be the most attractive feature of the book.

In the preparation of the book it has been assumed that the student has previously obtained some knowledge of gross and microscopic anatomy, or is taking courses in these subjects concurrently with his physiology. For this reason no systematic attempt has been made to present details of histology or anatomy, but each author has been left free to avail himself of material of this kind according as he felt the necessity for it in developing the physiological side.

In response to a general desire on the part of the contributors, references to literature have been given in the book. Some of the authors have used these freely, even to the point of giving a fairly complete bibliography of the subject, while others have preferred to employ them only occasionally, where the facts cited are recent or are noteworthy because of their importance or historical interest. References of this character are not usually found in elementary text-books, so that a brief word of explanation seems desirable. It has not been supposed that the student will necessarily look up the references or commit to memory the names of the authorities quoted, although it is possible, of course, that individual students may be led to refer occasionally to original sources, and thereby acquire a truer knowledge of the subject. The main result hoped for, however, is a healthful pedagogical influence. It is too often the case that the student of medicine, or indeed the graduate in medicine, regards his text-book as a final authority, losing sight of the fact that such books are mainly compilations from the works of various investigators, and that in all matters in dispute in physiology the final decision must be made, so far as possible, upon the evidence furnished by experimental work. To enforce this latter idea and to indicate the character and source of the great literature from which the material of the text-book is obtained have been the main reasons for the adoption of the reference system. It is hoped also that the book will be found useful to many practitioners of medicine who may wish to keep themselves in touch with the development of modern physiology. For this class of readers references to literature are not only valuable, but frequently essential, since the limits of a text-book forbid an exhaustive discussion of many points of interest concerning which fuller information may be desired.

The numerous additions which are constantly being made to the literature of physiology and the closely related sciences make it a matter of difficulty to escape errors of statement in any elementary treatment of the subject. It cannot be hoped that this book will be found entirely free from defects of this character, but an earnest effort has been made to render it a reliable repository of the important facts and principles of physiology, and, moreover, to embody in it, so far as possible, the recent discoveries and tendencies which have so characterized the history of this science within the last few years.

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CONTENTS OF VOLUME II.

I. GENERAL PHYSIOLOGY OF MUSCLE AND NERVE.

A. Introduction.

It is seldom that the physical and chemical structure of a tissue, as revealed by the microscope and the most careful analysis, gives even a suggestion as to its function. No one would conclude from looking at a piece of beef, or even microscopically examining a muscle, that it had once been capable of motion, nor would the most exact statement of its chemical composition give indication of such a form of activity. The most thorough histological and chemical examination of the bundle of fibres which compose a nerve would fail to suggest that a blow upon one end of it would cause to be transmitted to the other end an invisible change capable of exciting to action the cell with which the nerve communicated. To understand such a structure we must first learn the forms of activity of which the tissue is capable, the influences which excite it to action, and the conditions essential to its activity, and then seek an explanation of these facts in its physical and chemical constitution.

Contractility.—One of the most striking properties of living matter is its power to move and to change its form. At times the movements occur apparently spontaneously, the exciting cause seeming to originate within the living substance, but more often the motions are developed in response to some external influence. This power finds its best expression in muscle-substance. In its resting form a muscle, such as the biceps, is elongated, and when it is excited to action it assumes a more spherical shape, *i. e.* shortens and thickens, whence it is said to have the property of *contractility.* It is the shortening, the contraction, of the muscle which enables it to perform its function of moving the parts to which it is attached, as the bones of the arm or leg, and of altering the size of the structures of which it forms a part, as the walls of the heart, intestine, or bladder. Ordinary muscle-substance is arranged in fine threads, each one of which is enveloped in a delicate membrane, the sarcolemma; these muscle-fibres can be compared to long sausages of microscopic proportions. A muscle is composed of a vast number of fibres arranged side by side in bundles, the whole being firmly bound together by connective tissue. Since isolated muscle-fibres have been seen under the microscope to contract, each fibre can be looked upon as containing true muscle-substance and being endowed with contractility. The movements of muscles are the resultant of the combined activity of the many microscopic fibres of which the muscles are composed.

The rate, extent, strength, and duration of muscular contractions are adapted to the needs of the parts to be influenced, and it is found that the structure of the muscles differs according to the work which they have to perform. Thus we find two large classes of muscles: the one, like the muscles which move the bones, remarkable for the rapidity with which they change their form, but unsuited to long-continued action; the other, occurring in the walls of the intestine, blood-vessels, bladder, etc., sluggish of movement, but possessing great endurance. The first of these, when examined with the microscope, is seen to be composed of bundles of fibres, which are transversely marked by alternating dark and light bands, and hence are called striated or striped muscles; the other, though composed of fibres, shows no such cross markings, and therefore is known as smooth or non-striated muscle. Striated muscles are often called voluntary, because most of them can be excited to action by the will, whereas non-striated muscles are termed involuntary, because in most cases they cannot be so controlled. Within these two large classes of muscles we find special forms presenting other, though lesser, differences in function and structure. The muscle of the heart, though striated, differs so much from other forms of striped muscle as almost to belong in a special class.

FIG. 1.—Amœba proteus, magnified 200 times: *a*, endosarc; *b*, simple pseudopodium; *c*, ectosarc; *d*, first stage in the growth of a pseudopodium; *e*, pseudopodium a little older than *d*; *f*, branched pseudopodium; *g*, food-vacuole; *h*, food-ball; *i*, endoplast; *k*, contractile vesicle (after Brooks: *Handbook of Invertebrate Zoology*).

Since contractility is possessed by all forms of muscle-tissue, it is evident that it is independent of superficial structural differences. Nor is muscle the only substance possessing this property. Even isolated microscopic particles of living matter are capable of making movements, both spontaneously and when excited by external influences. As far back as 1755, Rosel von Rosenhof described the apparently spontaneous changes in form of a living organism composed of a single cell, a fresh-water amœba. Moreover, he noted that, if quiet, it could be excited to action by mechanical shocks.

The amœba (Fig. 1) is a little animal, of microscopic size, which is found in the ooze at the bottom of pools, or in the slime which clings to some of our fresh-water plants. Under the microscope it is seen to be composed of jelly-like, almost transparent matter, in which are a vast number of fine granules, a delicate tracery of finest fibrils, a small round body, called the nucleus or endoplast, a round hollow space termed the contractile vesicle, which is seen to change in size, appearing or disappearing from time to time, and small particles, which are bits of food or foreign bodies. In the resting state the body has a somewhat flattened, irregular form, which, if the slide on which it rests be kept warm, is found to alter from minute to minute. Little tongue-like projections, pseudopods (false feet), are protruded from the surface like feelers, and are then withdrawn, while others appear in new places. Evidently the little creature, though composed of a single cell, is endowed with life and has the power of making movements. Moreover, it may be seen to change its place, the method of locomotion being a peculiar one. One of the processes, or pseudopods, may be extended a considerable distance, and then, instead of being withdrawn, grow in size, while the body of the animal becomes correspondingly smaller; thus a transfer of material takes place, and this continues until the whole of the material of the cell has flowed over to the new place. This power of movement permits the animal to eat. If when moving over the slide it encounters suitable food material, a diatom for instance, it flows round it, engulfing it in its semifluid mass; and in a similar manner the animal gets rid of the useless substances which it may have surrounded, by flowing away from them. These movements may result from changes which have occurred within its own substance, and apparently independently of any external influence. On the other hand, if its body be disturbed by being touched, by an unusual temperature, by certain chemicals, or by an electric shock, it replies by drawing in all of its pseudopods and assuming a contracted, ball form.

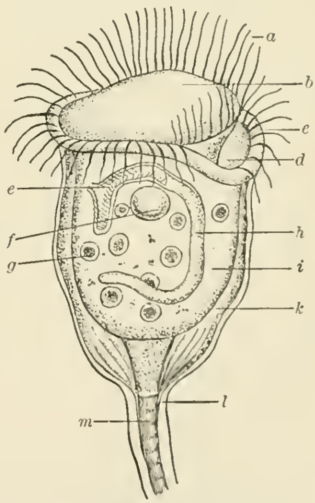

FIG. 2.—Vorticella nebulifera, × 600: *a*, cilia of ciliated disk; *b*, ciliated disk; *c*, peristome; *d*, vestibule; *e*, œsophagus; *f*, contractile vesicle; *g*, food-vacuoles; *h*, endoplast; *i*, endosarc; *k*, ectosarc; *l*, cuticle; *m*, axis of stem (after Brooks: *Handbook of Invertebrate Zoology*).

The movements of the leucocytes of the blood resemble in many respects those of the amœba.[1] The property of contractility is possessed by a vast variety of unicellular structures in lower forms of animal life. Another example is the Vorticella (Fig. 2).

The vorticella, like the amœba, is a little animal which, although consisting of a single cell, possesses within its microscopic form all the physiological properties essential to life and the perpetuation of its species. It consists of a bell, with ciliated margin, borne upon a contractile stalk. If touched with a hair, or jarred, the cell rapidly contracts; the edge of the bell is drawn in so as to make the body nearly spherical, and the stalk is thrown into a spiral and drags the body back toward the point of attachment. The contraction is rapid; the relaxation, which comes when the irritation ceases, is gradual. An interesting account of the movements of *Vorticella gracilis* is given by Hodge and Aikins[2] under the title of "The Daily Life of a Protozoan."

Other examples of contractile power possessed by apparently simple organisms are to be found in the tentacles of Actiniæ, the surface sarcode of sponges, the chromatoblasts of Pleuronectidæ,[3] which are controlled by nerves and under the influence of light and darkness change their size and so alter the color of the skin, and the vast variety of ciliated forms, including spermatozoa, and some of the cells of mucous membranes.[4]

Irritability.—We have thus far referred to but one of the vital properties of protoplasm, viz. contractility. Another property intimately associated with it is *irritability.* Irritability is the property of living protoplasm which causes it to undergo characteristic chemical and physical changes when subjected to certain external influences called irritants. Muscle protoplasm is very irritable, and is easily excited to contraction by such irritants as electric shocks, mechanical blows, etc. The muscles which move the bones rarely, if ever, in a normal condition, exhibit spontaneous alterations in form, and cannot be said to possess automatic power. By *automatism* is meant that property of cell-protoplasm which enables it to become active as a result of changes which originate within itself, and independently of any external irritant. Examples of this power may perhaps be found in the movements of ciliated organisms and the infusoria. Possibly the rhythmic movements of heart muscle are of this nature. Still another property of protoplasm, closely allied to contractility and irritability, and possessed by muscle-substance, is conductivity.

Conductivity is the property which enables a substance, when excited in one part, to transmit the condition of activity throughout the irritable material. For example, an external influence capable of exciting an irritable muscle-fibre to contraction, although it may directly affect only a small part of the fibre, may indirectly influence the whole, because the condition of activity which it excites at the point of application is transmitted by the muscle-substance throughout the extent of the fibre.

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[1] An excellent description of these movements, accompanied by illustrations, is given in *Quain's Anatomy,* vol. i., pt. 2, pp. 174–179.

[2] Hodge and Aikins: *American Journal of Psychology,* 1895, vol. vi., No. 4, p. 524.

[3] Krukenberg: *Vergleichend-physiologische Vorträge,* 1886, Bd. i. S. 274.

[4] A careful study of the different forms of movement exhibited by simple organisms has been made by Engelmann: *Hermann's Handbuch der Physiologie,* 1879, Bd i., Th. 1, S. 344.

Irritability and conductivity are not confined to contractile mechanisms. They are possessed in a still higher degree by nerve-cells, neurones, as they are called, which have not thus far been found to have the power of movement, except that which is associated with the growth of a cell. Each neurone is composed of a body and one or more branches. The bodies of the nerve-cells are located chiefly in the spinal cord and brain, a smaller number being found in the spinal ganglia and in the ganglia of the so-called sympathetic system. The branches of a neurone are of two kinds, an axis-cylinder process, or axone, which frequently carries at its extremity a specially formed organ, through which it is able to excite to action the cells with which it comes in contact, and protoplasmic processes, or dendrites, which have no such exciting mechanism, and are destined to receive excitation and transmit it to the body of the nerve-cell. Outside the central nervous system, at least, the axone and the dendrite acquire a delicate membranous sheath, the neurilemma, which invests it as the sarcolemma does the muscle-fibre. The branches of nerve-cells together with their sheaths form the nerve-fibres. There are two classes of nerve-fibres, medullated and non-medullated, which are distinguished by the fact that the former has between the axis-cylinder and the neurilemma another covering composed of fatty material, called the medullary sheath, while in the latter this is absent. Just as it is the special function of the muscle-fibre to change its form when it is excited, so it is the special function of the nerve-fibre to transmit the condition of activity excited at one end throughout its length, and to awaken to action the cell with which it communicates. Nerve-fibres are the paths of communication between nerve-cells in the central nervous system, between sense-organs at the surface of the body and the nerve-cells, and between the nerve-cells and the muscle- and gland-cells. Nerve-fibres are distinguished as afferent and efferent, or centripetal and centrifugal, according as they carry impulses from the surface of the body inward or from the central nervous system outward. Further, they receive names according to the character of the activity which they excite: those which excite muscle-fibres to contract are called motor nerves; those distributed to the muscles in the walls of blood-vessels, vaso-motor; those which stimulate gland-cells to action, secretory; those which influence certain nerve-cells in the brain and so cause sensations, sensory. Still other names are given, as "trophic" to fibres which are supposed to have a nutritive function, and "inhibitory" to those which check the activities of various organs. The method of conduction is the same in all these cases, the result depending wholly on the organ stimulated.

Nerve-fibres do not run for any distance separately, but always in company with others. Thus large nerve-trunks may be formed, as in the case of the nerves to the limbs, in which afferent and efferent fibres run side by side, the whole being bound together into a compact bundle by connective tissue. The separate fibres, though thus grouped together, are anatomically and physiologically as distinct as the wires of an ocean cable; that these many strands are bound together is of anatomical interest, but has little physiological significance.

The active substance of the nerve-fibre does not show contractility, but this does not prevent it from being classed with other irritable forms of living cell-substance as protoplasm. In spite of differences in structure and composition, nerve protoplasm and muscle protoplasm are found to have many points of resemblance. An explanation of the physiological resemblances may be found in their common ancestry. All the cells of the many structures of the animal body are descended from the two parent cells from which the animal is developed. The fertilized ovum divides, and two cells are formed, these new cells divide, and so the process continues, the developing cells through unknown causes becoming arranged to form more or less definite layers and groups, which by means of foldings and unequal growths develop into the various structures and organs of the fetus. At the same time that the division is going on, the total amount of material is increasing. Each of the cells absorbs and assimilates dead food-material, and this dead material is built into living substance. During this process of development and growth the cells of special tissues and organs acquire special anatomical and chemical characters. This development of specialized cells is termed cell-differentiation. Hand in hand with the anatomical and chemical differentiation goes a physiological differentiation. The protoplasm of each type of cell, while retaining the general characteristics of protoplasm, has certain physiological properties developed to a marked degree and other properties but little developed, or altogether lacking. The fertilized ovum does not have all the anatomical and chemical characteristics of all the cells which are descended from it, not at least in just the form in which they are possessed by these cells, and it cannot be assumed that its living substance possesses all the physiological properties which are owned by its descendants. Many of these properties it must have, for many of them are essential to the continuance of life of all active cells,—such as the power to take in, alter, and utilize materials which are suitable for the building up and repair of the cell-substance, the power of chemically changing materials possessing potential energy so that the form of actual energy which is essential to the performance of the work of the cell shall be liberated, and the power to give off the waste materials which result from chemical changes. The protoplasm of the ovum, to have these powers, has properties closely allied to absorption, digestion, assimilation, respiration, excretion ; and, in consideration of the special function of the ovum, we may add that it possesses the property of reproduction. The question of its possessing the characteristic properties of muscle and nerve protoplasm cannot be answered off-hand. Careful study, however, has shown the ovum of Hydra to possess irritability, conductivity, and contractility. It undergoes amœboid movements, as was first shown by Kleinenberg. Balfour,[1] in writing of the development of the ova of Tubularidæ, which is of a type similar to Hydra, says: "The mode of nutrition of the ovum may be very instructively studied in this type. The process is one of actual feeding, much as an amœba might feed on other organisms." Something similar seems to be true of the ova of echinodermata. During impregnation various movements are described implying the properties of irritability, conductivity, and contractility. Thus in the case of *Asterias glacialis*, when the head of the

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[1] *Comparative Embryology*, pp. 17, 29.

spermatozoon comes in contact with the mucilaginous covering of the ovum, "a prominence pointing toward the nearest spermatozoon now rises from the superficial layer of protoplasm of the egg and grows until it comes in contact with the nearest spermatozoon." "At the moment of contact between the spermatozoon and the egg, the outermost layer of protoplasm of the latter raises itself up as a distinct membrane, which separates from the egg and prevents the entrance of other spermatozoa." Some of the eggs of arthropods and other forms have likewise been observed to undergo amœboid movements as a result of the physiological stimulus given by the spermatozoon.[1]

Although irritability and contractility of the ovum have thus far been made out in but few forms, it is probable that they play an important part in all during fertilization and division. It would seem, then, that the ovum has all the principal properties which we ascribe to cell-protoplasm, and that these properties are inherited more or less completely developed by the many forms of cells descended from it. The protoplasm of specialized cells, in spite of their differences in structure, still retains its protoplasmic nature. Undoubtedly structural peculiarities are intimately related to specialized functions,—the striped muscle, for example, is especially adapted for rapid movements, and the nerve-fibre is remarkable for its power of conduction.

Physiological methods for the examination of individual cells are as yet in their infancy, and we must still seek for exact knowledge of the functional activity of cells by observing the combined action of many cells of the same kind.[2]

B. IRRITABILITY OF MUSCLE AND NERVE.

Irritability is the property of living protoplasm which causes it to undergo characteristic physical and chemical changes when it is subjected to certain influences, called irritants, or stimuli. By an irritant is meant an external influence which, when applied to living protoplasm, as of a nerve or muscle, excites it to action. Irritants may be roughly classed as mechanical, chemical, thermal, and electrical. The normal physiological stimulus is developed within some of the nervous mechanisms of the body as the result of the activity of the nerve-protoplasm, this having been excited as a rule by some form of irritant. The degree of irritability of a given form of protoplasm is measured by the amount of activity which it displays in response to a definite irritant, or by the minimal amount of irritation required to excite it to action. If the irritant be applied directly to a muscle, the height to which the muscle contracts and raises a given weight may be taken as an indication of its activity. As the nerve gives no visible evidence of activity, the effect of the irritant upon it is usually estimated by the extent to which the organ stimulated by the nerve reacts; in the case of motor nerves, the strength of the contraction of the corresponding muscle is taken as an index.

To determine the exact relation of an irritant to its irritating effect we should

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[1] Korschelt: *Zoologisches Jahrbuch*, 1891, Anat. Abtheil., Bd. iv., Heft 1, S. 1. Hertwig: *Morphologisches Jahrbuch*, 1876, Bd. 1. Herbst: *Biologische Centralblatt*, 1891, xiii. S. 22.

[2] For the physiology of the lower forms of animal life, see *General Physiology*, by Verworn; translation by F. S. Lee, London and New York, 1899.

be able to accurately measure them. This we cannot do. We are unable to state in irritation-units the relative value of different kinds of irritants. Even if we could accurately estimate the amount of energy which each form of irritant can expend in iritation, we should have only one of the many factors which determine its efficiency. It is equally difficult to compare the irritating effect of irritants upon different forms of protoplasm; *e. g.* we cannot state what degree of activity of a nerve-fibre corresponds to a certain amount of activity in a muscle-fibre. In spite of the lack of exact quantitative measurements, we have gained a clear idea of the way different forms of irritants act when applied to nerves and muscles in certain ways, and have learned to control the methods of excitation sufficiently to permit the influences which alter the irritability of nerves and muscles to show themselves. The effect of irritants can best be studied upon the nerves and muscles of cold-blooded animals, because these retain their vitality and irritability for a considerable time after they have been separated from the rest of the body. It is a common observation of country folk that the body of a snake remains alive for a long time after the head has been crushed, while the body of a chicken loses all signs of life in a comparatively short time after it has been decapitated. More careful examination would show that in neither case do all parts of the body die simultaneously. Each of the myriad cells has a life of its own, which it loses sooner or later according to its nature and to the alterations to which it is subjected by the fatal change. The cells of cold-blooded animals, as the snake and frog, are much more resistant than those of warm-blooded animals, because the vital processes within the cells are less active, and the chemical changes which precede and lead to the death of the part occur more slowly. For instance, the nerves and muscles of a frog remain irritable for many hours, or even days, after the animal has been killed and they have been removed from the body. This fact is of the greatest use to the student. It enables him to study the nerve or muscle by itself, and under such artificial conditions as he cares to employ. Experience shows that the facts learned from the study of the isolated nerve and muscle hold good, with but slight modification, for the nerves and muscles when in the normal body. Moreover, it has been found that the nerves and muscles of warm-blooded animals, and even man, resemble physiologically as well as anatomically those of the frog. The correspondence is by no means complete, but it is so great as to make the facts discovered by a study of the nerves and muscles of the frog of the utmost importance to us. We are driven to such sources of information because of the great difficulty of keeping the muscles of warm-blooded animals alive and in a normal condition after removal from the circulation.

Irritability of Nerves.—The following preparation suffices to illustrate the more striking effects of irritants upon a nerve. A frog is rapidly killed, and then the sciatic nerve is cut high up in the thigh and dissected out from its groove, the branches going to the thigh-muscles being divided. The leg is then cut through just above the knee. This gives a preparation consisting of the uninjured lower leg and foot, and the carefully prepared nerve supplying the muscles of these parts. The leg may be placed foot upward, and fastened in this position by a clamp which grasps the bones at the knee, the clamp being supported by an upright (see Fig. 3). This preparation can then be subjected to a variety of tests.

Mechanical Irritation.—If the nerve be cut, pinched, suddenly stretched, or subjected to a blow, the muscles of the leg will contract and the foot will be quickly moved.

Chemical Irritation.—If acid, alkalies, various salts, glycerin, or some other chemical substances be placed upon the nerve, the muscles of the leg begin to twitch irregularly, and as the chemical enters more and more deeply into the nerve the movements will become more and more marked, until finally all the muscles are actively contracted and the foot is held straight up.

Thermal Irritation.—If hot glass, or the flame of a match, be applied to the nerve, a condition of activity will be developed in the rapidly heated nerve-fibres, and be responded to by more or less vigorous muscular contractions.

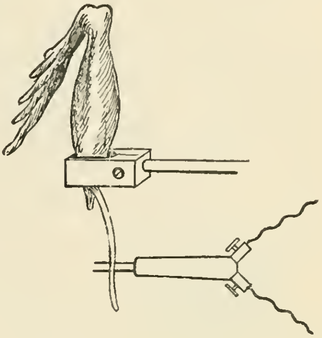

FIG. 3.—Experiment for determining the irritability of nerves.

Electrical Irritation.—If the wires connected with the two poles of a galvanic cell, static machine, or induction apparatus be brought in contact with the nerve, the muscles will twitch each time there is a sudden change in potential.

Physiological Irritation.—By all these methods the nerve was excited by irritants applied to it from without, and the muscle was excited to action by the physiological stimulus coming to it from the excited nerve. The irritant produced no visible change in the nerve, but the movement of the muscles was an evidence that the nerve had undergone a change at the point of stimulation, and that the active state thus produced had been transmitted through the length of the nerve, and had been sufficiently marked to stimulate the muscle to contraction. This condition of activity which was transmitted along the nerve is called the nerve-impulse. The same condition is excited in the nerve-fibre when the body of the cell becomes active.

Independent Irritability of Muscle.—In the above instances the irritants were applied to the nerve, and the muscle was indirectly stimulated. Muscle protoplasm, like nerve protoplasm, may be directly excited to action by various forms of irritants. A nerve after entering a muscle branches freely, and the nerve-fibres are distributed quite generally through the muscle. An irritant, if directly applied to muscle, would probably excite the nerve-fibres present as well as the muscle-fibres, and to obtain proof of independent irritability of muscle-substance it would be necessary to prevent the nerves from stimulating the muscle. This can be done by paralyzing the nerve-endings with curare.

Curare, the South American arrow-poison, is used by the Indians in hunting. The bird shot by these poisoned arrows gradually becomes paralyzed, and, losing power to move its muscles, is easily captured. The following experiment reveals the method of the action of this drug, and at the same time shows, first, that the muscle protoplasm can be irritated directly, and secondly, that the nerves do not communicate directly with the muscles, but stimulate them through the agency of terminal end-organs, called *motor end-plates.*[1]

Curare Experiment.—Rapidly destroy the brain of a frog with a slightly curved, blunt needle, and, to prevent hemorrhage, plug the wound by thrusting a pointed match through the foramen magnum into the brain-cavity. Expose the sciatic nerve of the left thigh, carefully pass a ligature under it, and tie the ligature tightly about all the tissues of the thigh excepting the nerve, thus cutting off the circulation from all the leg below the ligature without injury to the nerve. Inject into the dorsal lymph-sac or the abdominal cavity a few drops of a 2 per cent. solution of curare. In from twenty to forty minutes the drug will have reached the general circulation and produced its effect.

Although the brain has been destroyed and the frog is incapable of having sensation, it will be found that muscular movements will be made if the skin be pinched soon after the drug has been given. These are reflex movements, and are due to excitation of the spinal cord by the nerves connected with the skin. As the paralyzing action of the drug progresses, these reflex actions become feebler and feebler until altogether lost in the parts exposed to the drug, although they may still be shown by the parts from which the drug has been excluded. The condition of the nerves and muscles can be examined as soon as reflex movements of the poisoned parts cease.

To ascertain the action of the poison, expose the nerves of the two legs, either high up in the thigh or inside the abdominal cavity, where they have been subjected to the poison, and test their irritability by exciting them with electric shocks. Stimulation of the motor nerve of the right leg (*a*, Fig. 4) causes no contraction of the muscles of that leg, while stimulation of the motor nerve of the left leg (*b*), results in active movements of the muscles of that leg. The response of the left leg shows that nerve-trunks are not injured by the poison, and that the paralysis of the right leg must find some other explanation. On testing the muscles it is found that they are irritable and contract when directly stimulated. Since neither nerve-trunks nor muscles are poisoned, it is necessary to assume that the cause of the paralysis is something which prevents the nerve-impulse from passing from the nerve to the muscle. Microscopic examination shows that the nerve-fibre does not communicate directly with the muscle-fibre, but ends inside the sarcolemma in an organ which is called the motor end-plate (see Fig. 31). It appears that the nerve acts on the muscle through this organ, and its failure to act on the side which was exposed to the curare was because the end-plate had been paralyzed by the drug. By the use of curare, therefore, we are enabled to prevent the nerve-impulse from reaching the muscles, and, when we have done this, we find that the muscle is still able to respond to direct excitation with all forms of irritants, viz.,

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[1] Ch. Bernard: "Analyse physiologique des Propriétés des Systèmes musculaires et nerveux au moyen du Curare," *Comptes-rendus,* 1856, p. 825. Kölliker: "Physiologische Untersuchungen über den Wirkungen einiger Gifte," *Archiv für pathologische Anatomie,* 1856.

electrical, mechanical, thermal, and chemical. Evidently the muscle-protoplasm is irritable and is capable of developing a contraction independently of the nerves. There are a number of natural plant bases that have a "curare-like" action—*e. g.*, brucin, strychnin, leucin, nicotin, conin, etc.[1] If a nerve-muscle preparation be dissected out and placed in a 0.7 per cent. solution of sodium chloride containing one of these drugs, sooner or later the nerve-ends will be poisoned, and it will be found that excitation of the nerve has no effect on the muscle, although the muscle responds well to direct excitation.

Other Proofs that the Muscle-protoplasm can be Directly Irritated.—Muscles with long parallel fibres, such as the sartorius of the frog, contain no nerves at their extremities, the nerve-fibres joining the muscle-fibres at some little distance from their ends. The tip of such a muscle, where no nerve-fibres can be discovered by the most careful microscopical examination, is found to be irritable. The fact that in some of the lower animals there are simple forms of contractile tissue in which nerves cannot be discovered, and which are irritable, is interesting as corroborative evidence, although it is not a proof, of the independent irritability of a highly differentiated tissue such as striated muscle. Another similar piece of evidence is to be found in the fact that the heart of the embryo beats rhythmically before nerve appears to have been developed. A proof can be found in the observation that if a nerve be cut it begins to undergo degeneration and loses its irritability and conductivity in four or five days, and the excitation of such a nerve has no effect upon the muscle although direct stimulation of the muscle itself is followed by contraction. As degeneration involves not only the whole course of the nerve, but also the nerve end-plates, the contraction must be attributed to the irritability of the muscle-substance. Another point of interest in this connection is the behavior of a dying muscle. If it be struck, instead of contracting as a whole it contracts at the place where it was irritated, the drawing together of the fibres at the part forming a local swelling, or welt. If such a muscle be stroked, a wave of contraction spreads over it, following the instrument, instead of extending, as under normal conditions, by means of the excited nerve-fibres to other parts. Under these circumstances the circumscribed contraction would seem to show that the nerves had lost their irritability, or that the nerve-ends no longer transmitted the stimulus to the muscle, and the response was due to the direct excitation of the dying muscle-fibres. This phenomenon is known as an idiomuscular contraction.

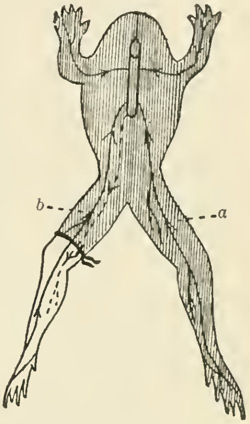

FIG. 4.—Curare experiment: the shaded parts show the region of the body to which the drug had access; the unshaded part, the portion which was protected by the ligature from the action of the drug. The unbroken lines represent the sensory nerves which carry sensory impulses from the skin to the central nervous system; the broken lines indicate the motor nerves, which carry motor impulses from the central nervous system out to the muscles (after Lauder Brunton: *Pharmacology, Therapeutics, and Materia Medica*).

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[1] Santesson: *Archiv für experimentelle Pathologie und Pharmakologie*, 1895, Bd. 35, S. 23.

CONDITIONS WHICH DETERMINE THE EFFECT OF EXCITATION.

The result of the irritation of nerve and muscle is dependent on two sets of conditions—namely, conditions which determine the irritability; conditions which determine the efficiency of the irritant.

It will be necessary for us to study the second set of conditions first—for, before we can judge of the irritability and the effect of various influences upon it, we must consider how far the activity of the nerve and muscle is dependent on the character, strength, and method of application of the irritant.

Conditions which Determine the Efficiency of Irritants.—Some of these conditions can be best studied on nerves, while others are more apparent in their effects on muscles. The most useful irritant for purposes of study is the electric current. Mechanical, thermal, and chemical irritants are likely to injure the tissue, and are not manageable, whereas electricity, if not too strong, can be applied again and again without producing any permanent alteration, and can be accurately graded as to strength, place, time, duration of application, etc. Of course, the results obtained by the use of a given irritant cannot be accepted for others until verified. The conditions which determine the effectiveness of the electric current as an irritant may be classed as follows: (*a*) The rate at which the intensity changes. (*b*) The strength of current. (*c*) The density of current. (*d*) The duration of application. (*e*) The angle of application. (*f*) The direction of flow.

Irritating Effect of the Electric Current.—Luigi Galvani, Professor of Physics at Bologna, 1791 (or, according to some, his wife Lucia), observed the legs of frogs which had been prepared for the kitchen, and had been suspended by brass hooks from an iron balcony, make convulsive movements every time the wind blew them against the iron. He repeated the experiment in his laboratory, and decided that the frogs had been excited to action by electric currents developed within themselves; he looked upon the metals which he had used merely as conductors for this current. Volta, Professor of Natural Philosophy at Pavia, repeated Galvani's experiment, and concluded that there had been an electric current developed from the contact of the dissimilar metals with the moist tissues of the frog. In accordance with this idea he constructed the voltaic pile, and this was the starting-point of the science of electricity of to-day.

Although it is true that, under certain conditions, differences in electric potential sufficient to excite muscles to contraction can be developed in the animal body, the contractions of the frog's leg which Galvani observed were due to the metals which he employed. The experiment can be easily performed by connecting a bit of zinc to a piece of curved copper wire, and bringing the two ends of the arc against the moist nerve and muscle of a frog. A stronger and more efficient shock can be obtained from a Daniell or some other voltaic cell.

A Daniell cell (Fig. 5) is composed of a zinc and copper plate, the former dipping into dilute sulphuric acid, the latter into a strong copper-sulphate solution. Although gravity will keep these liquids separated, if the cell is to be moved about it is better to enclose one of them in a porous cup. A common form of cell consists of a glass jar, in the middle of which is a porous cup; outside the cup is the sulphuric acid and the zinc plate, and inside the cup is the copper sulphate solution and the copper plate. The zinc plate is acted upon by the sulphuric acid, and, as a result of the chemical change, a difference of electric potential is set up between the metals, so that if the zinc and copper be connected by a piece of metal, what we call an electric current flows from the zinc to the copper inside the cell, and from the copper to the zinc outside the cell. The zinc plate, being the seat of the chemical change, is called the positive plate, and the copper the negative plate. Several such cells may be connected together to form a battery, each cell adding to the electro-motive force, and hence to the strength of the current. As the current is always considered to flow from + to —, we call the end of the wire connected with the copper (negative plate) the positive pole, or *anode*, and the end of the wire connected with the zinc (positive plate) the negative pole, or *kathode*. If one of these wires be touched to a nerve, under ordinary circumstances no effect is produced; but when the other wire is likewise brought in contact with the nerve, the moist tissues of the nerve form a conductor, complete the circuit, and an electric current at once flows through the nerve from the anode to the kathode. The effect of the sudden flow of electricity into the nerve is to give it a shock—as we say, it irritates the nerve—and the muscle which the nerve controls is seen to contract.

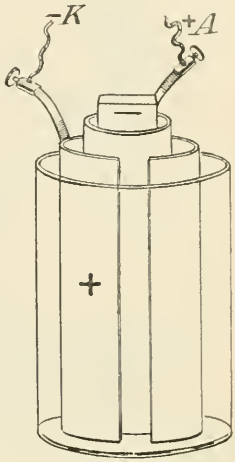


Fig. 5.—Daniell cell.

In the place of using ordinary wires for applying the electricity, we use electrodes. These are practically the same thing, but have insulated handles, and have a form better suited to stimulate nerves or other tissues. The two wires may be held in two different handles, in which case we speak of the positive and negative electrodes, or the anode and the kathode, or they may be held in the same handle (Fig. 6).

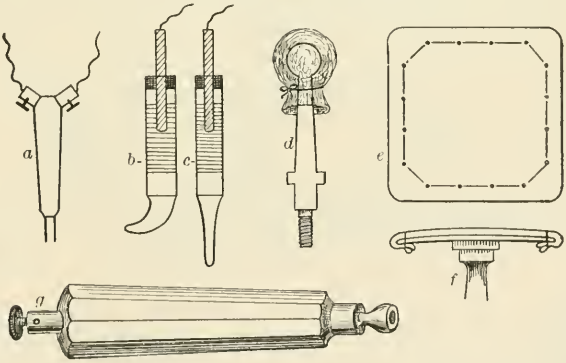


Fig. 6.—*a*, Ordinary electrode for exciting exposed nerves and muscles, consisting of two wires enclosed, except at their extremities, in a handle of non-conducting material; *b*, *c*, non-polarizable electrodes. When metals come in contact with moist tissues a galvanic action is likely to occur and polarizing currents to be formed. These extra currents would complicate or interfere with the results of many forms of experiment, and they are avoided by the use of non-polarizable electrodes. A simple form consists of a short glass tube, at one end of which is a plug of china clay mixed with a 0.6 per cent. solution of sodium chloride, and at the other end a cork through which an amalgamated zinc rod is thrust. The zinc rod dips into a saturated solution of zinc sulphate, which is in contact with the clay. The clay plugs touch the tissue to be excited, and the current passes from the zinc rods through the zinc-sulphate and sodium-chloride solutions in the clay to the tissues; *d*-*f*, electrodes for exciting human nerves and muscles through the skin (after Erb): these may be of various forms and sizes, and are arranged to screw into handles (*g*), to which the wires are attached; they are usually made of brass and covered with sponge or other absorbent material wet with salt-solution. The smaller electrodes are used when a dense, well-localized stream is required, and the larger electrodes when little action is wished and it is of advantage to have the stream diffuse.

Keys.—It is not as convenient to stimulate a nerve by touching it with the electrodes as it is to place it upon the electrodes and close the connection between the zinc and copper at some other part of the circuit; this may be done by what is called a key. Any mechanism which can be used to complete the circuit could receive this name, and there are a number of convenient forms. The one most used by physiologists is that devised by Du Bois-Reymond, and which bears his name (see Fig. 7). This has the advantage of being capable of being used in two different ways—one simply as a means to close the circuit, and the other to short-circuit the current. These two methods are shown in Figure 8.

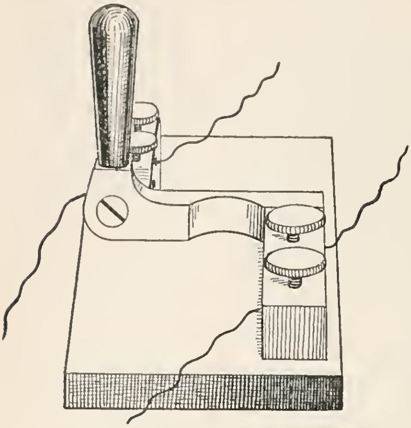


FIG. 7.—Electric key.

By the former method the key supplies a movable piece of metal by which contact between the two ends of the wires may be made as in *a* (Fig. 8), or broken as in *b*, and the current be sent through the nerve, or prevented from entering it. By the latter method the battery is all the time connected with the electrodes, and the key acts as a movable bridge between the wires, and when closed gives a path of slight resistance by which the current can return to the battery without passing through the nerve. The current always takes the path of least resistance, and so, if the key be closed as in *c*, all the current will pass through the key and none will go to the nerve, which has a high resistance, whereas if the key be opened as in *d*, the bridge being removed, all the current will go through the nerve. It is often better to let the cell or battery work a short time and to get its full strength before letting the current enter the nerve, and the short-circuiting key permits of this. Moreover, there are times when a nerve may be stimulated if connected with the source of electricity by only one wire; when the nerve is so excited, it is called unipolar stimulation; this may be prevented by the short-circuiting key.

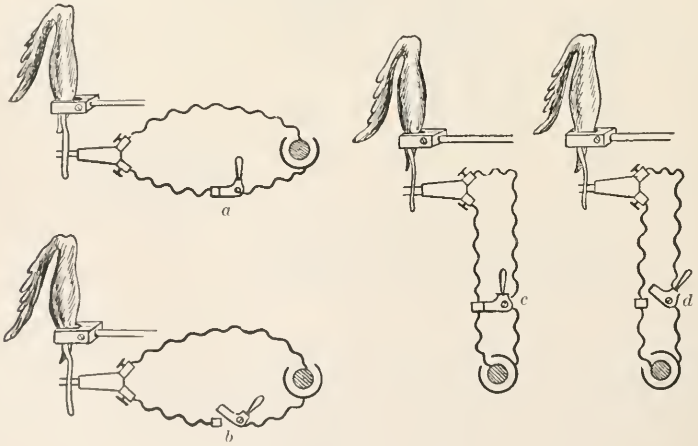


FIG. 8.—Electric circuiting.

As has been said, a nerve is irritated if it be connected with a battery and an electric current suddenly passes through it. Unless the current be very strong the irritation is transient, however; the muscle connected with the nerve gives a single twitch at the moment that the current enters the nerve, and then remains quiet; and thus we meet with the remarkable fact that an electric current, though irritating a nerve at the moment that it enters it, can flow through the nerve continuously without exciting it. Further, although the current while flowing through the nerve does not excite it, a sudden withdrawal of the current from the nerve irritates it, and causes the muscle connected with it to contract. It is our custom to speak of closing, or making, the circuit when we complete the circuit and let the current flow through the nerve, and of opening, or breaking, the circuit when we withdraw the current from the nerve. Since the closing of the circuit acts as a sudden irritant to the nerve, we speak of this irritant as a "making" or "closing" shock, and the corresponding contraction of the muscles as a making or closing contraction; similarly we speak of the effect of opening the circuit as an "opening" or "breaking" shock, and the resulting contraction as an opening or breaking contraction. As we shall see later, the making contraction excited by the direct battery current is stronger than the breaking contraction: the explanation of this must be deferred (see page 38).

(*a*) *Effect of the Rate at which an Irritant is Applied, Illustrated by the Electric Current.*—As has been said, an electric current of constant medium strength does not irritate a nerve while flowing through it, but the nerve is irritated at the instant that the current enters it, and at the instant that the current leaves it. Is it the change of condition to which the nerve is subjected, or is it the suddenness of the change, which produces the excitation? Would it be possible to turn an electric current into a nerve and remove it from a nerve so slowly that it would not act as an irritant?

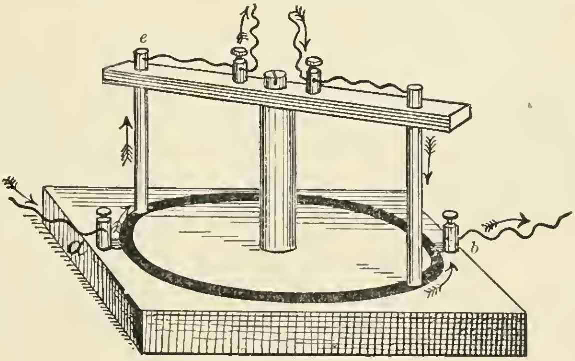


Fig. 9.—Rheonome.

The experiment has been tried, and it has been found that if the nerve be subjected to an electric current the strength of which is increased or decreased very gradually, no change occurs in the nerve sufficient to cause a contraction of the muscle. In this experiment, instead of using the ordinary key, we close and open the circuit by means of a rheonome (see Fig. 9).

This instrument contains a fluid resistance, which can be altered at will, thereby permitting a greater or less strength of current to pass from the battery into the circuit containing the nerve. The wires from the battery are connected with binding-posts, *a*, *b* (Fig. 9), at opposite sides of a circular groove containing a saturated solution of zinc sulphate. Strips of amalgamated zinc connect the binding-posts with the fluid, and so complete a circuit which offers much resistance to the passage of the current. From the centre of the block containing the groove rises an upright bearing a movable horizontal bar, from each extremity of which an amalgamated zinc rod, *e* and *f*, descends and dips into the zinc-sulphate solution. The zinc rods are connected with binding-posts on the movable bar, and from these wires pass to the electrodes on which the nerve rests. The bar revolves on a pivot on the top of the upright, and thus the zinc rods can be readily approached to or removed from the zinc strips, the poles of the battery. When the zinc rods hold a position midway between these poles, the current all passes by the way of the fluid. As the bar is turned, so as to bring the zinc rods nearer and nearer the two poles of the battery, the current divides, and more and more of it passes through the path of lessening resistance of which the nerve is a part. When the zinc rods are brought directly opposite the poles of the battery nearly all the current passes by the way of the nerve. If the bar be turned more or less rapidly, the current is thrown into, or withdrawn from, the nerve more or less quickly.

By this arrangement we can not only observe that the nerve fails to be irritated when the current is made to enter or leave it gradually, and when it is flowing continuously through it, but that sudden variations in the density of the current flowing through the nerve, such as are caused by quick movements of the bar, although they do not make or break the circuit, serve to excite. This experiment shows that electricity, as such, does not irritate a nerve, but that a sudden change in the density of the current, whether it be an increase or decrease, produces an alteration in the nerve-protoplasm which excites it to action and causes the development of what we call the nerve-impulse.

Du Bois-Reymond's Law.—Du Bois-Reymond formulated the following rule for the irritation of nerves by the electrical current: "It is not the absolute value of the current at each instant to which the motor nerve replies by a contraction of its muscle, but the alteration of this value from one moment to another; and, indeed, the excitation to movement which results from this change is greater the more rapidly it occurs by equal amounts, or the greater it is in a given time."

We shall have occasion to see that this rule has exceptions, or rather that there is an upper as well as lower limit to the rate of change of density of the electric current which is favorable to irritation.

Similar observations may be made with other forms of irritants. Pressure, if brought to bear on a nerve gradually enough, may be increased to the point of crushing it without causing sufficient irritation to excite the attached muscle to contract, although, as has been said, a very slight tap is capable of stimulating a nerve. Temperature, and various chemicals, likewise, must be so applied as to produce rapid alterations in the nerve-protoplasm in order to act as irritants. The same rule would seem to hold good for the nerve-cells of the central nervous system. It is a matter of daily experience that the nervous mechanisms through which sensory impressions are perceived are vigorously excited by sudden alterations in the intensity of stimuli reaching them, and but little affected by their continuous application; the withdrawal of light, a sudden alteration of temperature, an unexpected noise, or the cessation of a monotonous sound, as exemplified by the common experience that a sleeper is awakened when reading aloud abruptly ceases, attract the attention, although a continuous sensory irritation may be unnoticed. This physiological law of the nervous system would seem to have a psychological bearing as well.

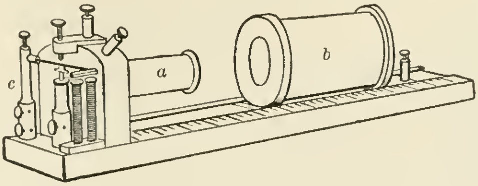


FIG. 10.—Induction apparatus: *a*, primary coil; *b*, secondary coil; *c*, the automatic interrupter.

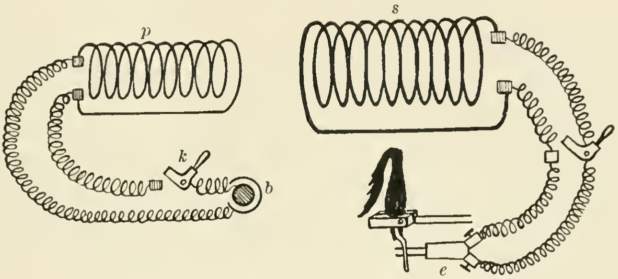


FIG. 11.—Schema of induction apparatus.

Irritating Effect of Induced Electric Currents.—Within certain limits, the more rapid the change in intensity of an electric current the greater its power to irritate. This probably accounts in part for the fact that the induced current is a more powerful irritant to nerves than the direct galvanic current. Induced currents are usually obtained by means of an induction apparatus (see Fig. 10).

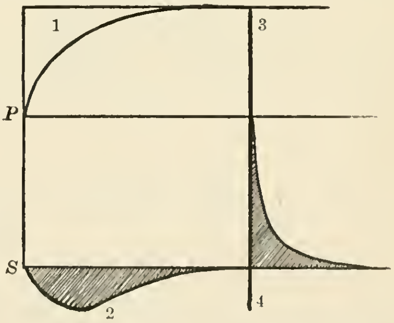


FIG. 12.—Schema of the relative intensity of induction currents (after Hermann, *Handbuch der Physiologie*, Bd. ii. S. 37): *P*, abscissa for the primary current; *S*, abscissa for the secondary current; 1, curve of the rise of intensity of the primary current when made; 2, curve of the rise and fall of intensity of the corresponding induced current; 3, curve of fall of the intensity of the primary current when it is broken; 4, curve of the rise and fall of intensity of the corresponding induced current.

The ordinary induction apparatus employed in the laboratory (see Fig. 11) consists of a coil of wire, *p*, which may be connected with the terminals of a battery, *b*, and a second coil, *s*, wholly independent of the first, which is connected with electrodes, *e*. At the instant that the key, *k*, in the primary circuit is closed, and the battery current enters the primary coil, an induced current is developed in the secondary coil, and the nerve resting on the electrodes is irritated. The induced current is of exceedingly short duration, suddenly rising to full intensity and falling to zero. As long as the battery current continues to flow constantly through the primary coil, there is no change in the electrical condition of the secondary coil, but at the instant the primary current is broken another induced current of short duration is set up in the secondary coil, and again the nerve receives a shock. The rise and fall of the density of the current in the secondary coil is very rapid, and this rapid double change in density of the current causes the induction shock to be a very effective irritant. The breaking induction shock, as we call that which is produced by breaking the primary current, is found to act more vigorously than the making shock, which is the reverse of what is found with direct battery currents. The cause of this lies in the nature of the apparatus. At the moment that the current begins to flow into the primary coil, it induces not only a current in the secondary coil, but also currents in the coils of wire of the primary coil. These extra induced currents in the primary coil have the opposite direction to the battery current and tend to oppose its entrance, and thereby to prevent it from immediately gaining its full intensity. This delay affects the development of the induced current in the secondary coil, causing it to be weaker and to have a slower rise and fall of intensity than would otherwise be the case. When the primary current is broken, on the other hand, there is no opposition to its cessation, and the current induced in the secondary coil is intense and has a rapid rise and fall. These differences are illustrated in Figure 12.

Myogram.—To accurately test the effect of the making and breaking induction shocks, it is necessary to record the reaction of the nerve; this can be done by recording the extent to which the corresponding muscle contracts in response to the stimulus which it receives from the nerve. In such an experiment it is customary to use what is known as a nerve-muscle preparation. The gastrocnemius muscle and sciatic nerve of a frog, for instance, are carefully dissected out, the attachment of the muscle to the femur being preserved, and the bone being cut through at such a point that a sufficiently long piece of it shall be left to fasten in a clamp, and so support the muscle (see Fig. 13).

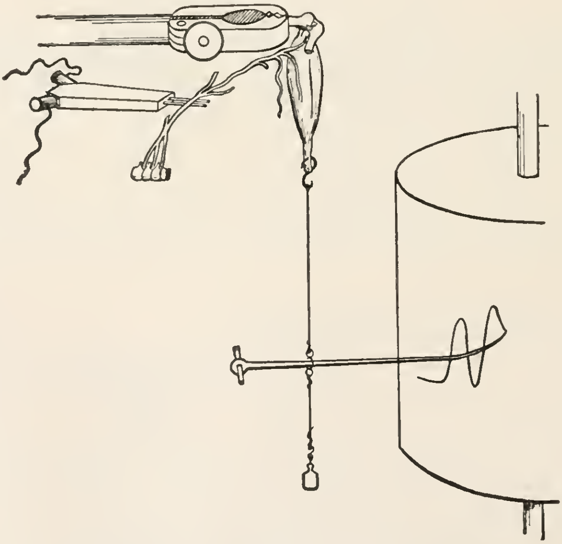


FIG. 13.—Method of recording muscular contraction.

The simplest method of recording the extent of the muscular contraction is to connect the muscle by means of a fine thread with a light lever, and let the point of the lever rest against a smooth surface covered with soot, so that when the muscle contracts it shall draw up the lever and trace a line of corresponding length upon the blackened surface. The combination of instruments employed to record the contraction of a muscle is called a *myograph,* and the record of the contraction is termed a *myogram.* If, when the muscle of a nerve-muscle preparation is thus arranged to write its contractions, the nerve be irritated with alternating making and breaking induction shocks of medium strength, the muscle will make a series of movements, which, if the surface be moved past the writing-point a short distance after each contraction, will be pictured in the record as a row of alternating long and short lines, the records of the breaking contractions being higher than those of the making contractions (Fig. 14). Similar results are obtained if, instead of irritating the nerve, we irritate the curarized muscle directly.

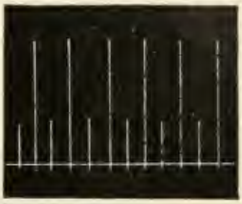


FIG. 14.—Effect of making and breaking induction shocks.

Stimulating Effects of Making and Breaking the Direct Battery Current.—On account of the construction of the induction apparatus, breaking induction shocks are more effective stimuli than making induction shocks. The reverse is true of the stimulating effects which come from making and breaking the direct battery current. The excitation which results from sending a galvanic current into a nerve or muscle is stronger than that which is caused by the withdrawal of the current. This difference is due to the physiological alterations produced by the current as it flows through the irritable substance, and is without doubt closely associated with changes in the irritability which occur at the moment of the entrance and exit of the current.

The making contraction starts from the kathode, and the breaking contraction from the anode. The irritation process which results from making the current is developed at the kathode, and that which results from breaking the current is developed at the anode. This was first demonstrated on normal muscles by Von Bezold,[1] and has since been substantiated for nerves as well as muscles by the experiments of a great many observers. Perhaps the most striking demonstration is to be obtained by Engelmann's method. The positive and negative electrodes are applied to the two extremities of a long curarized sarto-

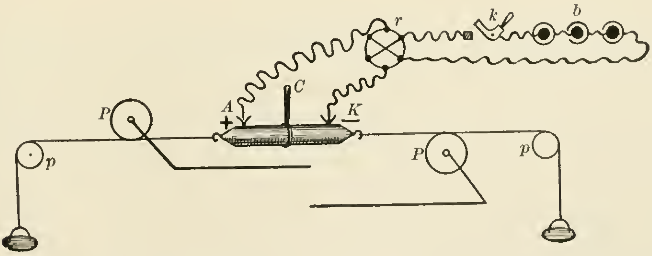
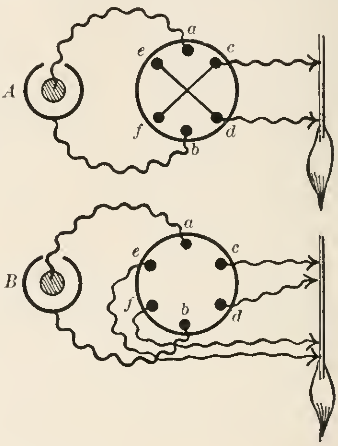


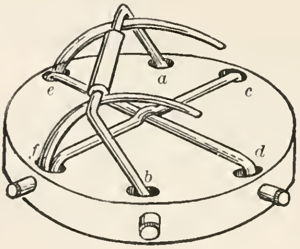
FIG. 15.—Schema of Hering's double myograph: *C,* clamp holding middle of muscle; *P,P,* pulleys to the axes of which the recording levers are attached; *p,p,* pulleys for the light weights which keep the muscle under slight tension; *A,* positive electrode; *K,* negative electrode; *r,* commutator for reversing the current; *k,* key; *b,* battery.

[1] *Untersuchungen über die elektrische Erregung von Muskeln und Nerven,* 1861.

rius muscle, which is clamped in the middle firmly enough to prevent the contractions of one half from moving the other, but not enough to interfere with the conduction-power of the tissue. The record of the contractions is best obtained by the double myograph of Hering (Fig. 15), which permits the recording levers attached to the two ends of the muscle to write directly under each other, so that any difference in the beginning of the contraction of the two halves of the muscle is immediately recognizable from the relative positions of the records of their contractions.

The current is applied to the two extremities of the muscle by non-polarizable electrodes. In all experiments with the direct battery current it is essential to employ non-polarizable electrodes. The form devised by Hering is very useful where the current has to be applied directly to the muscle, because the two electrodes are hung from pivots in such a way that they move with the movements of the muscle, and hence do not shift their position when the muscle contracts. Some kind of apparatus has to be employed for quickly reversing the direction of the current. A convenient instrument for this purpose is Pohl's mercury commutator (Fig. 16). This instrument consists of a block of insulating material in which are six little cups containing mercury, which is in connection with binding-posts on the sides of the block. Two of the mercury cups on the opposite sides of the block *a* and *b* (Fig. 17, *A*), are connected by wires with the battery; two others, *c* and *d*, are connected with wires which pass to the electrodes; the remaining two on the opposite side of the block, *e* and *f*, are joined by movable good conducting wires with the cups *c* and *d* in such a way that *c* connects with *f*, and *d* with *e*. Two anchor-like pieces of metal are connected by an insulated handle, and are so placed that the stocks of the anchors dip into the mercury cups *a* and *b* (Fig. 16). The anchors can be rocked to one side or the other, so that the ends of the curved arms shall dip into the cups *c* and *d* (in which case cup *a* will be connected with cup *c*, and cup *b* with cup *d*), or so that the other ends of the arms shall dip into cups *e* and *f* (in which case cup *a* will be connected with cup *e*, and by means of the cross wire with cup *d*, and cup *b* will be connected with cup *f*, and by means of the cross wire with cup *c*). By the arrangement shown in Fig. 17, *A* the current can pass from the battery by way of *a* and *c* down the nerve, and by way of *d* and *b* back to the battery; or it can pass from the battery by way of *a*, *e*, *d*, and in the reverse direction, up the nerve and back to the battery, by way of *c*, *f*, *b*. There are many other forms of apparatus, generally known as pole-changers, which may be employed to reverse the current.

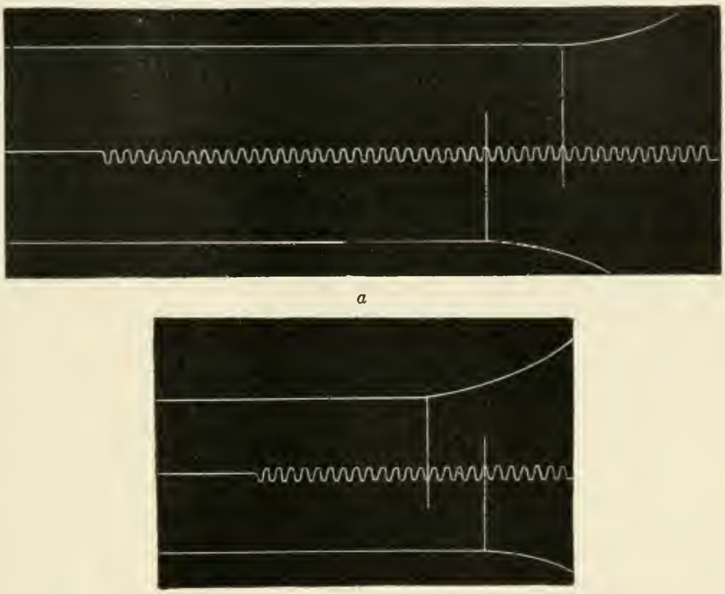




Figs. 16, 17.—Pohl's mercury commutator.

The commutator can be used in another way (see Fig. 17, *B*). If the battery be connected with it as before, and the cross wires be removed, the current can be sent at will into either one of two separate circuits. For instance, if the cups *c*, *d* be connected with the electrodes on one part of the nerve, and the cups *e*, *f* with the electrodes on another part, the anchors have only to be rocked to one side or the other to complete the communication between the battery and one or the other of these pairs of electrodes.

In experiments with the double myograph, in which the *making* of the current is used to irritate, records are obtained such as are shown in Figure 18.



a

b

Fig. 18.—The making contraction starts at the kathode (after Biedermann).

In these records the beginning of the tuning-fork waves shows the moment that the current was made and the irritation given. In the experiment from which record *a* was taken the anode was at the knee-end of a curarized sartorius muscle and the kathode at the pelvic end—*i. e.* the current was ascending through the muscle. The lower of the two curves was that got from the *kathode* half, the arrangement being that shown in Figure 15, and the lower curve began before that got from the anode half; *i. e.* the contraction originated at the kathode and spread thence over the muscle. In *b* the current was reversed, and the upper curve was obtained from the kathode half and the lower from the anode half; in this also the *kathode* end contracted first. In the above experiments the making of the current was used to irritate, and the muscular contraction began at the kathode; in experiments in which the breaking of the current was employed the opposite was observed, the anode end being seen to contract first, regardless of the direction of the current.

If strong currents be used, the fleeting contractions which result from opening and closing the current are followed by continued contractions, the closing, Wundt's, and the opening, Ritter's tetanus, as they are called. These continued contractions, which last for a considerable time, remain strictly located at the region where they originate, and Engelmann proved by his experiments that the tetanus which results from closing a strong current remains located at the kathode, and the tetanus following the opening of the current remains located at the anode.

The same is true of the nerve as of the muscle; the irritating process which is called out by the sudden entrance of a battery current into a nerve starts from the negative pole, the kathode, and spreads thence throughout the nerve, while the irritating process excited by the cessation of the flow of the current starts from the region of the positive pole, the anode, and spreads from that point throughout the nerve. A proof of this was obtained by Von Bezold, who observed the difference in the time between the moment of excitation and the beginning of the contraction of the muscle, when the nerve was excited by opening and by closing the current, with the anode next to the muscle, and with the kathode next to the muscle. He found the time to be longer when the current was closed if the kathode was the more distant, and to be longer when the current was opened if the anode was farther from the muscle. Evidently in the case of the nerve as of the muscle, the irritable substance subjected to the current is not all affected alike. The current does not set free the irritating process at every part of the nerve, but produces peculiar and different effects at the two poles, the change which occurs at the kathode when the current is closed being of a nature to cause the development of the excitatory process which awakens the closing contraction, and the change which occurs at the anode when the current is opened being such as to cause the development of the excitatory process which calls out the opening contraction.

Closing contractions are stronger than opening contractions. The irritation developed at the kathode is stronger than that developed at the anode. It is true of both striated and unstriated muscles that an efficient irritation can be developed at the kathode with a weaker irritant than at the anode. Moreover, a greater strength of current is required to produce opening than closing continued contractions.

The same may be said of nerves. If one applies a very weak battery current to the nerve of a nerve-muscle preparation, he notices when he closes the key a single slight contraction of the muscle, and when he opens the key, no effect. If he then increases the strength of the current very gradually, and tests the effects of the making and breaking of the current from time to time, he observes that each time the strength of the current is increased the closing contraction, which is due to irritation originating in the part of the nerve subject to the kathode, grows stronger, and finally contractions are also seen when the circuit is broken, the irritation process developed at the anode having become strong enough to excite the muscle. These opening contractions at first are weak, but gradually increase in strength, until with a medium strength of current vigorous contractions are seen to follow both opening and closing of the current. If the strength of the current be still further increased, it is found that either the closing or opening contraction begins to decrease in size, and if a very strong current be employed, the closing or opening contraction will be absent. It has been ascertained that the direction in which the current is flowing through the nerve determines which of these contractions shall cease to appear. The cause of this will be explained a little later.

(*b*) *Effect of Strength of Irritant.*—As a rule, the stronger an electric current the greater its irritating effect. This can be readily tested upon a nerve with the induction current, the strength of which can be varied at pleasure. The strength of the induced current obtained from a given apparatus depends upon the strength of the current in the primary coil, and on the distance of the secondary from the primary coil. In ordinary induction machines (see Fig. 10, p. 33) the secondary coil is arranged to slide in a groove, and can be easily approached to or removed from the primary coil, thus placing the coils of wire of the secondary coil more or less under the influence of the magnetic field about the primary coil. This permits the strength of the current to be graded at will. The strength of the induced current does not increase, however, in direct proportion to the nearness of the coils. As the secondary approaches the primary coil, the induced current increases in strength at first very slowly, and later more and more rapidly, reaching its greatest intensity when the secondary coil has been pushed over the primary.

The relation of the strength of a current to the irritating effect upon a nerve can be readily tested with such an induction apparatus. The secondary coils can be connected with a pair of electrodes on which the nerve of a nerve-muscle preparation rests (as in Fig. 11, page 33), and the muscle can be arranged to record the height of its contractions (as in Fig. 13, p. 34). The experiment can be begun by placing the secondary coil at such a distance from the primary that the making and breaking shocks are too feeble to have any effect upon the nerve. Then the secondary coil can be gradually approached to the primary, the primary current being made and broken at regular intervals. At a certain point the breaking shock will excite a very feeble contraction, the making shock producing no effect. If this contraction is barely sufficient to be recognized, we call it the minimal breaking contraction (see Fig. 19, *a*). In seeking the minimal contraction care must be taken not to excite the preparation at too short intervals of time, for, as we shall see, an irritation too slight to excite even a minimal contraction may, if repeated at short intervals, increase the irritability of the preparation and so become effective. By using a short-circuiting key in the secondary circuit we can cut out the making shocks, and test the effect of a further increase in the strength of the current by the response of the muscle to the breaking shocks. As the contractions become larger, care must be taken not to irritate the muscle too frequently, lest it be fatigued and so fail to give the normal response. As the current is strengthened the breaking contractions will become higher and higher until a point is reached beyond which the strength of the current may be increased to a considerable extent without any further heightening effect (Fig. 19, *b*). If the current be still further increased, this first maximum is succeeded by a still further growth in the height of the contractions, until finally a second maximum (Fig. 19, *d*) is reached, beyond which no further increase is to be obtained, however much the current may be strengthened.[1]

FIG. 19.—Effect of increase of strength of current on the efficiency of breaking induction shocks (after Fick): *a*, minimal contraction; *b–c*, first maximum; *d–e*, second maximum.

If both the making and breaking contractions be recorded, inasmuch as the making shocks are weaker stimuli than the breaking (see p. 35), the making contractions do not appear until after the breaking contractions have acquired a considerable height. After the making minimal contraction has been obtained, the making contractions rapidly gain in height as the current is strengthened, and finally acquire the same height as the maximal breaking shocks.

The relation of the strength of the electric current to its irritating power can be demonstrated equally well by using the direct galvanic current. The strength of the galvanic current depends upon the character and number of the cells employed, and the total resistance in the circuit. The strength of the current can be easily varied by altering the resistance, and there are a number of forms of apparatus for this purpose.

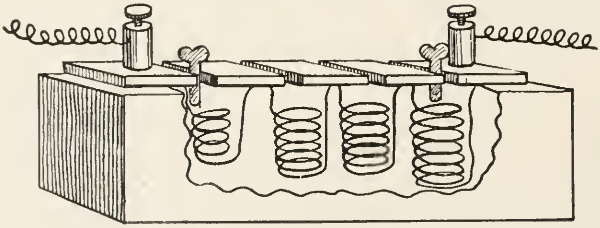


FIG. 20.—Rheostat.

A convenient instrument is the rheostat (Fig. 20). This is a box containing coils of wire of known resistance. These coils are connected with a series of heavy brass blocks on top of the box. The current enters the box by a binding-post attached to the first of the brass blocks and passes thence from block to block, by going through the coils of wire connecting them, until it reaches the binding-post at the other end of the series. The blocks can be also connected by good conducting brass plugs, which can be pushed in between them, and when this is done, as the current passes directly from block to block instead of going through the resistance coils beneath, the resistance is reduced to a corresponding amount.

Another method of altering the strength of the current flowing through the nerve is to employ some form of shunt to split the current so that only a part of it shall pass by way of the nerve. A current takes the path of least resist-

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[1] Fick: *Untersuchungen über elektrische Nervenreizung*, Braunschweig, 1864.

ance, and if two paths are opened to it, more or less can be sent through one of them by decreasing or increasing the resistance in the other.

A useful instrument for dividing the current is the rheocord. The schema given in Figure 21 illustrates the way in which it is used. The amount of current passing to the nerve will vary with the relative resistance in *a*, *b*, *c*, *d*, *e*, *f*, and in *a*, *b*, *g*, *h*, *e*, *f*. The bridge *c*, *d* can be slid along the fine German-silver wires *b*, *i* and *e*, *j*, and thus the resistance *a*, *b*, *c*, *d*, *e*, *f*, and the amount of current passing through the nerve, can be varied at pleasure.

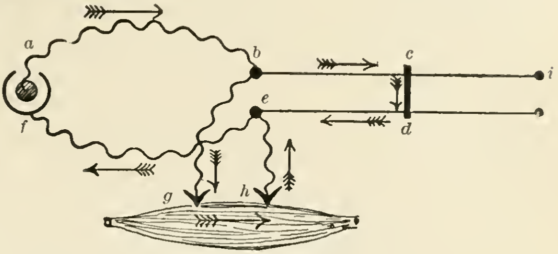

FIG. 21.—Rheocord.

With such an arrangement we should find that the irritating effect of the current is largely dependent upon its strength. In the case of strong currents, however, the results may be complicated by alterations in the irritability and conductivity, which we will consider later. It is true also of other forms of irritants, and of muscles as of nerves, that the effect of stimulation, up to a certain limit, increases with the strength of the irritant.

(*c*) *Effect of Density of the Current.*—Although the strength of the current is an all-important factor in its excitatory action, the effectiveness of the current as an irritant depends very largely on the density of the stream. When the current enters into a conductor, it spreads widely through the conducting substance, and though the larger part of it takes the path of least resistance, which is usually the shortest path to the point of exit, many of the threads of current make a comparatively wide circuit to reach the outlet. If the conductor is equally good at all points, but is irregularly shaped, the density of the stream will be greatest where the diameter of the conductor is least. Thus it happens that if a current be made to flow from end to end of a muscle, like the sartorius of the frog, which is smaller at the knee end than at the pelvic end, the density of the current will be greater at the lower than at the upper end, and the irritating power of the current will be greater at the lower end.[1]

This question of the effect of the density of the current is important, as it helps to explain the peculiar reactions to the electric stream obtained when a current is applied under normal conditions through the skin to the human nerve (see p. 51).

Spread of Electric Current.—The tendency of electric currents to spread widely through moist conductors is a common source of error in electrical excitation, and should be always guarded against. For example, if it is necessary to excite a nerve at the bottom of a deep wound, shielded electrodes should be used—*i. e.*, electrodes in which the metal terminals are insulated by vulcanite, except at the part which the nerve is to touch. Moreover, care should be taken that there is no fluid communication between the electrodes and the surrounding tissues. If these precautions are not observed,

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[1] Biedermann: *Elektrophysiologie*, 1895, Bd. i. S. 185.

the current may excite other parts than those which it is intended to excite and false conclusions may be reached.

In case currents of high potential are employed, another source of error may arise through electrostatic charging of distant parts.

Spread of Electrostatic Charges.—If the primary coil of an induction apparatus be connected with a battery by the closure of a key in the primary circuit, the sudden flow of current through the coil is accompanied by a transient change in the stress of the magnetic field about the coil. This change in the magnetic field induces an alteration in the electrical condition of the wire of the secondary coil of the apparatus, and the terminals of this coil undergo a rapid change of electrical potential, the one becoming positive, the other negative. If two electrodes be connected with the binding posts of the secondary coil, they become the terminals of the coil and are given, one a positive, the other a negative charge. The same thing happens when the key in the primary circuit is opened. In both cases the change of potential is only momentary in its duration. The effect of opening the primary circuit is considerably stronger than that of closing the circuit, for reasons stated on page 33.

If the two electrodes are connected by a conducting material, an electric current will flow from one to the other at the instant the change of potential takes place. If the electrodes be connected by the nerve of a nerve-muscle preparation, an electrical current will flow through the nerve; the nerve will be excited, a nerve-impulse will be developed and be transmitted along the nerve to the muscle and cause it to contract. It not infrequently happens, if the current entering the primary coil is strong and a large electromotive force is developed in the secondary coil, that the exciting effect of the sudden electrical change is not confined to the part of the nerve directly connecting the electrodes, but spreads to distant parts of the nerve, and even to the muscle. This is shown by the fact that the muscle will contract even after a moist ligature, tied tightly about the nerve, has broken the continuity of its protoplasm and so prevented the nerve impulse from reaching the muscle. In such a case the contraction of the muscle is due to an irritation of the nerve beyond the point to which the ligature was applied or to the direct excitation of the muscle itself.[1]

If it is found that the muscle will contract after the nerve has been crushed by the ligature, it will also be found that it will contract in case one electrode be removed from the nerve, so that it remains connected with only one pole of the induction apparatus. To understand this, we must look upon the muscle as the terminal of the pole of the secondary coil with which it is in connection. When the potential of the poles of the secondary coils is suddenly changed, the change of potential spreads through all conducting bodies connected with these poles, and in the case in question it passes, by way of the wire, electrode, and nerve, to the muscle. In short, the muscle, like any conductor, is charged up, and in the process of charging there is a flow of current which excites the nerve and muscle.

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[1] Du Bois-Reymond: *Untersuchungen über thierische Electricität,* Bd. i. S. 423.

A much stronger contraction is obtained if the muscle be connected with a large conductor, such as the human body, a large surface of tin-foil, a condenser, or the earth, for in the process of charging and discharging these bodies there is a large flow of current through the preparation. Further uniting the free pole of the secondary coil with the earth, because increasing the difference in the potential of the two poles, increases the effect. In case the free pole of the secondary coil be united to a large insulated conductor, and this be brought near the nerve-muscle preparation without touching it, the amount of excitation will be increased through what is known as "influence" action. For example, if the observer touch the free pole of the secondary coil with one hand and approaches the other to the nerve preparation a larger contraction will be seen when the primary current is made or broken. The effect produced on the preparation by the presence of a conductor, which is suddenly given an electrostatic charge of opposite sign, as in the case just mentioned, cannot be discussed here; suffice it to say, it is analogous to the influence exerted by the primary coil of an induction apparatus on the secondary coil at the time that the battery current is made and broken.[1]

In all cases which we have cited the excitation of the nerve and muscle was caused not by the change of electric potential, but by the sudden flow of current accompanying the change. The exciting effect of the current depends not only on the quantity of current, but also on the density of the stream. In the unipolar experiments thus far described the nerve-muscle was brought into connection with the secondary coil only at the point where the nerve touched the electrode; the electrical charge had to pass the length of the nerve to reach the muscle, and all the charging current had to flow in a dense stream the length of the nerve. This can be obviated by greatly enlarging the electrode and letting it come in contact with a large part of the nerve and muscle—*e. g.*, by using for an electrode a piece of thin tin-foil, or better gold-foil, and applying this to a large part of the surface of the nerve and muscle (see Fig. 22). By this arrangement the change in electric potential will be transmitted practically instantaneously throughout the good conducting foil, and the nerve and muscle will be charged from a vast number of points of contact and will at no part be subjected to a large quantity of electricity flowing in a dense stream. The whole of the nerve-muscle preparation will be charged, as before, to the potential of the pole with which it is connected, but it will not be stimulated. That the nerve-muscle receives an electrostatic charge under the above conditions can be readily observed by approaching the finger to the muscle at the time that the primary circuit is closed or opened. If the body of the observer has a large capacity, a large amount of current will flow through the nerve and muscle to the finger. This current will pass in a dense stream from the muscle at the point of contact with the finger, and the muscle-fibres at this part, because subjected suddenly

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[1] Hermann: *Handbuch der Physiologie*, Bd. ii. Thl. 1, S. 87; Biedermann: *Electro-physiology* (translated by F. A. Welby), 1897, vol. ii. p. 219.

to a dense flow of current, will be excited and the muscle will contract. Unless the primary current is very strong the electromotive force developed in the secondary coil on the closing of the primary circuit may be too weak to cause contraction, and only the effect of opening the circuit may be observed; in any case, the effect of breaking the primary circuit will be the stronger. More striking results will be obtained if the primary current be rapidly made and broken by an automatic interrupter introduced into the primary circuit; the muscle will then be excited by a series of rapidly following shocks.

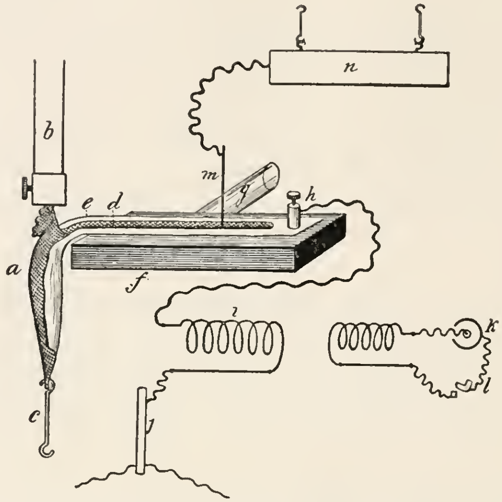

Fig. 22.—Unipolar, localized excitation of nerve. By this arrangement a large part of the surface of the nerve and muscle is brought into immediate connection with the secondary coil through the sheet of gold-foil. The nerve is locally excited at the point that is touched by the needle, because the current going to charge the tin-foil conductor passes out of the nerve at this point as a dense stream. The muscle (*a*) is supported by an insulating clamp of lead-glass and vulcanite (*b*), and is connected to the writing lever by a dry lead-glass hook (*c*); the nerve (*d*) lies on a sheet of gold-foil (*e*), which is also wrapped about the muscle, and which rests on a block of vulcanite (*f*) supported by a glass rod (*g*); the gold-foil is in close contact with the binding-post (*h*), and this is connected with one terminal of the secondary coil (*i*) of an induction apparatus, the other terminal being connected with a gas pipe (*j*), and so with the earth; in the primary induction circuit there are a battery (*k*) and a key (*l*); the needle (*m*) is connected with a large conductor (*n*), which is composed of a board covered with tin-foil, and is suspended from glass hooks.

For the sake of simplicity we have thus far only spoken of the charging of the preparation from the secondary coil. It must be borne in mind, however, that the change in the electrical condition of the secondary coil lasts only an instant, and the terminals of the coil and the tissues connected with them immediately return to their original potential, this change being accompanied by a backward surge of the electrical wave from the muscle through the nerve, electrodes, and wire to the coil, and this reverse current acts like the charging current to cause excitation. The charging and discharging processes follow each other with such rapidity, however, that they act upon the tissues as a single excitation.

To Prevent the Spread of Current.—As we have seen when the nerve of a nerve-muscle preparation is connected by two electrodes with the poles of the secondary coil of an induction apparatus, if a large electromotive force is developed in the secondary coil, a current not only passes through the part of the nerve bridging the electrodes, but through the part of the nerve between the electrodes and the muscle. This spread of current may be in part prevented by connecting the electrode nearest to the muscle with a gas-pipe and leading the charge through this to the earth (Hermann). Another method which has been suggested is to connect the two sides of the nerve beyond the electrodes by a loop of good conducting metal, so that the spreading currents shall be short-circuited (Hering).

Application of the Unipolar-excitation Method to the Localization of Excitation.—The principle that a flow of current will excite at the point where the current is dense can be employed to obtain definitely localized excitations by the unipolar method of irritation. For example, Kühne employs the following arrangement to show isolated contraction of muscle-fibres by localized excitation. A thin parallel-fibred sartorius muscle of a frog is curarized to shut out the effect of excitation of the nerve so that only the muscle-fibres which are directly excited will contract. The preparation is then placed on an insulated copper plate, which is connected with one pole of the secondary coil of an induction apparatus, the other pole being connected with the earth (see Fig. 23). The muscle makes no contractions when the key in the primary circuit is closed or opened. Its potential is undoubtedly changed, but its capacity is small, and it is charged from many points; the charging current is at no place sufficient in quantity or density to excite. If now the experimenter touch the top of the muscle near one side with the point of a needle held in the hand, the muscle twitches on the side touched each time the current is opened, and if the current is strong each time it is closed. The contraction is limited to the fibres just below the needle, because this is the point where the current charging the body of the observer passes through the muscle in a dense stream. The effect is more striking if, instead of using single shocks, the primary current be frequently interrupted. The fibres on the side stimulated will then be continuously contracted and the muscle will curl toward the stimulated side.

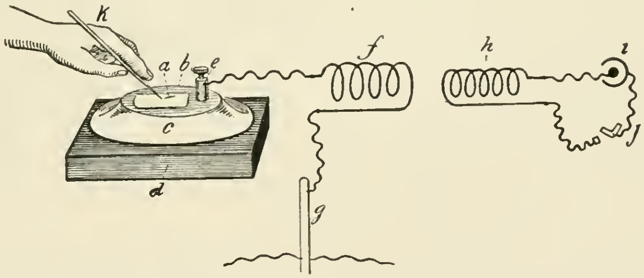

FIG. 23.—Unipolar localized excitation of the sartorius muscle. The muscle (*a*) rests on a sheet of copper (*b*), which is on a plate (*c*), resting on a sheet of vulcanite (*d*); the binding-post (*e*) on the copper plate is connected with one terminal of the secondary coil of the apparatus (*f*), the other terminal being connected with a gas pipe (*g*), and so with the earth; the primary coil (*h*) is connected with a battery (*i*) and a key (*j*); the muscle is locally excited by the current, which passes in a dense stream through it to the needle (*k*) held in the hand.

In a like manner if a nerve-muscle preparation be isolated, as shown in Fig. 22, and a needle, held in the hand or connected with a large metallic conductor or a condenser, be brought in contact with some point of the nerve, the excitation which occurs on the opening and, with a strong current, on the closing of the primary circuit will be strictly limited to the part of the nerve touched by the needle. This method can be used to advantage in studying the rate of conduction in nerves or any problem which requires strict localization of electric excitation.

(*d*) *Effect of the Duration of the Electric Current on its Power to Irritate Nerves and Muscles.*—As we have seen, a constant battery current, when flowing uninterruptedly through a motor nerve, does not ordinarily excite it; very slow variations in the strength of the current also fail to irritate; but rapid alterations in the strength, whether in the direction of increase or decrease, act as vigorous stimuli. For example, medullated nerves are irritated more vigorously by the rapid changes of intensity of induced currents than by the somewhat slower changes occurring at the make and break of battery currents. Within certain limits, at least, the more rapidly the intensity of the current changes, the greater the irritating effect upon nerves. That there is a limit even for the rapidly reacting protoplasm of medullated nerves is shown by the fact that by unipolar excitation the charging and discharging of the condensers through a nerve is the more effective the greater the capacity of the condensers. The process is more prolonged if the condenser is large, and the effect is greater.[1] Not all nerves are equally susceptible to rapid alterations of the intensity of the current. Non-medullated nerves do not appear to react as readily as medullated to electric currents of short duration. For instance, the nerves of the claw muscles of the crab are not readily excited by induced currents, and respond better to the more prolonged influence of the closing and opening of battery currents.[2]

The question now arises, Is the reaction of muscle to electric currents the same as that of nerves? Experiment shows that muscles which have been removed from the action of nerves, by means of curare, differ from medullated nerves in that they are excited more vigorously by the opening and closing of battery currents; less vigorously by making and breaking induction currents. This latter fact is well seen in experiments in which two gastrocnemius muscles from the same frog, one of which has been curarized and the other not, are connected with an induction apparatus in series, so that the current shall flow through them both in the same direction. If the primary current be made and broken, the non-curarized muscle will respond to a weaker induction shock than the curarized. By the curarized muscles the maximal contraction got on opening and closing a battery current is both higher and more prolonged than that to be obtained with a single induction shock. Unstriated muscles exhibit this difference to a still greater degree than striated muscle; they react well to the closing of battery currents of medium

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[1] Hermann: *Handbuch der Physiologie*, Bd. ii. Theil 1, S. 88.

[2] Biedermann: *Elektrophysiologie*, 1895, Bd. ii. S. 546.

strength, provided these last some little time, but respond to induced currents only when they are very strong. Thus the unstriated muscle which closes the shell of some of the fresh-water mussels, as the Anodontà, gives larger and larger contractions as the duration of the current is increased from one-quarter of a second to three seconds. Much the same is true of the unstriated muscles of the ureters;[1] the battery current must remain closed quite a while for the closing contraction to be called out, the length of time depending upon the strength of the current; and induction shocks have little or no effect unless very strong. Such a comparison makes it evident that the duration of the current is an important element in the influence exerted by electric currents on various forms of protoplasm. Unstriated muscles require that the current shall last from one-quarter of a second to three seconds to produce maximum contractions. Striated muscles require that a current shall last 0.001 second (Fick), and even medullated nerves fail to react if the current lasts too short a time. Various forms of irritable tissue can be arranged in series according to their ability to respond to electric currents of short duration, viz. medullated nerves, non-medullated nerves, striated muscles, non-striated muscles, and the little-differentiated forms of protoplasm of many of the protozoa. On the other hand these tissues are found to respond in the reverse order to currents which are more prolonged and which change their intensity slowly. It would seem as if the less perfectly differentiated the form of protoplasm, the less its mobility and its susceptibity to passing influences.

The same form of tissue reacts differently in different animals. For instance, the sluggish striated muscles of the turtle do not respond as well to induced currents as the more rapid striated muscles of the frog. Further, the condition of the tissue at the time is found to have an influence on its irritability and its power to respond to stimuli of short duration. Von Kries reports that nerves, if cooled, react better to slow variations in the intensity of the electric current, and, if warmed, to rapid variations. Under pathological conditions the reaction of nerve and muscle to electric currents may become blunted, and, as the tissue degenerates, its power to respond to rapid changes of the electric current is lessened. If a nerve be cut, the part which is separated from the influence of the nerve-cells degenerates. The irritability at first increases and then very rapidly decreases, in from three to four days being wholly lost. As the nerve regenerates, the irritability is recovered very gradually, and the power to respond to the relatively prolonged action of mechanical stimuli is regained sooner than the ability to reply to changes as rapid as those of induced currents. Howell and Huber observed that regenerating nerve-fibres when they have reached the stage resembling embryonic fibres, *i. e.* are strands of protoplasm without axis-cylinders, fail to respond to induction currents, though they can be excited by mechanical stimuli. It was found that it is not until the axis-cylinder has grown down into the regenerating fibres that the nerve is capable of responding to induction shocks.

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[1] Engelmann: *Pflüger's Archiv*, 1870, Bd. iii. S. 263.

When human striated muscle undergoes degeneration as a result of an injury to its nerve, the degenerating muscle comes to resemble normal unstriated muscle in its reactions to electricity, responding feebly to induced currents, at a time when irritability to mechanical stimuli and to direct battery currents is even increased. This is used by clinicians as a means of diagnosis of the condition of the nerve and muscle.

From what has been said it is evident that the rule laid down by Du Bois-Reymond (see p. 32) must be modified in so far that there is for each tissue a limit to the rate at which a change of intensity of the electric current acts as an irritant.

(e) *Effect of the Angle at which the Current Enters and Leaves the Muscle and Nerve.*—The angle at which the current acts on the muscle-fibre has been found to have a bearing upon its power to stimulate. Leicher[1] succeeded in obtaining definite experimental evidence that when the current is so sent through a muscle as to cross it at right angles to its fibres it has no irritating effect, and that its power to stimulate increases as the angle at which the threads of current strike the muscle-fibres decreases, being greatest when the current passes longitudinally through the fibres.

Similarly, it was found by Albrecht and Meyer[2] that the irritating effect of the electric current is most active when it flows longitudinally through the nerve, and that it is altogether absent when it flows transversely through it. This view is doubted by some observers, who would attribute the difference observed to differences in the electrical resistance. It is true that the resistance to cross transmission is greater than to longitudinal transmission, but it is not likely that this difference suffices to explain the lack of response to currents applied at right angles to the nerve-axis.

Relative Efficacy of the above Conditions upon the Irritating Power of the Electric Current.—When a current is applied to an irritable part of a nerve or muscle at an angle suitable to excitation, the stimulating effect of the current depends upon the rate at which its intensity is changed, the strength and density of the current, *i. e.* its intensity, and the duration of the current.

Fick[3] gives the following schema (Fig. 24) for the different ways in which the intensity of the electric current may be varied, and compares the effects of these different methods of application of the current. It must be remembered that a decrease of intensity acts no less than an increase to produce excitation. In the above schema the abscissa represents the time, and the ordinates the strength, of the current. Suppose the rise of intensity has a form such as is represented in *a*, Figure 24—that is, that the strength of the current increases to a considerable height, but very slowly. Such a rate of change, even though the rise of intensity were continued until the strength of current was very great, would have no exciting effect upon a nerve and might

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[1] *Untersuchungen aus dem physiologischen Institut der Universität Halle,* Heft i. S. 5.

[2] *Pflüger's Archiv,* 1880, Bd. xxi. S. 462.

[3] *Beiträge zur vergleichende Physiologie der irritablen Substanzen,* Braunschweig, 1863.

fail to irritate a striated or non-striated muscle. A more rapid rise, such as is shown in *b*, might irritate a non-striated muscle, but fail to irritate a nerve or a striated muscle. With currents which rapidly gain their full intensity and then return again to zero, the following cases would be possible: A rapid rise and fall of intensity (see *c*), such as occurs by an induction shock or by the momentary closure of a battery current, might suffice to excite a nerve but not be an effective irritant to a striated, much less a non-striated muscle, unless the short duration of the current were compensated for by a considerable increase in the intensity (see *d*). On the other hand a form of variation such as is shown in *e*, where the rate of change is very rapid, although the intensity is not great, might act to irritate nerves, and, because of the longer duration of the current, striated muscles, though having no effect on non-striated muscles; and the slower rate of change, and considerable duration, illustrated by *f*, though not affecting nerves, might suffice for striated muscles and be favorable to the excitation of non-striated muscles.

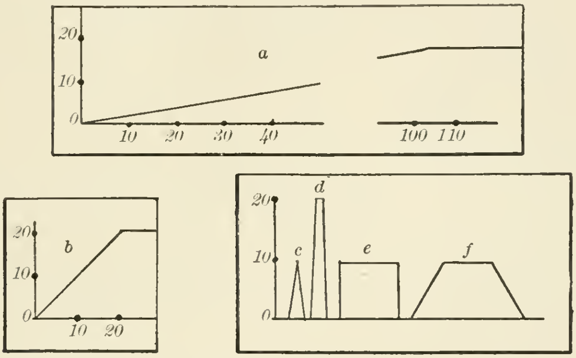

FIG. 24.—Schema of relation of the method of application of the electric current to the irritating effect.

In the case of nerves, duration of current is less important than a rapid change of intensity. In the case of striated muscles the advantage to be gained by rapid variations can be easily overstepped, and the importance of the duration of the current is greater; while in the case of non-striated muscles duration of current is of the first importance and rapid variation may fail to excite. In the case of all tissues, strength and density of current, what we may call intensity of current, is favorable to excitation.

(*f*) *Effect of the Direction in which the Current flows along the Nerve.*—The result of the irritating change produced in a nerve by a battery current has been found to depend upon whether the current flows toward or away from the organ stimulated by the nerve. This fact can be most readily observed in the case of isolated motor nerves. In the case of these nerves, the effects produced by opening and closing the current are different according as the current is descending, *i. e.* flows through the nerve in the direction of the muscle, or ascending, *i. e.* flows through the nerve in the opposite direction.

Moreover, by a given rate of change of intensity, the stimulating effect varies with the strength of the current employed. Pflüger in his celebrated monograph, *Untersuchungen über die Physiologie des Elektrotonus*, published in Berlin, 1859, p. 454, formulated the following rule for the result of excitations under varying conditions:

Pflüger's Law of Contraction.

	Ascending Current.		Descending Current.	
	Closing.	Opening.	Closing.	Opening.
Weak current	Contr.	Rest.	Contr.	Rest.
Medium "	Contr.	Contr.	Contr.	Contr.
Strong "	Rest.	Contr.	Contr.	Rest.

To understand this so-called "law of contraction" we must bear in mind certain fundamental facts, namely:

a. When a nerve is subjected to a battery current, an excitatory process is developed in the part of the nerve near the kathode when the current is closed, and in the part of the nerve near the anode when the current is opened (see p. 38).

b. The excitatory process developed at the kathode is stronger than that developed at the anode (see p. 38).

c. A third fact which is of no less importance, and which will be considered in detail when we study the effects of the constant current on the irritability and conductivity of nerve and muscle (see p. 95), is the following: During the time that a strong constant current is flowing through a nerve, the conducting power is somewhat lessened in the part to which the kathode is applied, and is greatly decreased, or altogether lost, in the region of the anode; moreover, at the instant that the current is withdrawn from the nerve the conducting power is suddenly restored in the region of the anode, and greatly lessened, or lost, in the region of the kathode.

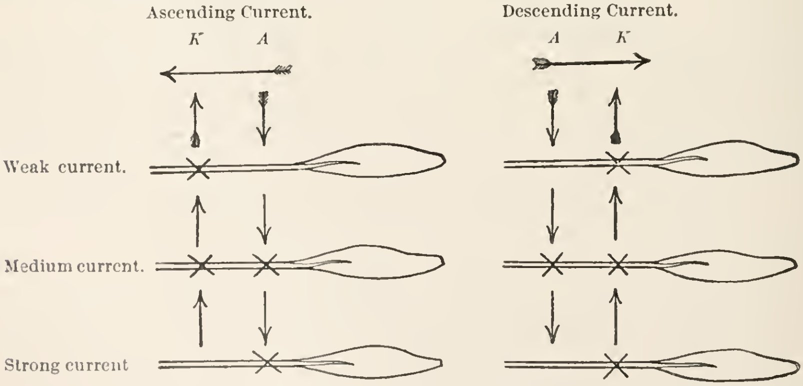

FIG. 25.—Diagram illustrating Pflüger's law.

The twelve cases included in the above table can be represented in the following diagram (Fig. 25), in which a cross is marked at the part of the nerve from which the irritation that is effective in producing a contraction takes its rise.

In the case of fresh motor nerves of the frog, when the current is weak, only closing excitations, *i. e.*, those originating at the kathode, are effective by both directions of the current. As the strength of the current is increased, at the same time that the closing kathodic contractions grow stronger, opening anodic contractions begin to appear; and with currents of medium strength both closing and opening contractions are obtained with both directions of the current. If the strength of the current be still further increased, a change is observed; with a strong current, the closing of the ascending and the opening of the descending current fails to excite a muscular contraction. This fact is demonstrated most clearly if we employ two nerve-muscle preparations, and lay the nerves in opposite directions across the non-polarizable electrodes, so that the current from the battery shall flow through one of the nerves in an ascending direction and through the other in the descending direction (see Fig. 26). If under these conditions a strong battery current be employed, muscle *a* (through the nerve of which the current is descending) will contract only when the circuit is closed, and muscle *b* (through the nerve of which the current is ascending) will contract only when the circuit is opened.

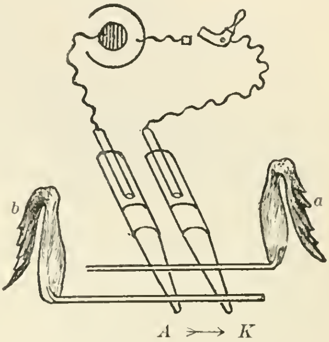

FIG. 26.—Effect of direction of current as shown by simultaneous excitation of two nerve-muscle preparations.

Since in the case of currents of medium strength, both opening and closing the circuit, when the current is ascending and when it is descending, develops a condition of excitation in the nerve sufficient to cause contractions, the failure of the contraction by the closing of the strong ascending current, and by the opening of the strong descending current, can scarcely be supposed to be due to a failure of the exciting process to be developed in the nerve; and it would seem more likely that the nerve-impulse is for some reason prevented from reaching the muscle—which, as has been said, is the fact, the region of the anode being incapable of conducting during the flow of a strong current, and the region of the kathode losing its power to conduct at the instant such a current is opened.

Effect of Battery Currents upon Normal Human Nerves.—In experiments upon normal human nerves, the current cannot be applied directly to the nerve, but has to be applied to the skin over the nerve. As it passes from the anode, the positive electrode, through the skin, the threads of current spread through the fluids and tissues beneath, somewhat as the bristles of a brush spread out, and the current flows in a more or less diffuse stream toward the point of exit, where the threads of current concentrate again to enter the kathode, the negative electrode. This spread of the current is illustrated in Figure 27.

The density of the current entering any structure beneath the skin will depend in part upon the size of the electrode directly over it—that is, the amount to which the current is concentrated at its point of entrance or exit—in part on the nearness of the structure to the skin, and in part on the conductivity of the tissues of the organ in question as compared with the tissues and fluids about it. If the conditions be such as are given in Figure 27, the current will not, as in the case of the isolated nerve, enter the nerve at a given point, flow longitudinally through it, and then leave it at a given point; most of the threads of current will pass at varying angles diagonally through the part of the nerve beneath the positive pole, then flow through the fluids and tissues about the nerve, until, at a point beneath the negative pole, the concentrating threads of current again pass through the nerve. A distinction is to be drawn between the physical and physiological anode and kathode. The physical anode is the extremity of the positive electrode, and the physical kathode is the extremity of the negative electrode; the physiological anode is the point at which the current enters the tissue under consideration, and the physiological kathode is the point where it leaves it. There is a physiological anode at every point where the current enters the nerve, and a physiological kathode at every point where it leaves the nerve; therefore there is a physiological anode and kathode, or groups of anodes and kathodes, for the part of the nerve beneath the positive electrode, and another physiological anode and kathode, or collection of anodes and kathodes, for the part of the nerve beneath the negative electrode.

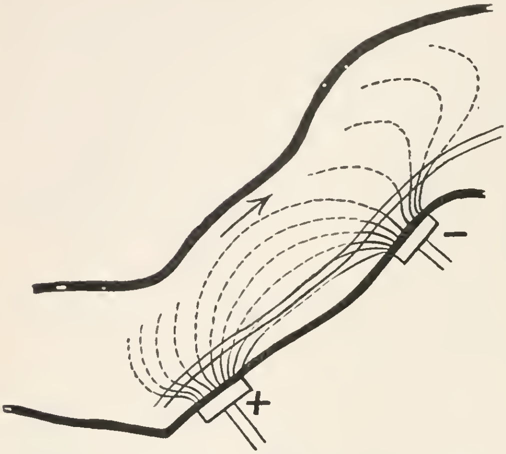

Fig. 27.—Rough schema of active threads of current by the ordinary application of electrodes to the skin over a nerve (ulnar nerve in the upper arm). The inactive threads are given in dotted lines (after Erb: *Ziemssen's Pathologie und Therapie*, Bd. iii. S. 76).

To understand the effect upon the normal human nerve of opening and closing the battery current, it is necessary to bear in mind three facts, viz.:

1. At the moment that a battery current is closed, an irritating process is developed at the physiological kathode, and when it is opened, at the physiological anode.

2. The irritating process developed at the kathode on the closing of the current is stronger than that developed at the anode on the opening of the current.

3. The effect of the current is greatest where its density is greatest.

The amount of the irritation process developed in a motor nerve is estimated from the amount of the contraction of the muscle. The contraction which results from closing the current, the closing contraction as it is called, represents the irritating change which occurs at the physiological kathode, while the contraction which results from opening the current, the opening contraction, represents the irritating change developed at the physiological anode. Since there are physiological anodes and kathodes under each of the two electrodes—the physical anode and physical kathode (see Fig. 28)—four possible cases may arise, namely:

1. *Anodic closing contraction*—*i. e.* the effect of the change developed at the physiological kathode, the place where the current leaves the nerve, beneath the physical anode (the positive pole).

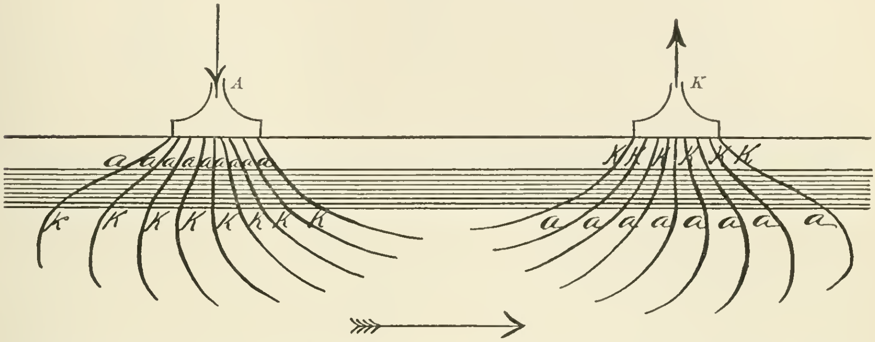

FIG. 28.—Diagram showing physical and physiological anodes and kathodes: *A*, the physical anode, or positive electrode; *K*, the physical kathode, or negative electrode; *a*, *a*, *a*, physiological anodes; *k*, *k*, *k*, physiological kathodes.

2. *Anodic opening contraction*—*i. e.*, the effect of the change developed at the physiological anode, where the current enters the nerve, beneath the physical anode (the positive pole).

3. *Kathodic closing contraction.*—*i. e.* the effect of the change developed at the physiological kathode, where the current leaves the nerve, beneath the physical kathode (the negative pole).

4. *Kathodic opening contraction*—*i. e.*, the effect of the change developed at the physiological anode, where the current enters the nerve, beneath the physical kathode (the negative pole).

For convenience these four cases are represented by the abbreviations ACC, AOC, KCC, and KOC.

Since the irritation process developed at a physiological kathode by closing a current, is, other things being equal, stronger than that developed at a physiological anode by opening the current, we should expect that the two closing contractions, KCC and ACC, would be stronger than the two opening contractions, KOC and AOC. This is the case, and as the current is more dense in the region of the physiological kathode, beneath the physical kathode, than at the physiological kathode, beneath the physical anode, KCC is stronger than ACC.

Of the two opening contractions, AOC is stronger than KOC because of the greater density of the current in the region of the physiological anode, beneath the physical anode, than in the region of the physiological anode, beneath the physical kathode.

These differences in the strength of the irritation process developed in these different regions is well shown by examining the reaction of nerves to currents of gradually increasing strength. The effect of the opening and closing irritation is seen to be as follows:

Weak currents.	Medium currents.	Strong currents.
KCC	KCC	KCC
——	ACC	ACC
——	AOC	AOC
——	——	KOC

The natural order, therefore, would be KCC, ACC, AOC, KOC. Sometimes, however, AOC is stronger than ACC; this happens when on account of the relation of the surrounding tissues to the nerve the density of the current at the physiological anode is great as compared with the density at the physiological kathode. Bordier[1] tested the strength of battery current necessary to awaken minimal sensations by unipolar excitations, and found the effect to be greatest by KC, then AC, then AO; and that it was least by KO—*i. e.*, sensory behave like motor nerves.

In testing the effect of the battery current on the nerves and muscles of man, it is customary to use one small and one large electrode (Fig. 6, *d*, *e*, *f*). The small electrode is placed over the part to be stimulated, while the large electrode is put over some distant portion of the body. This arrangement causes the current to be condensed, and hence efficient, when it enters or leaves the small exciting electrode, and to be diffused, and hence ineffective, at the large indifferent electrode. For example, the indifferent electrode may be placed on the sternum or over the back of the neck, while the exciting electrode may be put over the ulnar nerve at the elbow. The two poles may be connected with the battery, a pole-changer, rheostat, milliampèremeter, and exciting-key being introduced in the circuit. The pole-changer permits the exciting pole to be made A or K at the wish of the operator, the rheostat allows the strength of current to be raised gradually, and the milliampèremeter shows the strength of the current employed. With this arrangement the reaction of the nerve can be readily tested.

When the currents employed are strong, it occasionally happens in the case of men that not only are the make and break followed by the usual rapid contractions of short duration, but during the closure of the current there is a continued contraction—galvanotonous, as it is sometimes called. This is especially seen under certain pathological conditions.

When the nerve or muscle is diseased we may have the above order changed, and ACC obtained with weaker currents than KCC, and KOC than AOC (Babinski)[2]. This is known as the reaction of degeneration. Under

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[1] Bordier: *Archives de Physiologie normale et Pathologique*, 1897, pp 543–553.

[2] Babinski: *Comptes rendus de la Société de Biologie*, 1899, p. 343.

such circumstances the nerve might respond well to the direct battery current and yet fail to respond to the induced current. This would be still more markedly the case with the muscle, which at the same time that it gave no response to induction shocks would react better than normally to battery currents. At such times galvanotonus is easily excited. Thus during degeneration the irritability of the nerve and muscle approaches that of slowly reacting forms of protoplasm (see p. 70).

Conditions which Determine the Irritability of Nerves and Muscles.—We have thus far considered the conditions which determine the efficiency of such an irritant as the electric current. Other irritants are subject to like conditions, their activity being controlled to a considerable extent by the suddenness, strength, density, duration, and, possibly, direction of application. It is not necessary for us to consider how each special form of irritant is affected by these conditions; it will be more instructive for us to study how different irritants alter the irritability of nerve and muscle, and the relation of irritability to the state of excitation.

The power to irritate is intimately connected with the power to heighten irritability—for a condition of heightened irritability is difficult to distinguish from a state of excitation. The irritability of cell-protoplasm is very dependent upon its physical and chemical constitution, and even slight alterations of this constitution, such as may be induced by various irritants, will modify the finely adjusted molecular structure upon which the normal response to irritants depends. If this change be in the direction of increased irritability, the result may be irritation. But we must defer the discussion of the relation of irritability to irritation until we have considered the conditions upon which the irritability of nerve and muscle depends. These conditions can be best studied in connection with the influences which modify them—namely:

(*a*) Irritants.

(*b*) Influences which favor the maintenance of the normal physiological condition.

(*c*) The effects of functional activity.

(*a*) *The Influence of Irritants upon the Irritability of Nerve and Muscle.—Effect of Mechanical Agencies.*—A sudden blow, pinch, twitch, or cut excites a nerve or muscle. All have experienced the effect of a mechanical stimulation of a sensory nerve, through accidental blows on the ulnar nerve where it passes over the elbow, "the crazy bone." The amount of mechanical energy required to cause a maximal excitation of an exposed motor nerve of a frog is estimated by Tigerstedt[1] to be 7000 to 8000 milligrammillimeters, which would correspond roughly to a weight of 0.500 gram falling fifteen millimeters—at least a hundred times less energy than that given out by the muscles in response to the nerve-impulse developed. Such stimuli can be repeated a great many times, if not given at too short intervals, without interfering with the activity

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[1] Studien über mechanische Nervenreizung," *Acta Societatis Scientiarum Fennicæ*, 1880, Bd. xi. S. 32.

of the nerve. A nerve can be irritated thirty to forty times, at intervals of three to four minutes, by blows from a weight of 0.485 gram, falling 1 to 20 millimeters, the contractions of the muscle, weighted with 30 to 50 grams, varying from minimal to from 3 to 4 millimeters in height. Rapidly following light blows or twitches applied to a motor nerve, by the tetanomotor of Heidenhain or Tigerstedt, excite a series of contractions in the corresponding muscles which fuse more or less into a form of continuous contraction, known as tetanus.

Not only may a nerve be excited by bringing sudden pressure to bear on it, but the sudden removal of weights or a sudden lessening of tension irritates.[1] Kühne long ago called attention to the excitation of sensory fibres of the ulnar nerve of man on the removal of pressure. The cause is probably the irregular return of the semi-fluid parts of the nerve to their normal relations.

Mechanical applications to nerve and muscle first increase and later lessen and destroy the irritability. Thus pressure gradually applied first increases and later reduces the power to respond to irritants. Stretching a nerve acts in a similar way, for this also is a form of pressure; as Valentin said, the stretching causes the outer sheath of the nerve to compress the myelin, and this in turn to compress the axis-cylinder. Tigerstedt states:[2] "From a tension of 0 up to 20 grams the irritability of the nerve is continually increased, but it lessens as soon as the weight is further increased."

Surgically the stretching of nerves is sometimes employed to destroy their excitability. Slight stretching heightens the excitability and even quite vigorous stretching has only a temporary depressing effect unless it be carried to the point of doing positive injury to the axis-cylinder, and of causing degeneration. As nerves have the power to regenerate, they may recover from even such an injury.

The irritability of muscles is likewise increased by moderate stretching and destroyed if it be excessive. Thus slight stretching produced by a weight causes a muscle to respond more vigorously to irritants. Similarly tension of the muscles of the leg, produced by slight over-flexion or extension, makes them more irritable to reflex stimuli, as in the case of the knee-jerk and ankle-clonus. Tension must be very marked to permanently alter the irritability of the muscles.

Effect of Temperature.—Changes in temperature, if sudden and extreme, irritate nerves and muscles. If the nerve or muscle be quickly frozen or plunged into a hot fluid it will be excited and the muscle be seen to contract. The cause of the irritation has been attributed to mechanical or chemical alterations produced by the change of temperature. The ulnar nerve at the elbow is excited if the part be dipped into ice-water and allowed to remain there until the cold has had time to penetrate; as is proved by the fact that in addition to the sensations from the skin, pain is felt which is attributed by the subject of the experiment to the region supplied by the nerve. As the effect

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[1] v. Uxhull: *Zeitschrift für Biologie*, 1894, Bd. xxxi. S. 148; 1895, Bd. xxxii. S. 438.

[2] *Op. cit.*, S. 43.

of the cold becomes greater the pain is replaced by numbness, both the irritability and power of conduction of the nerve being reduced. Gradual cooling of motor nerves or muscles, and gradual heating, even to the point of death of the tissue, fails to excite contractions. It is stated that if a frog whose brain has been destroyed is placed in a bath the temperature of which is very gradually increased, the heating may be carried so far as to boil the frog without active movements having been called out. If a muscle be heated to 45° C. for frogs and 50° C. for mammals, it undergoes a chemical change, which is accompanied by a form of shortening different from the contraction induced by irritants. This form of contraction, though extensive, is feeble and is associated with a stiffening of the muscle, known as *rigor caloris* (see p. 164).

In general it may be said that raising the temperature above the usual temperature of the animal increases, while cooling decreases, the irritability of the nerves and muscles. This statement requires to be amplified, because the character of the stimulus has a marked effect upon the result. Cooling the nerve increases its irritability for mechanical and chemical stimuli, for the constant current if it lasts at least 0.005 sec., for condenser discharges, and for sine currents of at least 0.005–0.01 sec. duration: heating the nerve increases its irritability for these forms of electrical excitation when of shorter duration, and also for induced currents.[1] If a nerve be excited by charging or discharging a condenser through it, the size of the condenser plays an important part, because it determines the duration of the stimulus; for example a slow, prolonged rate of discharge may excite a nerve at 4° C. and fail to excite one at 30° C., while a rapid, brief fall of energy will excite a nerve at 30° C. and fail to excite one at 4° C.[2] Not only does temperature influence the ability of the nerve to take on the change which is associated with the development of what we call the nerve impulse, but it alters its power of recovery. This appears in experiments in which the ability of the nerve to respond to two rapidly following stimuli is tested by different temperatures. A nerve, like the heart-muscle, shows a "refractory period" for a short interval after excitation, and during this period it is incapable of responding to stimulation. The length of the interval varies with the temperature. If the two stimuli are separated by an interval of 0.001 sec., the second stimulus will be effective at 15° C., but it will fail at 3° C.; at this temperature, even with an interval of 0.006 sec., the second stimulus will be without effect, as much as 0.01–0.02 sec. being needed for the recovery of nerve at this low temperature.[3]

Cold, unless excessive and long continued, though it temporarily suspends, does not destroy the irritability; while heat, if at all great, so alters the chemical constitution of the cell-protoplasm as to destroy its life.

The higher the temperature the more rapid the chemical changes of the body and the less its power of resistance; low temperature, on the other hand,

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[1] Gotch and Macdonald: *Journal of Physiology*, 1896, xx. p. 247.

[2] Waller: *Ibid.*, 1899, xxiv. p. 1.

[3] Gotch and Burch: *Ibid.*, 1899, xxiii. p. 22; Boycott: *Ibid.*, 1899, xxiv. p. 144.

slows chemical processes and increases the endurance. It is noticeable that nerves and muscles remain irritable much longer than ordinarily in case the body be cooled before their removal. In the case of a mammal, the irritability may last from six to eight hours instead of two and a half, while in the case of frogs it may be preserved at 0° for ten days, although at summer heat it lasts only twenty-four hours. In the case of frogs which have been kept at a low temperature the irritability becomes abnormally high when they are warmed to ordinary room-temperature.

Effect of Chemicals and Drugs.—The irritability of nerve and muscle protoplasm is markedly influenced by even slight changes in its constitution. If a nerve or muscle be allowed to lie in a liquid of a different composition from its own fluid, and especially if such a liquid be injected into its blood-vessels, an interchange of materials takes place which results in an alteration of the constitution of the tissue and a change in its irritability. Indeed, the only solutions which fail to alter the irritability are those which closely resemble serum and lymph. Fluids having other than the normal percentage of salts have a marked effect, while even the absence of proteids appears to have little influence unless continued for a considerable time.

Pure water acts as a poison to protoplasm, soon destroying its life. Through diffusion and osmosis it is imbibed into the cells at the same time that the salts pass out, and the resulting change in the physical and chemical condition of the tissue cause if rapid, first an increase, and in any case later a decrease, and finally a total loss of irritability. Thus water injected into the blood-vessels of muscles first excites contraction and later destroys the irritability, and results in the condition known as water rigor. These effects are prevented by the presence of small amounts of salt. A sodium chloride solution, of a strength of 6 parts per 1000 of distilled water, has been called the physiological solution, because it was supposed to have no effect on the irritability of nerves and muscles of cold-blooded animals; even this solution, if long continued, gradually increases and later decreases the irritability. A solution containing 7 parts of sodium chloride per 1000 is more nearly isotonic to the fluids of cells of the frog, and one containing 9 parts per 1000 is approximately in osmotic equilibrium with the fluids of the cells of the mammal. Such fluids cannot be properly regarded as physiological solutions, however, for this would mean that they would cause no change in constitution of the cells. They contain only one of the salts essential to the normal activity of the tissues, and the difference in the partial pressure of the other salts of the muscle would cause the muscle cells to lose some of each of these, and, as a result, to have their irritability altered. The importance of the individual salts present in the fluids normally surrounding the tissues, and the need that they should be present in definite proportions, were most strikingly demonstrated by experiments, by Ringer and others, on the nature of the fluid which is essential to the maintenance of the activity of the isolated heart of the frog. These experiments have shown that not only Na, but Ca and K are essential. The heart of the terrapin can be kept beating for more than forty-eight hours in a solution containing NaCl, CaCl, and KCl, even when there are no energy-giving substances present in the fluid. Howell[1] says that NaCl is needed in the proportion in which it occurs in the blood, to preserve the osmotic relations of the tissues, while Ca and K are essential to the development of the rhythmic movements of the heart-muscle. Loeb[2] made a careful study of the relation of salts of the blood to the activity of striated and non-striated muscles. He found, as others had done before, that a striated muscle if left in 0.7 per cent. NaCl solution in time develops more or less rhythmic automatic contractions. He considers that Na, Ca, and K are held in the muscle, not only as salts, but in combination with the proteids, and that all of these are necessary to the normal functional activity of the protoplasm. A fluid to deserve the name of physiological must contain all these ions. The muscle contracts rhythmically in a solution of pure NaCl because the Na drives some of the Ca and K out of their ion-proteid combinations. If Ca and K are present in the solution, this cannot occur. He goes so far as to say that were it not for the Ca and K in the blood, the human skeletal muscles would show rhythmic contraction.

A truly physiological solution would contain all the constituents of the fluid of the blood, and a physiological salt solution would contain all the salts of the blood, in the proportion in which they exist in the blood. The salts would appear to have a twofold function: they would maintain the normal imbibition relations of the cells, and they would supply the Na, Ca, and K ions which are required for the ion-proteid compounds in the muscle. The quantities of inorganic salts are different in different tissues of the same animal, which shows that the presence of these inorganic substances is dependent not merely on the amount presented to them by the fluids in which they are bathed, but also on the chemical conditions within the cells, each type of cell requiring a definite supply for its normal functional activity. Howell reports a fact of interest in this connection: the muscle of the ventricle of the heart of the terrapin does not make automatic rhythmic movements in a Ringer's solution containing Na, Ca, and K in amounts equal to those occurring in the blood, but the large veins at the base of the heart do make such contractions and supply the excitation necessary to rhythmic contraction of the whole heart.

The presence of inorganic salts is essential to the normal functional activity of nerves, as it is of muscles. If the nerve be subjected to distilled water, it gradually loses its salts through osmosis, and imbibes water, and the resulting chemical and physical change in its constitution is accompanied by a loss of irritability. Likewise the withdrawal of water from a motor nerve by drying, or by strong solutions of urea, glycerin, etc., causes a change of irritability. The irritability is first increased, due to a concentration of the salts within the nerve and to the mechanical excitation resulting from the shrinkage of the tissue. If the change is a rapid one, it is frequently accompanied by an active irritation, and the muscle connected with the nerve

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[1] *American Journal of Physiology*, 1898, ii. p. 47.

[2] *Ibid.*, 1900, iii. p. 383.

shows irregular contractions, as the different fibres of the nerve are one after the other affected. If the drying has not been continued too long, the normal irritability may be restored by supplying water. Muscles behave like nerves in these respects.

Most drugs and chemicals capable of altering the irritability of nerves and muscles first increase and later destroy the irritability. If the change in the chemical constitution of the nerve is sufficiently rapid, it may be accompanied by the phenomena of excitation. For example, veratria, eserin, digitalis, most mineral acids, and many organic acids, free alkalies, most salts of heavy metals, destroy the irritability of nerves and muscles, as a rule after first producing increased excitability. Potash salts, if concentrated, rapidly kill, but excite less than soda compounds. Verworn says: Acids, alkalies, and salts have a similar effect on the protoplasm of a thick pseudopod of one of the rhizopods of the Red Sea; they first excite and later paralyze, acting like narcotics on the central nervous system.

Ammonia, carbon disulphide, and ethereal oils may destroy the irritability of nerves without causing excitations, at least not in sufficient amount to produce visible muscular contractions. If applied directly to the muscle, however, these substances excite contractions.

The attempt to ascertain some exact relation between the molecular weight of different salts and acids and their destructive power has encountered too many exceptions for the establishment of any definite rule; in general, however, the higher the molecular weight the stronger the effect on the muscle.[1] Many gases and vapors have a marked effect on the irritability and activity of protoplasm.[2] Carbonic-acid gas, tobacco-smoke, the fumes of ether, alcohol, and chloroform, applied directly to exposed nerves, first stimulate, later anæsthetize, and finally kill. CO_2 has a very powerful effect, even a fiftieth of a milligram sufficing to influence profoundly the activity of the protoplasm of the nerve, a fact of considerable importance if we recall that this gas is produced by the normal oxidation of carbon within the tissues of the body. Tobacco-smoke acts like CO_2 and probably because of the CO_2 which it contains. Alcohol first excites and then paralyzes the nerve. If the fumes of alcohol have not acted for too long a time, the paralyzed nerve may recover its function, and the same is true for ether and chloroform. These vapors, if present in considerable quantities act rapidly upon exposed nerves; thus ether (diethyl oxide) will anæsthetize a nerve in three minutes; if the drug be then removed, the nerve can completely recover in five minutes. Chloroform would appear to be a more dangerous anæsthetic than ether, as recovery of the nerve is less likely to occur in case the anæsthetic action is somewhat prolonged. Many other gases and fumes chemically irritate and kill nerve-muscle protoplasm.

From all these results it becomes evident that the normal irritability of

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[1] Blumenthal: *Pflüger's Archiv*, 1896, Bd. 62, S. 513.

[2] Waller: *Lectures on Physiology*, first series, "On Animal Electricity," London, 1897, pp. 42–46.

nerves and muscles requires that a certain chemical constitution be maintained, and that even slight variations from this suffice to alter, and, if continued, to destroy, the irritability. Further, it is noticeable that in most cases the first step toward deterioration is a rise of irritability, which, if sudden and marked, is accompanied by a condition of irritation. If the cause of the increase in irritability and excitation be continued, sooner or later exhaustion supervenes, the irritability lessens, and finally is lost.

Effect of the Electric Current upon Muscles.—If a constant-battery current of medium strength be sent through a muscle for a short time, the muscle will give a single short contraction at the moment that the current enters it, and again when the current leaves it. If a strong current be used, the short closing contraction may be followed by a prolonged contraction (Wundt's closing tetanus), which, though gradually decreasing, may last as long as the current is closed; and when the current is broken, the usual opening contraction may be likewise followed by a prolonged contraction (Ritter's opening tetanus), which only gradually passes off. The closing contraction originates at, and the closing continued contraction may be limited to, the region of the kathode; and the opening contraction originates at, and the opening continued contraction may be limited to, the region of the anode.

In case a very weak current is used, no contraction will be observed; nevertheless, while the current is flowing through the muscle it modifies its condition; a state of latent excitation is produced at the kathode, which shows itself in a considerable increase of irritability of that part of the muscle. On the other hand, the irritability of the muscle at the kathode will be found to be lessened after the withdrawal of the polarizing current, because the condition of excitation which it causes fatigues that part of the muscle.

The effects of the battery current at the region of the anode are just opposite to those produced at the kathode. While the current is flowing, the irritability at the anode is lessened, and when the polarizing current is removed, irritability at the anode is found to be greater than it was before the battery current was applied.

The lessened irritability which is produced at the anode during the flow of the battery current may be shown by an inhibition of a condition of excitation which may be present at the time that the current is applied to the muscle. For example, in the case of unstriated muscles, not only does closing the battery circuit never cause a contraction at the anode, but if the part of the muscle exposed to the influence of the anode happens to be at the time in a condition of tonic contraction, the entrance of the current causes that part of the muscle to relax. The inhibitory influence exerted by the anode, as a result of the lowering of the irritability, is seen to a remarkable degree in its effect upon the heart.[1] If the anode rest on the ventricle of the frog's heart, and the kathode at some indifferent point, relaxation is seen in the region of the anode with each systole of the ventricle. Inasmuch as the rest of the ventricle contracts, the pressure of the blood causes the wall of the ventricle to bulge

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[1] Biedermann: *Elektrophysiologie*, 1895, S. 195.

out, and make a little vesicle at the region of the anode. A similar inhibitory influence may be observed upon an ordinary striated muscle at the point of application of the anode, if it be in a condition of tonic contraction when the battery current is sent into it. During the flow of the constant current through a muscle, the irritability is increased in the region of the kathode and decreased in the region of the anode. When the current is withdrawn from the muscle, on the other hand, the irritability of the kathode is found to be decreased, and at the anode to be increased.

Effect of the Electric Current upon Nerves.—The polarizing effects of a continuous constant current are the same upon a nerve as upon a muscle, with the exception that in the case of the nerve the condition of altered irritability is not so strictly limited to the point of application of the anode and kathode, but spreads thence throughout the part of the nerve between the two electrodes, the intrapolar region, as it is called, and for a considerable distance into the parts of the nerve through which the current does not flow, *i. e.* the extrapolar region. The term electrotonus has been applied to the effects of battery currents on nerves and muscles, and includes two sets of changes—(1) manifested by the alterations of irritability which we are considering; (2) exhibited in changes of the electrical condition of the tissue.

There can be little doubt that both of these sets of changes are the result of electrolytic alterations of the nerve protoplasm, caused by the flow of the polarizing current. We shall consider here only the former of these sets of changes. The true nature of the electrotonic changes of the electrical condition of the nerve, and their relation to the nerve impulse, embrace a number of difficult problems, which are still under discussion and cannot be profitably considered here.[1]

The most important work on the influence of the constant current on the irritability of nerves was done by Pflüger.[2] He ascertained the electrotonic effects of the polarizing current to be most vigorous in the immediate vicinity of the anode and kathode, and to spread thence in both directions along the nerve. He called the change produced in the nerve in the region of the anode "anelectrotonic," and the condition itself "anelectrotonus;" while the change at the kathode was termed "katelectrotonic," and the condition "katelectrotonus." The same names are given to the effects of battery currents upon muscles.

To test the effect of a constant battery current upon the irritability of a nerve, put the nerve of a nerve-muscle preparation upon two non-polarizable electrodes (*A*, *K*, Fig. 29) which are placed at some little distance apart and at a considerable distance from the muscle. Connect these electrodes with a battery, introducing into the circuit a key (*k*), which permits the current to be quickly thrown into or removed from the nerve, and a commutator (*C*), which allows the current to be reversed and to be sent through the nerve in

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[1] Waller: *Lectures on Animal Electricity*, London, 1897; Biedermann: *Electrophysiology*, translated by F. A. Welby, 1898, vol. ii.

[2] Pflüger: *Untersuchungen über die Physiologie des Electrotonus*, Berlin, 1859.

either the ascending or descending direction. Connect the muscle with a myograph lever, arranged so as to record the height of the muscle contractions. Then apply to the nerve at some point between the polarizing electrodes and the muscle a pair of electrodes (*I*) connected with the secondary coil of an induction apparatus, which is placed near enough to the primary coil to cause excitations of medium strength, and introduce into the secondary circuit a short-circuiting key (*S*), by which the closing shocks can be prevented from reaching the nerve.

If, with this arrangement, a breaking induction shock of medium strength be given, the nerve will be excited, and the height of the muscular contraction which results may be taken as a test of the irritability of the nerve at *I*. Now send the polarizing current through the nerve, in the ascending direction, that is, with the anode nearer the muscle. At the moment the current is closed, if it be of medium strength, a closing contraction will be observed; then comes a period during which the muscle is not contracting and the polarizing current is apparently producing no effect on the nerve; if, however, after the current has acted a short time, the irritability of the nerve at the point *I* be again tested with a breaking induction shock, it will be found to be decreased, on account of the condition of anelectrotonus which has been induced. If the key in the polarizing current be then opened, the usual opening contraction will be recorded. After the polarizing current has been removed, the condition of the nerve at *I* can be again tested, and it will be seen that the irritability has returned to the normal, or is even greater than it was at the start.

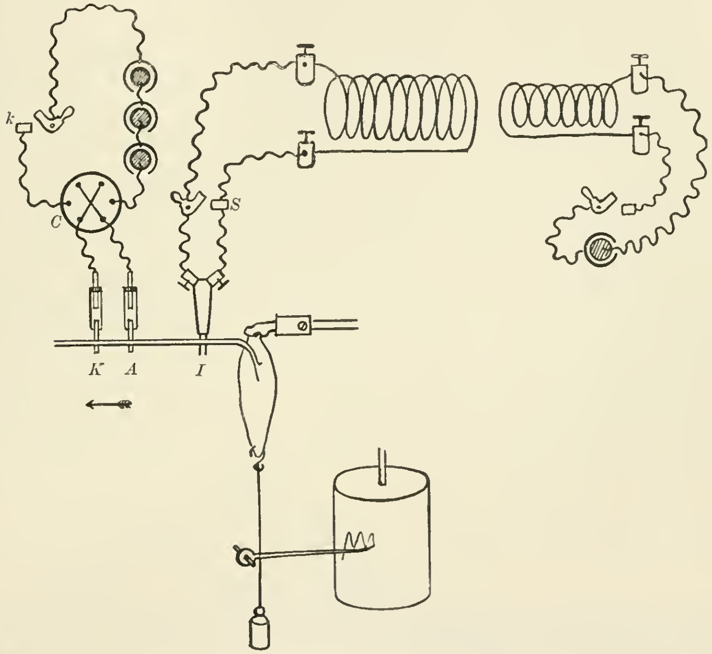

FIG. 29.—Method of testing anelectrotonic and katelectrotonic alterations of irritability in nerves.

The effect of the kathode on the irritability may be tested in a similar way, by reversing the polarizing current and again sending it into the nerve. This time the current will be descending, *i. e.* the kathode nearest the muscle. As before, a closing contraction will be seen when the circuit is made, but on testing the irritability at *I* with an induction shock of the same strength as before, it will be found to be increased, the shock causing a larger contraction. On opening the polarizing current the usual opening contraction will be seen, and if after the current has been removed the irritability be again tested, it will be found to have returned to the normal, or to be decreased. The changes in irritability described can be ascertained by using mechanical or chemical stimuli as well as induction shocks. Alterations of the irritability induced by anelectrotonic and katelectrotonic changes of the nerve-substance are to be found not only in the part of the nerve between the point to which the polarizing current is applied and the muscle, but in the extrapolar region at the central end of the nerve, and in the intrapolar region. The experimental evidence of this is not so readily obtained, but there is no doubt of the fact.

The effect of the polarizing current is the greater, the better the condition of the nerve; moreover, the stronger the current employed, the more of the nerve influenced by it. Of course, in the intrapolar region there is a point where the effect of the anode to decrease the irritability comes into conflict with the effect of the kathode to increase it, and where, in consequence, the irritability remains unchanged. This indifferent point may be observed to approach the kathode as the strength of the current is increased. The following schema is given by Pflüger to illustrate the way in which the irritability is changed in the anelectrotonic and katelectrotonic regions as the strength of the current is increased:

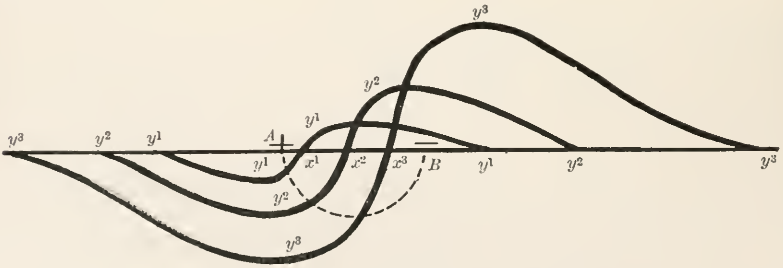

Fig. 30.—Electrotonic alterations of irritability caused by weak, medium, and strong battery currents: *A* and *B* indicate the points of application of the electrodes to the nerve, *A* being the anode, *B* the kathode. The horizontal line represents the nerve at normal irritability; the curved lines illustrate how the irritability is altered at different parts of the nerve with currents of different strengths. Curve y^1 shows the effect of a weak current, the part below the line indicating decreased, and that above the line increased irritability, at x^1 the curve crosses the line, this being the indifferent point at which the katelectrotonic effects are compensated for by anelectrotonic effects; y^2 gives the effect of a stronger current, and y^3, of a still stronger current. As the strength of the current is increased the effect becomes greater and extends farther into the extrapolar regions. In the intrapolar region the indifferent point is seen to advance with increasing strengths of current from the anode toward the kathode.

As in the case of the muscle, so of the nerve, the constant current leaves behind it important after-effects. In general it may be stated that wherever during the flow of the current the irritability is increased, there is a decrease of irritability immediately after the removal of the current, and *vice versa.* When the current is withdrawn from the nerve, the irritability in the region of the kathode is lowered, and in the region of the anode raised. It must be added, however, that the decrease of irritability seen at the kathode gradually passes over into a second increase of irritability, while the increase seen at the anode upon the removal of the current continues a considerable time and is not reconverted to a decrease; therefore the total after-effect is an increase of irritability. The effect of the battery current to alter the irritability of the human nerve can be made out by the following experiment.[1] Test the irritability of the nerve by giving it a series of light blows through the medium of the electrode itself, which is made anodic or kathodic. The electrode is pressed carefully upon the nerve, and is regularly tapped by a light mallet just hard enough to give distinct twitches of the fingers; if while this is going on the electrode is made kathodic, the twitches become stronger, and if it be made anodic they are abolished.

The fact that when the current is closed the irritation starts from the kathode, and when the current is opened from the anode, may well be associated with the changes in irritability which take place at the kathode and anode upon the closing and the opening of the current. The setting free of an irritation appears to be associated only with an increase of irritability. When the current is closed the establishment of the condition of katelectrotonus is accompanied by a rise of irritability at the kathode, and when the current is opened the cessation of the condition of anelectrotonus is likewise accompanied by a rise of irritability. In the first case the irritability rises from the normal to something above the normal, and in the second case the irritability rises from the condition of decreased irritability up to something above the normal irritability. The change from the normal to the anelectrotonic condition of decreased irritability, or from the katelectrotonic condition of increased irritability down to normal irritability, does not irritate. As has often been said, it is hard to distinguish between increase of irritability and irritation.

Effect of Frequency of Application of the Stimulus on Irritability.—We have seen that influences which act as irritants may also have an effect upon the irritability of the nerve or muscle. In order to produce this change they must be as a rule powerful, or act for a considerable time. Nevertheless, in the case of muscles, at least, even a weak irritant of short duration, if repeated frequently, tends to heighten irritability. For example, if a muscle be stimulated by separate weak induction shocks at long intervals, the effect of each shock is slight, and the change produced by it is compensated for by restorative processes which occur within the living protoplasm during the following interval of rest, and each of the succeeding irritations finds the mechanism in much the same condition; if, however, the shocks follow each other rapidly, each stimulation leaves an after-effect which may have an influence upon the effectiveness of the stimulus following it. As a result of this, induction shocks too feeble to excite contractions may, if frequently repeated, after a little time cause a visible

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[1] Waller and de Watteville: *Philosophical Transactions of the Royal Society,* 1882.

movement, and shocks of medium strength, if given at short intervals, may each cause a larger contraction than its predecessor, until a certain height of contraction has been reached, beyond which there is no further increase possible. We shall consider these so-called "staircase contractions" more carefully later (see page 112). When irritations follow each other very rapidly the whole character of the contraction is changed, and the muscle, instead of making rapid single contractions, enters into the condition of apparently continuous contraction known as tetanus, during which it shortens considerably more than it does when making single contractions. Increase in irritability plays only a comparatively small part in the production of this remarkable phenomenon, which we shall study more carefully when we come to the mechanical problems involved in muscular contractions.

Rapidly repeated stimuli, though at first favorable to activity of a muscle, soon exert an unfavorable influence by causing the lessened irritability which is associated with fatigue.

When a nerve is excited there is a change in its electrical condition, and the extent of the change is generally believed to be an indication of the extent to which the protoplasm of the nerve has become active in response to excitation. Waller,[1] taking the amount of change in the electrical condition of the nerve as an evidence of the ability of the protoplasm to react under varying conditions, found that repeated excitation increases the activity of the nerve as it does of the muscle. Repeated excitation of a nerve at suitable, regular intervals causes a staircase-like increase in the strength of the electrical response, the record resembling that got by staircase contractions of muscles (see page 112). Moreover, if the electrical condition of the nerve is tested by a series of excitations of equal strength before and after it is subjected to a tetanizing current, the strength of the variations is found to be increased.

If a second stimulus follows the first too soon, it may be wholly ineffective; at least this has been found to be the case with certain forms of protoplasm. It has been shown that heart muscle has a "refractory period," as it is called, responding very imperfectly to stimuli applied to it just before and during its systole.[2] Apparently much the same is true of the nerve. Boycott,[3] using contraction of muscle as a test, and Gotch and Burch,[4] using the current of action as a test, have lately discovered that for a brief period after the nerve has been stimulated it is incapable of responding to a second stimulus. The length of the period of lessened excitability is greatly influenced by temperature; at 4° C., with maximal stimuli, the "critical period" may be 0.007–0.008 second; at higher temperatures it is shorter.

(*b*) *Influences which favor the maintenance of the Normal Physiological Condition of Nerve and Muscle.—Effect of Blood-supply on Nerve and Muscle.*—The vascular system is a path of communication between the several organs

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[1] Waller: *Lectures on Physiology*, first series, 1897, p. 68.

[2] Cushing: *Journal of Physiology*, 1897, vol. xxi. p. 214.

[3] Boycott: *Ibid.*, 1899, vol. xxiv. p. 144.

[4] Gotch and Burch: *Ibid.*, p. 410.

and tissues, and the circulating blood is a medium of exchange. The blood carries nutritive materials from the digestive organs and oxygen from the lungs to all the tissues of the body, and it transports the waste materials which the cells give off to the excretory organs. In addition to these functions it has the power to neutralize the acids which are produced by the cells during action, and so maintain the alkalinity essential to the life of the cell; it supplies all parts with moisture; by virtue of the salts which it contains, it secures the imbibition relations which are necessary to the preservation of the normal chemical constitution of the cell-protoplasm; it distributes the heat, and so equalizes the temperature of the body; finally, in addition to these and other similar functions, it is itself the seat of important chemical changes, in which the living cells which it contains play an active part. It is not strange that such a fluid should exert a marked influence upon the irritability of the nerves and muscles. Since the metabolism of muscles is best understood, we will first consider the importance of the circulation to the muscle. Muscles, even in the so-called state of rest, are the seat of chemical changes by which energy is liberated, and when they are active these changes may be very extensive. If the cell is to continue its work, it must be at all times in receipt of materials to replenish the continually lessening store of energy-holding compounds; moreover, as the setting free of energy is largely a process of oxidation, a free supply of oxygen is likewise indispensable to action. These oxidation processes result in the formation of waste products—such as carbon dioxide, water, lactic acid—and these are injurious to the muscle protoplasm, and if allowed to accumulate would finally kill it. Of the services which the blood renders to the muscle there are, therefore, two of paramount importance, viz. the bringing of nutriment and oxygen and the removal of waste matter, and surplus energy, as heat.

A classical experiment illustrating the effect of depriving tissues of blood is that of Stenson, which consists in the closure of the abdominal aorta of a warm-blooded animal by a ligature, or by compression. In the case of a rabbit, for example, the blood is shut off, not only from the limbs but from the lower part of the spinal cord. The effect is soon manifested in a complete paralysis of the lower extremities, sensation as well as power of voluntary and reflex movements being lost. The paralysis is due, in the first instance, to the loss of function of the nerve-cells in the cord by which the muscles are normally excited to action. Later, however, the nerves and muscles of the limbs lose their irritability. Of the peripheral mechanisms the motor nerve-ends are found to succumb before the nerves and muscles. This is shown by the fact that although the muscles are still capable of responding to direct irritation, they are not affected by stimuli applied to the nerve, although the nerve at the time, to judge from electrical changes which occur when it is excited, is still irritable. Since the nerve and muscle are irritable, the lack of response must be attributed to the nerve-ends. The response to indirect stimulation (*i. e.* excitation of a muscle by irritating its nerve) is lost in about twenty minutes, while the irritability of the muscle, as tested by direct excitation, is not lost for four or five hours. In this as in so many instances the loss of irritability of the muscle is due primarily to the disturbance of the respiration of the muscle. Of the substances supplied to the muscle by the blood, oxygen is one the want of which is soonest felt. The muscle contains within itself a certain store of oxygen, but one which is by no means equal to the amount of oxidizable substances. Of this oxygen, that which is in the least stable combinations, and which is available for immediate needs, is soon exhausted. A continual supply of oxygen is required even for the chemical changes which occur in the quiet muscle. Of the waste substances which the blood removes from the cell, carbon dioxide is the one which accumulates most rapidly and is the first to lessen the irritability. Lactic acid and waste products from the breaking down of nitrogenous materials of the cell are also injurious.

The dependence of nerve-fibres upon the blood-supply is by no means so well understood. The nerve-fibre is a branch of a nerve-cell, and it seems as if the nourishment of the fibre was largely dependent upon that of the cell-body (see Fatigue of Nerve, pp. 75 and 95). Nevertheless, the nerve-fibre requires a constant supply of blood for the maintenance of its irritability. The irritability of the nerve cannot long continue without oxygen, and a nerve which has been removed from the body is found to remain irritable longer in oxygen than in air, and in air than in an atmosphere containing no oxygen. Waste products liberated by active muscles have a deleterious effect on nerves; whether such substances are produced in the nerves themselves will be considered later.

The efficacy of the blood to preserve the irritability is to be seen in such experiments as those of Ludwig and Schmidt;[1] they succeeded in maintaining the artificial circulation of defibrinated, aërated blood through the muscles of a dog, and kept them irritable for many hours after death of the animal. If such an experiment is to be successful, the blood must be maintained at the normal temperature, be plentifully supplied with oxygen, and be kept as free from carbon dioxide as possible. Von Frey[2] made an elaborate experiment of this nature. A dog was killed, the body was cut in halves, and the aorta and inferior vena cava were quickly connected with an apparatus for pumping the blood at a regular rate through the hind part of the body. Before the blood entered the arteries it passed through coils in which it was warmed to the normal temperature, and an artificial lung, where it received a supply of oxygen and was relieved of its carbon dioxide. Under these conditions the muscles were kept alive for more than seven hours, and so far retained their normal condition that throughout this period they were able to respond to stimuli sent to them through their nerves and contract with sufficient vigor to raise a considerable weight. H. N. Martin[3] made a similar experiment on the heart

[1] *Sitzungsberichte der math.-phys. Classe der k. sächs. Gesellschaft der Wissenschaften*, vol. xx., 1868.

[2] "Versuche über den Stoffwechsel des Muskels," *Archiv für Anatomie und Physiologie*, 1885; physiologische Abtheilung, S. 533.

[3] *Studies from the Biological Laboratory of Johns Hopkins University*, 1882, vol. ii. p. 188.

of a dog. The heart and lungs were isolated from the rest of the body, the heart was fed with defibrinated blood from a Mariotte flask, and the lungs were supplied with air by an artificial respiration apparatus. The heart, which was kept moist and at the normal temperature, continued to beat for four hours and more. Porter[1] has succeeded in keeping even small pieces of the ventricle of the mammalian heart alive by maintaining a good circulation of well-oxygenated blood through its vessels (see Section on Nutrition of the Heart).

Normally the blood-supply to the muscle is varied according to its needs. When the muscle is stimulated to action its blood-vessels are at the same time dilated, so that it receives a free supply of blood.[2] Moreover, if muscular work is extensive, the heart beats faster and the respiratory movements are quicker, so that a larger amount of oxygen is provided and the carbon dioxide is removed more rapidly. The importance of the blood-supply to a muscle can be best understood if we consider it in relation to the effects of fatiguing work upon the muscles (see p. 74). The relation of special substances in the blood to the needs of the muscle can be best considered together with the chemistry of the muscle (see p. 159).

Effect of Separation from the Central Nervous System.—If a motor nerve be cut, or if some part of it be so injured that the fibres lose their power of conduction, the portion of the nerve thus separated from the central nervous system sooner or later completely degenerates (see p. 77). Each of the motor nerve-fibres is a branch of a motor cell in the anterior horns of the spinal cord. These nerve-cells are supposed to govern the nutrition of their processes, though how a microscopic cell can thus influence a nerve-fibre a meter or so long is by no means clear. Soon after the nerve is separated from its cell it exhibits a change of excitability. In general it responds more readily to the kathode than the anode, which would imply an increased irritability; at the part near the cut, however, it responds best to the anode.[3] The increase is soon followed by a gradual decrease of irritability. In the case of mammalian nerves loss of irritability may be complete at the end of three or four days, but the nerves of cold-blooded animal may retain their irritability for several weeks. The immediate cause of the loss of irritability is the change in the chemical and physiological structure of the axis-cylinder. The degenerative changes result finally in the complete destruction of the nerve-fibres, and involve the motor end-organs as well, but do not immediately invade the muscle, which may be considered a proof that nerve and muscle protoplasm are not continuous.

Though no immediate change in the structure of the muscle is observable, the irritability of the muscle soon begins to alter. At the end of a fortnight the irritability of the muscle for all forms of stimuli is lessened. From this time on, the irritability gradually undergoes a remarkable change, the excitability

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[1] Porter: *American Journal of Physiology*, 1899, vol. ii. p. 127.

[2] Sczelkow: *Sitzungsber. d. k. Akad. Wien*, 1862, Bd. xlv. Abth. 1.

[3] Blix: *Skandinavisches Archiv fur Physiologie*, 1889, Bd. i, S. 184.

for mechanical irritants and for direct battery currents (see p. 54) beginning to increase, but the power to respond to electric currents of short duration, as induction shocks, continuing to lessen; indeed, the reactions of the muscle appear to take on more of the character of those of smooth muscle-fibres. The condition of increasing irritability to direct battery currents and mechanical irritants reaches its maximum by the end of the seventh week, and from that time on the power to respond to all forms of stimuli lessens, the excitability being wholly lost by the end of the seventh or eighth month. During the stage of increased excitability fibrillary contractions are often observed.

As in the case of a nerve, so of the muscle the loss of irritability is due to degenerative changes which gradually lead to the destruction of the muscle protoplasm. The cause of the change in the muscle is still a matter of doubt, some regarding it as due to the absence of some nutritive, trophic influence from the central nervous system, others consider it to be the result of circulatory disturbances, consequent upon the lack of a proper regulation of the blood-supply, due to the division of the vaso-motor nerves, and still others attribute it to a lack of exercise, it being no longer stimulated to action. As regards the second view, it may be said that muscles whose vaso-motor nerves are intact, the vessels being innervated through other nerves than those which supply the muscle-tissue proper, as is the case with some of the facial muscles, undergo similar changes in irritability when their motor nerves are cut. As regards the first and last views, it may be said that if the muscles be artificially excited, as by electric stimuli, and thus are exercised daily, the coming on of degeneration can be at least greatly delayed. The question as to whether the anabolic processes within the muscle-cell are dependent on the central nervous system, in the sense of their being specific trophic influences sent from the nerve-cells to the muscles, is still under discussion and need not be considered further in this place. Without doubt the reflex tonus impulses which during waking hours are all the time coming to the muscles are productive of katabolic changes and, indirectly at least, favor anabolism.

(c) *Effect of Influences which result from the Functional Activity of Nerves and Muscles.—Fatigue of Muscles.*—The condition of muscular fatigue is characterized by lessened irritability, decrease in the rate and vigor with which the muscle contracts and liberates energy, and a still greater decrease in the rate with which it relaxes and recovers its normal form. In a sense, whatever induces such a state can be said to cause fatigue, but it is perhaps best to restrict the term to the form of fatigue which is produced by excessive functional activity. The cause of exhaustion which results from overwork is in part the same as the cause of the loss of irritability and power which follows the cutting off of the blood-supply. The working cell liberates energy at the expense of its store of nutriment and oxygen, and through oxidation processes forms waste products which are poisonous to its protoplasm. The fatigue which results from functional activity has, therefore, a twofold cause, the decrease in energy-holding compounds available for work and the accumulation of poisonous waste matters.

It is evident that the length of time that the cell can continue to work will depend very much upon the rapidity with which the energy-holding explosive compounds are formed by the cell-protoplasm and the waste products are excreted. If a muscle is made to contract vigorously and continuously, as when a heavy weight is held up, fatigue comes quickly; on the other hand, a muscle may be contracted a great many times if each contraction is of short duration and considerable intervals of rest intervene between the succeeding contractions. The best illustration of this is the heart, which, though making contractions in the case of man at the rate of seventy or more times a minute, is able to beat without fatigue throughout the life of the individual. Each of the vigorous contractions, or systoles, is followed by an interval of rest, diastole, during which the cells have time to recuperate. The same is true of the skeletal muscles. It was found in an experiment that if a muscle of the hand, the *abductor indicis*, were contracted at regular intervals, a weight being so arranged that it was lifted by the finger each time the muscle shortened, a light weight could be raised at the rate of once a second for two hours and a half, *i. e.* more than 9000 times, without any evidence of fatigue. If, however, the weight was increased, which required a greater output of energy, or if the rate of contractions was increased, which shortened the time of repose, the muscle fatigued rapidly. In general, the greater the weight which the muscle has to lift, the shorter must be the periods of contraction in proportion to the interval of rest if the muscle is to maintain its power to work. Maggiora,[1] in his interesting experiments in Mosso's laboratory at Turin, made a very careful study of this subject, and ascertained that for a special group of muscles there is for each individual a definite weight and rate of contraction essential to the accomplishment of the greatest possible work in a given time. These experiments were made on men, and the height of the succeeding contractions was recorded by an apparatus devised by Mosso, the ergograph,[2] which made it possible to estimate the total amount of work done by the muscles studied. Many forms of apparatus have since been devised to accomplish this. Mosso's ergograph consisted of two parts, an arm rest equipped with suitable clamps for fixing the arm and hand, and a writing mechanism arranged to record the movements of the weight which was raised by the flexion of the second finger. Either increasing the weight or the rate of contraction hastens the coming on of fatigue and so lessens the power and the total amount of work. In such an exercise as walking the muscles are not continually acting, but intervals of rest alternate with the periods of work, and the time for recuperation is sufficiently long to permit the protoplasm of the muscle-cells to prepare the chemical compounds from which the energy is liberated as fast as they are used, and get rid of the

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[1] *Archiv für Anatomie und Physiologie*, 1890; physiologische Abtheilung, S. 191.

[2] Mosso: *Die Ermüdung*, Leipzig, 1892, S. 90; Lombard: *Journal of Physiology*, 1892, vol. xiii. Fig. 1, Plate 1.

waste products of contraction, so that vigorous muscles can be employed many hours before any marked fatigue is experienced. Sooner or later, however, the vigor of the muscle begins to decrease. The reason for this is not wholly clear. It is noticeable, however, that not only the muscles employed in the work, but other muscles, such as those of the arms for instance, even when purposely kept quiet, have their irritability reduced. This would suggest that the fatigue which finally asserts itself is due to some general rather than local influence. To understand this we must recall the fact that all parts of the body are in communication by means of the circulatory system. The ever-circulating blood as it is thrown out by the heart is divided into minute streams, which, after passing through the many organs of the body, unite again on their return to the heart. If materials be taken from the blood by one part, they are lost to all the rest, and if materials be added to the blood by any part, they are sooner or later carried to all the rest. During the course of a long march, the muscles of the leg take up a great deal of nutriment, and give off many waste products, and all the organs suffer in consequence. Mosso,[1] in his experiments upon soldiers taking long forced marches, found that lack of nutriment is not the only cause of the general fatigue produced by long-continued muscular work. The soldiers, though somewhat refreshed by the taking of food, did not recover completely until after a prolonged interval of rest. He attributed this to the fatigue-products which he supposed the muscles to have given off, and concluded that they were only gradually eliminated from the blood. To see if there were fatigue-products in the blood of a tired animal capable of lessening the irritability of organs other than those which had been working, he made the following experiment: He drew a certain weight of blood from the veins of a dog, and then put back into the animal an equal amount of blood from another completely rested dog. The dog which was the subject of the experiment appeared to be all right after the operation. On another day he repeated the experiment, but this time the blood which was put back was taken from a dog that was completely tired out by running. The effect of the blood from the fatigued animal was very marked; the dog receiving it showed all the signs of fatigue, and crept off into a corner to sleep. Mosso concluded from this experiment, that during muscular work fatigue-products are generated in the muscles, pass thence into the blood, and are conveyed to other muscles, where they produce the lowered irritability and loss of power characteristic of fatigue. Many years before, Von Ranke extracted from the tired muscles of frogs substances which he considered fatigue materials. Lee[2] would draw a sharp distinction between fatigue and exhaustion. He considers the former to be a transient change in the capacity for work induced by the presence of waste products, while the latter is a far more serious condition and is due to a lack of nutritive energy-giving substance. He considers that fatigue, by lessening the irri-

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[1] *Archiv für Anatomie und Physiologie*, 1890; physiologische Abtheilung.

[2] *Proceedings of the American Physiological Society*, Dec., 1898, published in *American Journal of Physiology*, 1899, vol. ii. p. 11.

tability, may exert a protective influence and prevent the work from being carried under ordinary conditions to the point of exhaustion. In favor of this view he states that the muscles even of starving animals, although incapable of long-continued work, do not make contractions of the type characteristic of fatigued muscles (see p. 115); on the other hand, muscles which have been subjected to lactic acid, one of the waste products resulting from muscular work, whether it be free or combined, as it probably is in the muscle, with potassium or sodium, do make contractions of the type shown by fatigued muscles. Waller[1] has of late laid much stress upon the action of CO_2 to stimulate protoplasm when present in small amounts and to anæsthetize it when in larger quantities. CO_2 is also a waste product of muscle, but it is doubtful whether the paralyzing effect of large amounts can be regarded as a fatigue effect.

Maggiora, in his experiments upon the fatigue of special groups of muscles, likewise found that the taking of food causes only a partial recovery of the tired muscles, and that an interval of rest is essential to complete recovery. In these experiments the irritability of the muscles was tested not only by volitional impulses, but by the strength of the electric current required to cause direct excitation. A curve of fatigue of human muscles by voluntary contractions is shown in Fig. 59, and one resulting from electrical excitation of the muscle in Fig. 58. In the case of vigorous men, one and a half hours suffice to restore the muscles of the forearm which have been completely tired out by raising a heavy weight many times. He also observed that the time required for recovery can be greatly shortened if the circulation of the blood and lymph in the muscles be increased by massage. This suggests that the power of the cell to give off its waste products to the blood is sufficiently rapid to keep pace with the ordinary production, but not with the more rapid formation taking place during fatiguing work. This would seem to be the case in spite of the fact that circulation of the blood and lymph in the muscles is increased during action. This increase in the circulation through the acting muscle is brought about in part by the fact that the muscle massages itself by its own contractions. It is a pumping mechanism, which acts at the time when the increased taking of oxygen and nutriment and giving off of waste products make the rapid renewal of the restoring fluids imperative. Every time the muscle contracts the swelling, tense fibres compress the lymphatics and blood-vessels between and about them, and when it relaxes the valves in the lymph vessels and veins prevent the return of the fluid which has been squeezed out. In addition to this, when muscles are stimulated to action by impulses coming to them from the central nervous system, the muscles in the walls of the blood-vessels of the muscle are acted upon by their vaso-dilator nerves, and, relaxing, permit a greater flow of blood through the muscle; when the muscles cease to be excited the muscles in the vessel walls gradually regain their tone, and the blood-supply to the muscle tissue is correspondingly lessened. This arrangement would seem to suffice for the

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[1] *Lectures on Physiology*, first series, on *Animal Electricity*, London, 1897, p. 47.

bringing of nutriment and oxygen and the removal of waste matters under ordinary conditions.

Considerable difference of opinion exists as to which of three classes of food-stuffs—proteids, carbohydrates, and fats—supply the energy used by the muscle in ordinary and excessive work, and how these are employed by the muscle.

The question has been studied by examining the character and quantity of waste products liberated from the body during and after excessive muscular work, as compared with those given off when the subject is at rest. Another method has been to test the strength of the muscle in ergographic experiments, and to find the effect of different kinds of food upon the time required for its recovery. Experiments of Fick and Wislicenus,[1] Voit and Pettenkofer,[2] Voit,[3] and others caused the view to become generally accepted that the energy of the muscle by violent muscular work comes largely from the non-proteid substances in the muscles. Later Pflüger and his pupils have gone to the other extreme and conclude that proteid is the chief source of energy.[4]

Very many others have written on both sides of the subject and still a final conclusion has not been reached.[5]

Probably the sugars, and possibly after these the fats are employed by the muscle as the most available form of energy, while the proteid forms a more permanent part of the muscular machine, and is only made use of when the work is exhaustive (see page 166). The taking of any one of these classes of food hastens the recovery from fatigue, and the sooner the more readily it is digested and assimilated (see Metabolism—effect of muscular work).

Normally the muscles are never completely fatigued. It would seem that as the muscles tire and their irritability is lessened, the central nerve-cells which send the stimulating impulses to them have to work harder, and that the nerve-cells give out sooner than the muscles. On the other hand, certain experiments seem to show that the nerve-cells recover from fatigue more rapidly than the muscles do, so that it is an advantage to the organism that they should cease to excite the muscles before muscular fatigue is complete. With the decreasing irritability of the muscle, a feeling of discomfort in the muscle and an increasing sense of effort are experienced by the individual, both of which tend to cause a cessation of contraction, and prevent a harmful amount of work. That such an arrangement would be of service was apparent in the experiments of Maggiora, in which he found that if muscles are forced to work after fatigue has developed, the time of recovery is prolonged out of all proportion to the extra work accomplished.

At the close of even exhaustive muscular work there is always a large amount of energy-holding materials in the blood and tissues, and the rapid,

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[1] *Vierteljahresschrift der naturforsche Gesellschaft in Zurich*, 1865, Bd. x. S. 317.

[2] *Zeitschrift für Biologie*, 1866, Bd. ii.

[3] *Ibid.*, 1876, Bd. vi. S. 305.

[4] *Pflüger's Archiv*, 1899, Bd. 77, S. 425.

[5] Schäfer's *Text-book of Physiology*, 1898, vol. i. p. 912.

though partial, improvement in the condition on the taking of food is perhaps best explained as the result of a stimulating effect on the central nervous system. This might be due to the change in the circulation which follows the taking of food, as well as the fact that a fresh supply of uncombined and hence available energy-holding substances is being received. The effect of the so-called stimulants, alcohol, tea, coffee, etc., to temporarily increase the ability to do work, is probably chiefly through their action on the central nervous system. Their influence is a temporary one, and only markedly increases the amount of work when the body has a plentiful supply of nutriment.[1]

Fatigue of Nerves.—Muscle-, gland- and nerve-cells—in fact, almost every form of protoplasm—if excited to vigorous long-continued action, deteriorate and exhibit a decline of functional activity. As we have seen, in the case of muscle there are a using up of available energy-holding compounds and a production of poisonous waste matters, and these two effects induce the condition known as fatigue. *A priori*, we should expect similar changes to occur in the active nerve-fibre; almost all the experimental evidence is, however, opposed to this view. The form of activity which is most characteristic of muscle is contraction; that which is most characteristic of nerve is conduction. In the case of the muscle it is exceedingly difficult to distinguish between the effects produced by the processes associated with the change of form and those which result from the transmission of the excitatory change. There is little doubt that fatigue is associated with the former; whether it is associated with the latter is not known. In the case of the nerve, where the transmission process may be studied by itself, conduction does not seem to fatigue (see p. 95).

Apparently the same may be said of the processes which result in the development of what we call the nerve-impulse. We have already seen that the nerve may undergo an alteration of irritability if subjected to artificial irritants. Such a change at the point of application of the irritant is hardly to be regarded as a fatigue effect, however, for in many cases, at least, it is due to the direct effect of the irritant on the physical or chemical structure of the nerve-protoplasm rather than to molecular changes which are peculiar to the development of the nerve-impulse. Thus the change of irritability which results from a series of light blows, such as may be given to a nerve by Tigerstedt's tetanomotor, cannot properly be said to be the result of fatigue. It has been found that a medullary nerve may be excited many times a second for hours, by an induced current, and still be capable of developing at the stimulated point what we call the nerve-impulse. The change which is developed at the point of excitation and which passes thence the length of the nerve, would seem to be the expression of a form of energy liberated within the nerve, and since the liberation of energy implies the breaking down of chemical combinations, the apparent lack of fatigue of the nerve is incomprehensible. It is the more remarkable since the nerve-fibre is to be considered a

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[1] Schumburg: *Archiv für Anatomie und Physiologie*, 1899, supplement, S. 289.

branch of a nerve-cell, and nerve-cells appear to fatigue if frequently excited to vigorous action. Inasmuch as we have as yet no definite knowledge of the nature of what we call the nerve-impulse, or of the character of the processes by which it is transmitted along the nerve, we can afford to leave this question open, and simply state that the evidence thus far obtained is opposed to the view that nerve-fibres fatigue.

Effect of Use and Disuse.—Different kinds of muscle-tissues possess very different degrees of endurance. By endurance we mean the capacity to liberate energy during long periods of time. This capacity is intimately associated with irritability, for one of the first marks of failure of power is a decline of irritability. In general, the more irritable a muscle the less its endurance, because with an increase of irritability there is associated a more rapid and extensive liberation of energy in response to irritants. For example, the rapidly responding and acting pale striated muscles of the rabbit have less resisting power than the red striated muscles, while the sluggish unstriated muscle-fibres can contract a long time without suffering from fatigue.

The endurance of muscles of even the same kind may differ very considerably in the same individual, but the differences are more striking in the case of different individuals. One of the causes of this is the extent to which the muscles are employed. Use, exercise, is the most effective method of increasing not only the strength, but the endurance of the muscle. Though this fact is so well known as to scarcely need repeating, the explanation of it is by no means so clear. Undoubtedly one of the causes is a more perfect circulation in a muscle which is often used, but this is not all. It would seem as if the protoplasm of the muscle-cell was educated, so to speak, to be more expert in assimilating materials containing energy, in building up the explosive compounds employed in its work, and in excreting deleterious waste matters.

The effect of exercise upon irritability has not been thoroughly worked out. It would seem as if there were a normal degree of irritability for each special form of muscle-tissue, and as if either an increase or decrease of the irritability above or below this level was a sign of deterioration. Exercise, if not excessive, is favorable to the maintenance of this normal physiological condition. Without doubt many of the differences which we attribute to the muscles of different men are really due to differences in the central nerve-cells, the action of muscles, rightly interpreted, being rather an expression of central nervous activity than the result of peculiarities of the muscles themselves. To voluntarily exercise the muscles is to exercise the nerve-cells, and the effects of exercise upon these nervous mechanisms is of as much importance as the effect upon the muscles. In admiring visible proportions we must always bear in mind that though "beef" is of use to the athlete, the muscles are merely the servants, and can accomplish nothing if the master is sick. The nerve-cells always give out before the muscles, and the man preparing for a contest should watch his nervous system more than his muscles. He who forgets this can easily over-train, and do himself a permanent injury, besides failing in the race.

Effect of Enforced Rest.—Not only is the strength of the muscles greatly increased by exercise, but a lack of exercise soon results in a loss of strength. This is seen when an individual is confined to his bed for even a comparatively short time, or when a limb is subjected to enforced rest by being placed in a splint. The cause is to be sought in changes peculiar to the muscle protoplasm itself, although reduced circulation may also play a part. The effect of prolonged rest on the irritability of muscles, is seen most markedly when they are separated from the central nervous system by injuries of their nerves (see p. 70). The lowered irritability which results from prolonged rest is not peculiar to muscles, but is shared by all forms of protoplasm.

C. CONDUCTIVITY.

Conductivity is that property of protoplasm by virtue of which a condition of activity aroused in one portion of the substance, by the action of a stimulus of any kind, may be transmitted to any other portion. For example, if the edge of the bell of a vorticella (see Fig. 2, p. 19) be irritated by a hair, not only do the movements of the cilia cease, but the contractile substance of the bell draws it into a more compact shape, and the fibrillæ of the stalk shorten and pull the bell away from the offending irritant. In such a case an exciting process must have been transmitted throughout the cell, and through several more or less differentiated forms of protoplasm. This property of conductivity is not known to be limited to any one peculiar structural arrangement of protoplasm distinguishable with the microscope, but is exhibited by a vast variety of forms of cell-protoplasm, and by plants as well as animals. The cytoplasm of cells, the part of the protoplasm surrounding the nucleus, appears to be composed of a semifluid granular material, traversed in all directions by finest fibrillæ which in some cases appear to form an irregular meshwork, the reticulum, and in others to be arranged side by side as more or less complete fibrils. It is not known whether the power of conduction is possessed by the whole of the protoplasmic substance or is confined to the reticular substance, but there are certain reasons why the former view may be considered the more probable. The rate and the strength of the conduction process varies greatly in different forms of protoplasm, and there appear to be differences in the facility with which the exciting process spreads through different parts of even the same cell.[1] Not only are such differences to be noticed in many of the ciliated infusoria, but even the substance of striated muscles seems to conduct in two different ways, the sarcoplasm appearing to conduct slowly, and the more highly differentiated fibrillary portion of the fibre rapidly. In general the process appears to be more rapid and vigorous where a fibrillated structure is observable. Smooth muscle-tissue, which has a somewhat simple structure, conducts comparatively slowly; striated muscle, which is more highly differentiated, more rapidly, and the fibrillated axis-cylinder of the nerve-fibre, most rapidly of all.

Protoplasmic Continuity is Essential to Conduction.—*Effect of a Break in Protoplasmic Continuity.*—A break of protoplasmic continuity in any

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[1] Biedermann: *Elektrophysiologie*, 1895, S. 137.

part of a nerve- or muscle-fibre acts as a barrier to conduction. If a nerve be cut through, the irritability and conductivity remain for a considerable time in the severed extremities, but communication between them is lost, and remains absent however well the cut extremities may be adjusted. The nerve-impulse is not transmitted through the nerve-substance as electricity is transmitted along a wire: join the cut ends of a wire, and the contact suffices for the passage of the current; join the cut ends of a nerve, and the nerve-impulse cannot pass. Any severe injury to a nerve alters the protoplasmic structure and prevents the chemical and physical processes through which conductivity is made possible. It is probable that the same may be said of all forms of living cells, and the absence of protoplasmic continuity would seem to be an explanation of the fact that nerve- and muscle-fibres which lie close together may physiologically act as separate mechanisms.

Even in the case of apparently homogeneous protoplasm there is probably a definite structural relation of the finest particles, and upon this the physiological properties of the substance depends. Slight physical and chemical alterations suffice to change the rate and strength of the conduction process, and the power to conduct is altogether lost if the protoplasm is so altered that it dies.

The relation of conductivity to structure of cell-protoplasm is illustrated in the effects of degeneration and regeneration upon the physiological properties of the nerve-fibre (see p. 69). The life of the nerve-fibre is dependent on influences exerted upon it by the body of the cell of which it is a branch. When any part of the fibre is injured it loses its power to conduct, and the portion of the fibre separated by this block from the body of the cell soon dies. The irritability and conductivity are wholly lost at the end of a period varying from four days to several weeks, the time differing in different kinds of nerves, and the fibre begins to undergo degeneration. The axis-cylinder and the myelin are seen to break up and are then absorbed, apparently with the assistance of the nuclei which normally lie just inside the neurilemma, and which at this time proliferate greatly and come to occupy most of the lumen of the tube. The process of absorption is nearly complete at the end of a fortnight after the injuy. Under suitable conditions, however, regeneration may occur, and as this takes place there is a recovery of physiological activities. The order in which conductivity and irritability return is instructive. Howell and Huber[1] made a careful study of this subject. They found that the many nuclei which develop during degeneration are apparently the source of new protoplasm, which is seen to accumulate in the old sheath until a continuous band of protoplasm is formed. About this thread of protoplasm a new membranous sheath develops, and thus is built up what closely resembles an embryonic nerve-fibre. The embryonic fibre formed in the peripheral end of the regenerating nerve joins that of the central end in the cicatricial tissue which has been deposited at the point of injury. Thus a temporary nerve-fibre is formed and united to the undegenerated part of the old fibre, and this

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[1] *Journal of Physiology*, 1892, vol. xiii. p. 381.

new structure, though possessing neither myelin nor axis-cylinder, is found to be capable of conduction and to have a low form of irritability, being excitable to violent mechanical stimuli but not to induction currents. The power of conduction appears to return before irritability, and may be observed first at the end of the third week. Apparently sensation is recovered before the power of making voluntary movements; this difference may well be due, not to any essential difference between sensory and motor fibres, but to the fact that extra time is required for the motor fibres to make connection with the muscle. The embryonic fibre gradually gives place to the adult fibre, new myelin being formed all along the fibre, and a new axis-cylinder growing down from the old axis-cylinder. As the axis-cylinder grows down, the irritability for induction shocks is recovered. Many months may be necessary for the complete recovery of function. Langley[1] reports that medullated fibres of the sympathetic, if cut, regenerate and recover the power to function before they regain a medullary sheath. Such experiments show the axis-cylinder to be the true conducting medium, and that the medullary sheath has a subordinate function.

The same is true of muscle as of nerve protoplasm,—the power of conduction ceases with the life of the cell-substance; thus, if the middle part of a muscle-fibre be killed, by pressure, heat, or some chemical, the dead protoplasm acts as a block to prevent the state of activity which may be excited at one end from being transmitted to the other, and the conduction power is only recovered on the regeneration of the injured tissue.

Isolated Conduction is the Rule.—(*a*) *Conduction in Nerve-trunks.*—The axis-cylinders of the many fibres which run side by side in a nerve-trunk are separated from each other by the neurilemma, and in the case of the medullary nerves by the myelin substance as well, so that there is not even contiguity, much less continuity of nerve-substance. Thus the many fibres of a nerve-trunk, some afferent and others efferent, though running side by side, conduct independently of one another. For example, if the skin of the foot be pricked, the excitation of its sense-organs is communicated to sensory nerve-fibres, and is transmitted along them to the spinal cord, where the stimulus awakens certain groups of cells to activity; these cells in turn, by means of their branches, the motor nerve-fibres, transmit the condition of excitation down to the muscle-fibres of the legs, which, when stimulated, contract and withdraw the foot from the offending irritant. The sensory and motor nerves concerned in this reflex act run for a considerable part of their course in the same nerve-trunk, but the sensory impulses have no direct effect on the motor nerve-fibres, and the roundabout course which has been described is the only way by which they can influence them.

Isolated conduction by separate fibres and their branches holds good within the central nervous system, as elsewhere, otherwise we could scarcely explain the localization of sensations, or co-ordinated movements.

The presence of a medullary sheath is not essential to isolated conduction,

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[1] *Journal of Physiology*, 1897, vol. xxii. p. 223.

for it occurs in the absence of this sheath, both in the peripheral nerves and in the central nervous system. The large class of non-medullated nerves have the power of isolated conduction, and Donaldson reports that new-born rats can make co-ordinated movements, although the nerves of both the peripheral and central nervous systems do not acquire a medullary sheath until several days after birth. It is not likely that the neuroglia cells are essential to isolated conduction within the central nervous system, for this occurs in its absence in the peripheral nerves. Although the neurilemma, by separating the axis-cylinders of adjacent fibres, may make the insulation more complete, it is probably not the real cause of isolated conduction. A break of the protoplasmic continuity of the nerve protoplasm stops conduction, and conduction fails wherever protoplasmic continuity is lacking.

An apparent contradiction to the rule that absolute continuity of nervous matter is essential to conduction by nerves, is to be found in the phenomenon known as "Hering's Paradoxical Contraction." This will be explained later (see p. 157, *d*).

(*b*) *Distribution of Excitation by Branches of Nerves.*—Nerve-fibres sometimes branch in their passage along the peripheral nerves, but most of the branches which are seen to be given off from the nerve-trunks are composed of bundles of nerve-fibres which have merely separated off from the rest. After the nerves have entered a peripheral organ, or the central nervous system, the axis-cylinders may give off branches. Thus in muscles, and to a still greater degree in the electric organs of certain fish, the nerve-fibre and its axis-cylinder may divide again and again, or after entering the spinal cord the fibre may be seen to give off a great many lateral branches—collaterals, as they are called. It is not known whether in such cases the fibrillæ of the axis-cylinder give off branches, or whether they simply separate, a part of them entering the branch while the rest of them continue on in the main fibre. Though the exciting process does not pass from fibre to fibre, it probably involves in a greater or less degree all the elements of the same fibre, and passes into all its branches. It is evident that where it is necessary for the irritation to be localized, branching could not occur; but where a more general distribution is permissible, especially where several parts of an organ ought to act at the same instant, conduction through a single fibre which branches freely near its termination would be useful.

(*c*) *Conduction in Muscles.*—Each fibre of the muscles which move the bones—the skeletal muscles, as they are sometimes called—is physiologically independent of the rest. The sarcolemma prevents not only continuity, but contiguity of the muscle-substance of the separate fibres, and there is no cross conduction from fibre to fibre. That this is so is proved by an experiment, such as was described on page 45, in which unipolar excitation of the part of the fibres of a curarized sartorius muscle results in a contraction strictly confined to the fibres which are subjected to the irritating current. Each of the separate muscle-fibres is supplied by at least one nerve-fibre or a branch of a fibre, and, under normal conditions, only acts when stimulated by the nerve. In the case of plant-cells, and of certain forms of muscle-cells, about which there is a more or less definite wall or sheath, there are little bridges of protoplasm binding the cells together. For example, Engelmann describes the muscle of the intestines of the fly as composed of striated cells, sheathed by sarcolemma, except where bound together by little branches of sarcoplasma, which may act as conducting wires between the cells.

There are certain cells, however, which have been supposed to be exceptions to the rule that protoplasmic continuity is essential to conduction. The striated muscle-fibres of the heart are quite different from those of ordinary skeletal muscles, physiologically as well as anatomically. They are stumpy, quadrangular cells, which are not known to have a sarcolemma, and which are united not only by their broad ends, but by lateral branches. Engelmann and lately Porter[1] and others have concluded that conduction takes place in the heart from cell to cell, without the intervention of nerves, and may occur in all directions. This question is considered at length in the section on the conduction of excitation in the heart.

The cells of the contractile substance of some of the medusæ (as Aurelia), have been supposed to communicate by contiguity rather than by continuity. The same has been thought to be the case with many forms of unstriated muscle-tissue;[2] moreover, there are groups of ciliated cells, the members of which act in unison although they have not been found to be connected either directly or by nerves. These cells have apparently no membranous covering, and though living as independent units, are so related that a condition of activity excited in one seems to be transmitted to the rest by means of contact, or through the mediation of cement-substance.

From what has been said it will be seen that protoplasmic continuity ensures free communication between different cells; that protoplasmic contiguity, either directly or through the mediation of the cement-substance, may possibly permit of conduction; but that normally the intervention of a different tissue, even as delicate as the sarcolemma, suffices to cause complete isolation of the cell from its neighbors. Under normal conditions there may be a spread of excitation from muscle-fibre to muscle-fibre, even in the skeletal muscles. Kühne's experiment with the sartorius muscle of the frog, described on page 45, gives a good proof that the activity of a striated muscle-fibre is not normally transmitted to its neighbors; nevertheless, Kühne[3] has found that if the extremities of two sartorius muscles be pressed firmly together by a suitable clamp, care being taken that the pressure shall not be enough to destroy the physiological activity of the protoplasm, excitation of one muscle may cause contraction of the other. A satisfactory explanation is lacking.

Biedermann[4] reported that when a frog's muscle was partly dried a slight

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[1] Porter: *Journal of Experimental Medicine*, 1897, ii. p. 391; *American Journal of Physiology*, 1899, ii. p. 127.

[2] Engelmann: *Pflüger's Archiv*, 1871, Bd. iv.

[3] Kühne: *Untersuchungen aus der physiologischen Institute in Heidelberg*, 1880, Bd. 3, S. 1.

[4] Biedermann: *Berichte der Wiener Akademie*, 1888, Bd. 97, Abth. 3, S. 145.

mechanical excitation of one part of it might lead to a contraction of the whole. Similarly, a partly dried-up frog may be seen, if mechanically excited, to make movements simulating life. The cause of these movements, also, is not understood. Drying of the muscle in its early stages greatly increases its irritability because of the concentration of the salts, but that does not account for the loss of insulation.

Transmission of Excitation by Means of End-organs.—In spite of the rapid advances which have been made in the histology and physiology of the nervous system during the past few years, we are still in doubt as to the exact way that the axone, the exciting branch of the neurone, stimulates the cell to which it is distributed. In many cases, at least, the axone terminates in an end-organ which is physiologically different from the rest of the cell, and this end-organ is the exciting agent. The relation of the protoplasm of the end-organ to the protoplasm of the cell which it stimulates, whether one of continuity or contiguity, is not certain, but most histological and physiological observations are distinctly in favor of the latter view.

FIG. 31.—Nerve-termination in voluntary muscle of the rabbit, stained in methylen-blue (*intra vitam*), fixed, sectioned, and counter-stained in alum carmin. *A*, surface view, *B*, longitudinal section through nerve-termination and muscle-fibre; *C*, cross-section; *S*, sarcolemma; *n. l.*, neurilemma. (From *Text-book of Histology*, Bohm and Davidoff, revised by G. C. Huber. W. B. Saunders, Philadelphia, 1900).

The physiology of the end-organs of motor axones distributed to striated muscles is best known.

Fig. 31 shows a surface view and a longitudinal and cross-section of the end-organ of an axone supplying a voluntary muscle of a rabbit. The axis-cylinder loses its medullary sheath shortly before reaching the fibre, and the neurilemma becomes continuous with the sarcolemma, so that the axis-cylinder on penetrating the sarcolemma comes into direct contact with the sarcoplasma of the muscle. The sarcoplasma is heaped together at this place, making a little mound, and the axis-cylinder, after dividing into a number of fine terminal twigs, ends in the midst of this mass of sarcoplasma. Evidently the nerve and muscle protoplasm come into very close relation. On the other hand, nerve and muscle protoplasm retain each its peculiar reaction to staining-fluids, and as far as these chemical reactions can show each maintains its peculiar chemical and histological structure. Moreover, the results of physiological experimentation have shown that, although no definite histological boundary has been found between the axone and its terminal organ, the exciting organ must be considered to be a specially differentiated structure, differing widely from the rest of the neurone.

The motor end-organ uses up more time in the excitation of the muscle than would be required for transmission of the excitation through a like amount of nerve- or muscle-substance. It is found by experiment that a muscle does not contract so quickly if it be excited through its nerve as when stimulated directly. Part of the lost time is spent in transmission of the excitation through the nerve; but after allowance has been made for this loss there is a balance to be accounted for, and this is credited to the motor end-organ. The time used by the motor end-plate is found to be 0.0032 second.[1]

Motor end-organs are, as we have seen, poisoned by curara (see p. 26) and a number of other drugs which have little influence on the rest of the axone or on the muscle.

If a muscle is continuously excited for a considerable time by irritants applied to its nerve, it will at last cease to contract. Direct excitation shows that, though weakened, it is still capable of contraction, and we know that the nerve-fibre does not fatigue. The cessation of contraction is due to fatigue of the motor ends.

The motor end-organ is found to lose its vitality quicker than the muscle or the nerve-fibre, if it be deprived of its normal blood-supply.

If a motor nerve be cut, the part of the axone separated from the body of the nerve-cell and the terminal organ degenerates, but the degeneration process stops at the muscle.

These facts show that the motor end-organ differs physiologically in many respects from the rest of the axone and from the muscle. Moreover, they favor the idea that excitation is not conducted directly from nerve to muscle protoplasm. That this is the case is also made probable by the fact that though a condition of excitation is transmitted in both directions through nerve and muscle protoplasm as long as there is continuity, a condition of excitation in muscle substance does not appear to be transmitted to the motor nerve. Apparently the protoplasm of the end-organ and the muscle are in contact, but are not physiologically continuous, and excitation of muscle protoplasm by the end-organ occurs through some special process. Various views have been advanced with reference to the probable nature of such a process, but as no one of them has received general acceptance they need not be dwelt upon here. One point more, of interest in this connection, is the fact that it is the sarcoplasma rather than the fibrillary elements of the muscle that comes in contact with the nerve end-organ, which would seem to show that this substance is capable of being excited and conducting the excitation. If this be true of muscle substance, it is likely that the semi-fluid part of the protoplasm of the nerve, as well as perhaps the fibrillary part, may have the power of conduction.

As a result of a series of remarkable histological investigations on the anatomy of the nervous system, the view has come to be generally accepted, that the afferent nerve-fibres entering the spinal cord do not communicate directly with the nerve-cells, but terminate in brush-like endings in close contact with some part of the cells which they excite. A similar arrangement has been found wherever nerve-cells are excited to action by nerve-fibres. As in the case of the motor end-organ, it has remained a matter of doubt whether the brush-like ends of the axones should be considered to be

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[1] Bernstein: *Archiv für Anatomie und Physiologie*, 1882, S. 329.

in contact with the bodies and dendrites of the cells to be excited, and whether this relation would be sufficiently close for a transmission of excitation, or whether they should be considered as specially differentiated exciting mechanisms, which do not simply transmit the condition of excitation by a process of conduction, but which develop a special form of physiological stimulus, and through this excite the second neurone to activity.

Of late, certain histologists claim to have traced the fibrillæ of the axone of one neurone into the cell-body of another neurone, and have even suggested that the nerve impulse from the first might be transmitted through the cell-body of the second and into its branches without the intervention of the protoplasm of the body of the cell.

It is possible that in some cases the axone of the exciting neurone may, instead of ending close to the neurone to be excited, penetrate it and end in its substance, just as the motor end-organ penetrates into the sarcoplasma of the muscle-fibre. This could happen, and yet the protoplasms of the two cells might preserve their individuality.

There are many facts which show that, physiologically at least, the two neurones act as wholly independent mechanisms. These will be dealt with more at length in the section devoted to the physiology of the central nervous system. Suffice it to say, the end-brush at the extremity of the axone can excite the cell body of another neurone, but cannot be excited by it. A reflex act involving only two neurones requires more time than could be used in simple conduction through the two cells. The character of the impulse sent out of the spinal cord by the efferent cell may be very different from that passing in along the afferent cell—*e. g.*, the efferent impulse may be stronger than the afferent ; the strength of efferent discharge may vary greatly within short intervals of time even when the strength of the afferent impulses remains the same ; weak afferent impulses may, by summation, lead to a strong efferent discharge, and continuous afferent stimulation may awaken rhythmic efferent discharges.

In short, physiological facts are all opposed to the idea that there is continuity of protoplasm of different nerve-cells, and in favor of the view that the end-brush, like the motor end-plate, acts as a specialized exciting mechanism.

Conduction in Both Directions.—(*a*) *In Muscle.*—Wherever protoplasmic continuity exists, conductivity would seem to be possible; moreover, the active change excited by an irritant would seem to be able to pass in all directions, though whether with the same facility is not known. Where the spread of the excitatory process is accompanied by a change in form, as is the case in many of the lower organisms and in muscle-tissue, it is not difficult to trace the process. The rate at which the excitation spreads through the irritable substance is very rapid, and special arrangements have to be employed to follow it, but the change is not so swift that its course cannot be accurately determined. It has been found that if a muscle-fibre be stimulated, as normally, by a nerve-fibre, the active condition produced at the point of stimulation spreads along the muscle-fibre in both directions to its extremities ; if the fibre be artificially irritated at either end, the exciting change runs the length of the fibre, regardless of the direction, and stimulates every part of it to contraction.

(*b*) *In Nerves.*—In the cases of nerves where excitation is accompanied by no visible manifestation of activity, a definite answer to the question is not so readily obtained. As long as a nerve is within the normal body, the activity of the nerve-fibre can only be estimated from the response of the cell which the nerve-fibre excites, and there is such an organ only at one extremity of the fibre.

Paul Bert made a well-known experiment, in which he tried to reverse a sensory nerve in the living animal. He succeeded in bringing about union of the end of the tail of a rat with the tissues of the back, and found, when the union was complete, after the tail was cut off at its base, it was still capable of giving sensations of pain. The experiment failed to throw light on the problem, however, for we now know that the peripheral part of the cut nerve dies, and the conduction power manifested in this case was dependent on new axis-cylinders which had grown down from the central nerve-stump (see p. 79).

Efforts have been made to elucidate the problem by attempting to unite the central part of a cut sensory nerve with the peripheral part of a divided motor nerve, and observing, after the healing was complete, whether excitation of the sensory nerve caused movements in the part supplied by the motor nerve. Most of these experiments have given doubtful results, but lately Budgett and Green[1] have succeeded where others have failed, and have made cut sensory fibres grow down the degenerated trunk of a motor nerve, and connect with muscle-fibres, so that the muscle contracted when the peripheral end of the sensory fibres was stimulated. The impulse went up the old sensory fibres, and then down the newly developed fibres in the old motor trunk. Their method was to cut the left pneumogastric nerve between the ganglion and the cranium, and to suture its peripheral cut end to the peripheral cut end of the hypoglossal. All the fibres of the hypoglossal and the efferent fibres of the pneumogastric must have degenerated, because these fibres were separated from the bodies of the cells of which they were branches. The sensory fibres of the pneumogastric, on the other hand, because still in connection with the nerve-cells of the ganglion, continued to live, and the part connected with the peripheral stump of the cut hypoglossal grew down this nerve and came into relation with the muscles of the tongue.

Two or three months after the operation the left pneumogastric was divided just above the thorax, and the combined vago-hypoglossal nerve, together with the tongue, was excised. When the peripheral end of the pneumogastric was excited the muscles of the tongue were seen to contract. Mechanical as well as electrical stimuli were effective, and there would seem to be no escape from the conclusion that the sensory fibres of the pneumogastric had conducted the impulse centripetally as far as the ganglion, and then centrifugally down to the muscle of the tongue.

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[1] Budgett and Green: *American Journal of Physiology*, 1899, iii. p. 115.

There is, however, an entirely different method of experimentation which seems to prove that nerve-, like muscle-protoplasm, can conduct in both directions. This method is based on the fact that though nerve-fibres rarely branch in the peripheral nerve-trunks on their way to an organ, they may divide very freely after reaching it. Such branchings of fibres occur in muscle, and Kuehne[1] found that if one of these branches was stimulated, the irritation passed up the branch to the nerve-fibre and then down the other branches to the muscle. For example, he split the end of the sartorius muscle of a frog by a longitudinal cut, and then found on exciting one of the slips that the other contracted (see Fig. 32). Since cross conduction between striated muscle-fibres does not occur, no other explanation presents itself. Perhaps a still more striking example is to be found in an experiment of Babuchin[2] on the nerve of the electric organ of an electric fish, the Malopterurus. The organ, consisting of many thousand plates, is supplied by a single enormous nerve-fibre which after entering the organ divides very freely so as to supply every plate. In this case mechanical stimulation of the central end of one of the cut branches of the nerve, sufficed to cause an electric discharge of the whole organ. The irritation must have passed backward along the irritated branch until the main trunk was reached and then in the usual direction down the other branches to the electric plates.

FIG. 32.—Kuehne's preparation of sartorius to show double conduction in nerve.

Still another method is that which was employed by Du Bois-Reymond,[3] on the fibres of the spinal nerve-roots. When a nerve is excited to action it undergoes a change in electrical condition, and this change progresses along the fibre at the same rate and in same direction as the nerve-impulse. This electrical change, though entirely different from the nerve-impulse itself, can be taken as an indication of the direction of movement of the process of conduction. Du Bois-Reymond found that if he stimulated the afferent fibres of the posterior spinal nerve-roots of the sciatic nerve of the frog, a "negative variation current," as the current resulting from the change in the electrical condition of the nerve is called, passed down the nerve in a direction opposite to that which the normal impulse takes. Further, it was found that if the sciatic nerve was excited, a negative variation current could be detected in the anterior as well as the posterior roots. Normally the irritation only passes up the posterior roots and down the anterior, for normally the sensory fibres of the posterior roots are excited only at the peripheral end and the motor fibres of the anterior roots only at the central end. The experiment showed both sensory and motor fibres to be capable of conducting in both directions. Normally a nerve is stimulated only at one end, and therefore conducts in only one direction.

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[1] *Archiv für Anatomie und Physiologie*, 1859, S. 595.

[2] *Ibid.*, 1877, S. 262.

[3] *Thierische Electricität*, 1849, Bd. ii. S. 587.

Rate of Conduction.—The activity of the conduction process varies greatly in different tissues. The nerves of warm-blooded animals conduct more rapidly than those of cold; in a given animal the nerve-fibres conduct more rapidly than muscle-fibres; striated muscle conducts more rapidly than smooth muscle; and even within a single cell different portions may transmit the exciting process at different rates; thus the myoid substance of the contractile fibres of one of the rhizopods conducts more rapidly than the less highly differentiated protoplasm of the cell. In general, it may be said that, "the power to conduct increases with increase of mobility and sensitiveness to external irritants, a fact which reveals itself in the protozoa, by a comparison of the slowly moving rhizopods with the lively flagellata and ciliata."[1] A study of different classes of muscle-tissue supports this view.

(*a*) *Rate of Conduction in Muscles.*—The conduction process is invisible, hence we estimate its strength and rate by its effects. It is most readily followed in such mechanisms as muscle, where the conducting medium itself undergoes a change of form as the exciting influence passes along it.

Rate of Transmission of Wave of Contraction.—If a muscle be excited to action by an irritant applied to one end, it does not contract at once as a whole, but the change of form starts at the point which is irritated and spreads thence the length of the fibres. At the same time that the muscle shortens it thickens, and under certain conditions the swelling of the muscle can be seen to travel from the end which is excited to the further extremity. In the case of normal, active, striated muscle, the rate at which the change of form spreads over the muscle is far too rapid to be followed by the eye, and hence the muscle appears to act as a whole. By suitable recording mechanisms, evidence can be obtained of the rate at which the exciting influence and contraction process pass along the fibre. Thus two levers can be so placed as to rest on the two extremities of a muscle, at the same time that the free ends of the levers touch a revolving cylinder, the surface of which is covered with paper blackened with lampblack. The writing-point of one lever must be directly under the point of the other. If, when the cylinder is revolving, one end of the muscle be stimulated, the record will show that the lever resting on that part is the first to move, making it evident that that part of the muscle begins to thicken first, and that the contraction does not begin at the further extremity of the muscle until somewhat later. The record given in Figure 33 was obtained in a similar experiment, but one in which the contraction of the muscle was registered by the *pince myographique* and recording tambour of Marey (see Fig. 34).

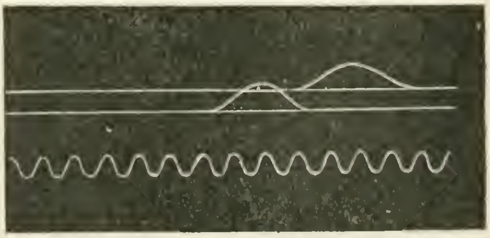

FIG. 33.—Rate of conduction of the contraction process along a muscle, as shown by the difference in the time of thickening of the two extremities. The tuning-fork waves record $\frac{1}{100}$ second (after Marey).

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[1] Biedermann: *Elektrophysiologie*, 1895, Bd. i. S. 124.

Bernstein[1] measured the rate at which the irritating process is transmitted along the muscle by recording the latent period, the time elapsing between the moment of irritation and the beginning of the contraction (see p. 102). A lever was so connected with one end of the muscle as to record the instant that it began to thicken. The muscle was stimulated in one experiment at the end from which the record of its contraction was taken, and in another immediately following experiment it was stimulated near the other end. The distance between the stimulated points being known, the rate of transmission was reckoned from the difference in the latent periods. In his experiments he found the rate of conduction in the semimembranosus of the frog to be from 3.2 to 4.4 meters per second. Hermann found the rate to be 2.7 meters for the curarized sartorius of the frog. The results obtained by Abey and some others are a little lower, but probably 3 meters per second can be accepted as the average normal rate for frog's muscle.

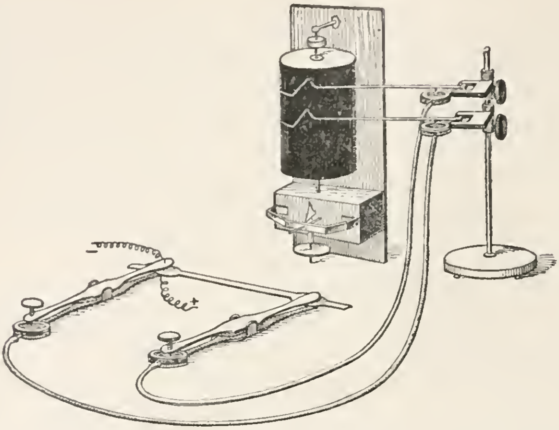

FIG. 31.—Method of recording the rate of passage of the contraction process along a muscle (after Marey). The movements of the muscle are recorded by means of air-transmission. The *pince myographique* consists of two light bars, the upper of which acts as a lever, moving freely on an axis supported by the lower. When the free end of the upper bar is raised, the other end presses down on a delicate rubber membrane which covers a little metal capsule, which is carried on the corresponding extremity of the lower bar. The capsule is in air-communication, by a stiff-walled rubber tube, with another capsule which is similarly covered with rubber membrane. A light lever is connected with the membrane of the second tambour, and records its movements on the surface of a revolving cylinder. The muscle is placed between the free ends of the bars of the *pince myographique*, and, when the muscle thickens in contraction, it raises one end of the lever, depresses the membrane at the other end, and drives air into the recording tambour, and thus, by automatically raising the writing-point, records its change in form on the cylinder.

Length of Wave.—By such experiments it becomes obvious that the contraction process passes over the muscle, in the form of a wave. In an experiment, such as Bernstein's, in which the thickening of the muscle is recorded, we can determine from the length of the curve written by the contracting muscle how long the contraction remains at a given place. Knowing this, and the rate at which the process passes along the fibre, we can estimate the length of the contraction wave, just as we could reckon the length of a train

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[1] *Untersuchungen über die elektrische Erregung von Muskeln und Nerven*, 1871, S. 79.

of cars if we knew how fast it was moving and how long it required to pass a given station. Thus, if the contraction is found to last at a given point on the muscle 0.1 second, and the rate at which the contraction process is travelling is 3000 millimeters per second, the length of the wave is 300 millimeters. According to Bernstein's determinations, the length of the wave of contraction in a frog's striated muscle is from 198–380 millimeters. The length of a striated muscle-fibre is, at the most, scarcely more than 40 millimeters, and normally the muscle-fibre is stimulated, not as in the above experiment at one end, but near its centre, at the point where the nerve joins it; the irritation process spreads along the fibre in both directions from this point, and would pass over the distance 20 millimeters so quickly that practically the whole muscle-fibre would be in the same phase of contraction at the same time.

Rate of Conduction in Different Kinds of Muscle.—The rate of conduction varies very considerably in the muscles of different animals, and in different kinds of muscle in the same animal, just as the contraction process itself differs in its rate and strength.

	Meters per second.	
Smooth muscle-fibres of the ureters of the rabbit	0.02–0.03	(Engelmann).
Muscle of the heart-ventricle of the frog	0.1	(Waller).
Contractile substance of medusæ	0.5	(Waller).
Neck-muscles of the turtle	0.1 –0.5	(Hermann and Abey).
Gracilis and semimembranosus of the frog	3.2 –4.4	(Bernstein).
Cruralis (red muscle) of the rabbit	3.4	(Rollet).
Sterno-mastoid of the dog	3. –6	(Bernstein and Steiner).
Semimembranosus (white muscle) of the rabbit	5.4 –11.4	(Rollet).
Human muscle	10. –13	(Hermann).

(*b*) *Rate of Conduction in Nerves.*—Conductivity is most highly developed in the case of the nerve-fibre. The distances through which it acts and the rapidity of the process excite our wonder. The process is accompanied by no visible change in the nerve-fibre itself, and the strength and rate have to be estimated by the effect produced on the organ which the nerve excites to action, or by the change which takes place in the electrical condition of the nerve as the wave of excitation sweeps over it.

Rate in Motor Nerves.—Helmholtz was the first to measure the rate of conduction in nerves.[1] Originally he employed Pouillet's method for measuring short intervals of time. The arrangement is illustrated in Figure 35. The moment that a current was thrown into the coils of a galvanometer (see p. 145) the current in the primary coil of an induction apparatus was broken and the nerve connected with the secondary coil received a shock. An instant after, the contraction of the muscle which resulted from the stimulation of the nerve broke the galvanometer circuit. The amount of deviation of the magnet of the galvanometer varied with the time that the circuit remained closed, and therefore could be taken as a measure of the interval elapsing between the stimulation of the nerve and the contraction of the muscle. The nerve was

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[1] Helmholtz: *Archiv für Anatomie und Physiologie*, 1850, S. 71–276; 1852, S. 199.

excited in two succeeding experiments at two points, at a known distance apart, and the difference in the time records obtained was the time required for the transmission of the nerve-impulse through this distance.

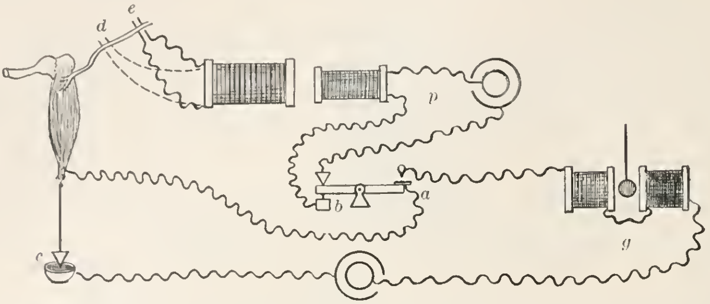

Fig. 35.—Method of estimating rate of conduction in motor nerve of frog, as used by Helmholtz. The horizontal bar *a-b* is supported on an axis in such a manner that when the contact is made at *a* it is broken at *b*, therefore at the same instant a current is made in the galvanometer circuit *g* and opened in the primary circuit of the induction apparatus *p*. When the muscle contracts, the galvanometer circuit is broken at *c*. The nerve was stimulated in two successive experiments at *d* and *e*.

Later, Helmholtz devised a method by which a muscle would record its contractions on a rapidly moving surface, and employed this to measure the rate of conduction in motor nerves. He stimulated the nerve as near as possible to the muscle and let the contraction be recorded; then he stimulated the nerve as far as possible from the muscle, and again had the contraction recorded. The difference in time between the moment of excitation and the beginning of the contraction in the two experiments was due to the difference in the distance that the nerve-impulse had to pass in the two cases, and, this distance being known, the rate of conduction could be readily calculated. By this means he found the rate of transmission in the motor nerves of the frog to be 27 meters per second. In similar experiments upon men he recorded the contractions of the muscles of the ball of the thumb, and noted the difference in the time of the beginning of the contractions when the median nerve was excited through the skin at two different places. He found the average normal rate for man to be about 34 meters per second, a rate which is considerably quicker than that of our fastest express trains, but a million times less than the rate at which an electric current is transmitted along a wire. These determinations are still accepted as approximately correct for human nerves, although they are found to vary very considerably under different conditions, a high temperature and strong irritation quickening the rate to 90 or more meters per second, while cooling may gradually slow the rate and finally stop conduction. Moreover, considerable differences exist in nerves controlling different functions, even in the same animal. Thus Chauveau gives the rate for the fibres of the vagus nerve, which supply the rapidly contracting striated muscles of the larynx, as 66.7 meters per second; and the rate for vagus fibres, controlling the slower smooth muscles of the œsophagus, as 8.2 meters per second. The rate of transmission in the non-medullated nerves of invertebrates appears to be still slower; the nerve for the claw-muscles of the lobster conducts at a rate of from 6 to 12 meters per second, according as the temperature is low or high (Fredericq and Vandervelde). The rate in non-medullated nerves of the Cephalopodia is 3.5–5.5 meters per second (Boruttan).

Contrary to the view frequently expressed (Pflüger[1] and others), all parts of the nerve have the same rate of conduction.[2]

Rate in Sensory Nerves.—We have no definite knowledge of the rate of conduction in sensory nerves. The attempt has been made to measure it by stimulating the sensory fibres of a nerve-trunk at two different points and noting the difference in the time of the beginning of the resulting reflex acts; or, in experiments on men, the difference in the length of the reaction time has been taken as an indication. By reaction time is meant the interval which elapses between the moment that the irritant is applied and the signal which is made by the subject as soon as he feels the sensation. Oehl found the mean normal rate of conduction in the sensory nerves of men to be 36.6 meters per second.[3] Dolley and Cattell,[4] by employing the reaction-time method, found the rate for the sensory fibres of the median nerve of one of them to be 21.1 meters per second, and for the other 49.5 meters per second, while the posterior tibial nerve gave rates, for one of them 31.2 meters, and for the other 64.9 meters. They attribute these wide variations in part to differences in the effectiveness of the irritant at different parts of the skin, but chiefly to differences in the activity of the central nervous processes involved in the act.

Schelske[5] observed similar differences in different men—for one 25.3 meters, for another 32.6 meters, and for still another 31.05 meters per second.

In spite of the great difficulty of getting definite measurements in experiments on men, we may conclude from the work of these and other observers that the rate of conduction in sensory fibres is about the same as in motor fibres; in the case of man about 35 meters per second.

Another method applicable to isolated nerves is based on the fact that the passage of the nerve-impulse along a nerve is accompanied by a change in its electrical condition. The rate of conduction can be ascertained by finding the rate at which this electrical change is transmitted.

Influences which Alter the Rate and Strength of the Conduction-process.—(*a*) *Effect of Death-processes.*—Normally, the rate of conduction in muscle-fibres is so rapid that the whole muscle appears to contract at the same time; but there are certain conditions under which the transmission of the exciting influence is very much slowed, or even altogether prevented, so that the stimulation of a given part of the muscle results in a local swelling, or welt, limited

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[1] Pflüger: *Untersuchungen über die Physiologie des Electrotonus*, Berlin, 1859, S. 465.

[2] R. du Bois-Reymond: *Centralblatt für Physiologie*, 1899, Bd. xiii. S. 513.

[3] Oehl: *Archives italiennes de Biologie*, 1895, xxi. 3, p. 401.

[4] Dolley and Cattell: *Psychological Review*, New York and London, 1894, i. p. 159.

[5] Schelske: *Archiv für Anatomie und Physiologie*, 1864, S. 151.

to the excited area. When a muscle is dying, the rate of conduction as well as the rapidity of contraction is lessened. The muscles of warm-blooded animals exhibit more striking differences than those of cold-blooded, but both are similarly affected. If a dying muscle be mechanically stimulated, as by a direct blow, a localized swelling develops at the place; and if the muscle be stroked with a dull instrument, a wave of contraction may be seen to follow the instrument, the contraction being quite strictly limited to the excited area, so that one can write on the muscle. The strict localization of the contraction to the irritated parts makes it evident that the nerves take no part in it, hence Schiff called it an idio-muscular contraction, in distinction from the normal neuro-muscular contraction. In the dying nerve as in the dying muscle the rate of transmission is found to be slowed.

(*b*) *Effect of Mechanical Conditions.*—The effect of pressure to lessen the conduction-power of nerves is one which everyone has had occasion to demonstrate on himself. For example, if pressure be brought to bear on the ulnar nerve where it crosses the elbow, the region supplied by the nerve becomes numb, "goes to sleep," so to speak. It is noticeable that only a slightly greater effort is required to move the muscles, at a time when no sensations are received from the hand. For some unexplained reason the sensory nerve-fibres appear to be less resistant than the motor. Gradually applied pressure may paralyze the nerve without exciting it, but on the removal of the pressure the recovery of function of the sensory fibres is accompanied by excitation processes, which are felt as pricking sensations referred to the region supplied by the nerve. The exact reason of the loss of functional power caused by pressure which is insufficient to produce permanent injury is not altogether clear. Stretching a nerve may act to lessen, and if severe destroy, conductivity. It is in one sense another way of applying pressure, since the calibre of the sheath is lessened and through the fluids pressure is brought to bear on the axis-cylinder. Of course, if the stretching were excessive, the nerve-fibres would be ruptured and degenerate.

Whether stretching can alter the rate of conduction in nerves is not known. Apparently it does not do so in muscles, although because of the greater length of the muscle it appears to do so.[1]

(*c*) *Effect of Temperature on Conduction.*—Helmholtz and Baxt found that by cooling motor nerves they could lower the rate of conduction, and by heating them they could increase it even more markedly. By altering the temperature of the motor nerves of man, they observed rates varying from 30 to 90 meters per second. The rate of the motor nerves of other animals is likewise greatly altered by heat and cold. This is true of the invertebrates as well as the vertebrates; the rate in the nerves of the claw-muscles of the lobster, for example, changes from 6 to 12 meters per second as the temperature is varied from 10° to 20° C. Sensory nerve-fibres are similarly influenced by temperature. Oehl[2] found by cooling and heating the nerves of men, variations of from 30 to 25 meters per second on cooling, and from 30 to 50 meters

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[1] Schenck: *Pflüger's Archiv*, 1896, Bd. 64, S. 179.

[2] Oehl: *Archives italiennes de Biologie*, 1895, xxiv. p. 231.

a second on heating. Both the sympathetic and the vagus nerve-fibres in the frog have their influence on the heart-beat decreased by cold and increased by heat.[1] The favorable influence of heat on the conduction power seems common to all nerves, but only within certain limits. The motor fibres of the sciatic of the frog lose their power to conduct at 41° to 44° C., but may recover the power if quickly cooled; if the temperature has reached 50° C. conductivity is permanently lost.

Nerves of like function in different animals may lose the power of conduction at different temperatures. Thus the motor fibres of the sciatic nerve of the dog cease to conduct at 6° C., those of the cat at 5° to 3° C., of the frog at about 0° C. The inhibitory fibres of the vagus nerve of the dog show diminished activity at 3° C., and become wholly inactive at 0° C.; the inhibitory fibres of the vagus of the rabbit become inactive at 15° C.

Different kinds of fibres in the same nerve-trunk may be differently affected by temperature, and this difference may be sufficiently marked in some cases to be used as a means of distinguishing them.[2] For example, the temperature limits at which the vaso-constrictor fibres of the sciatic of the cat can conduct are 2°–3° C. to 47° C., while the limits for the dilator fibres are both lower and higher than for the constrictors. If cold be applied to the sciatic nerve, the fibres supplying the extensor muscles seem to fail before those which innervate the flexors.

Further, it has been observed that if cold be applied locally to a nerve, the part affected loses its power to conduct, and acts as a block to the passage of the nerve-impulse generated in another part of the nerve. Application of extreme cold to the ulnar nerve of man at the elbow results in a complete loss of feeling in the parts which the nerve supplies.[3] On the other hand, the strength of an impulse is increased by passage through a region which has been warmed. These facts remind us of the effect of heat and cold on the activity of other forms of protoplasm and would find a comparatively easy explanation were we content to look upon conduction as the result of chemical change in the axis-cylinder. The fact that conduction does not cause fatigue is opposed to such an explanation, and so we take refuge in the idea that heat is favorable and cold unfavorable to molecular activity in general.

(*d*) *Effect of Chemicals and Drugs.*—The conductivity, like the irritability, of nerve and muscle is greatly influenced by anything which alters the chemical constitution of active substance. In general, influences which increase or decrease the one have a similar effect upon the other. There are important exceptions to the rule, however. The direct application of alcohol, ether, etc., to the nerve may destroy the conductivity without greatly lessening the irritability, while carbon dioxide[4] or cocain will destroy the irritability very much sooner than the conductivity. Such observations suggest that con-

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[1] Stewart: *Journal of Physiology*, 1891, vol. xii. No. 3, p. 22.

[2] Howell, Budgett, and Leonard: *Journal of Physiology*, vol. xvi. Nos. 3 and 4, 1894.

[3] Weir Mitchell: *Injuries of Nerves and their Consequences*, Philadelphia, 1872, p. 59.

[4] Grünhagen: *Pflüger's Archiv*, 1872, vi. S. 180.

ductivity is dependent on other properties of the nerve than irritability, and there are some other facts pointing in the same direction; for example, regenerating nerves acquire the power to conduct before they recover their irritability. The usual explanation of those who regard conduction as due to the excitation of each succeeding part of the nerve by the one just preceding it is, that external excitation is a coarse affair as compared with the normal internal excitation process, and the effect of the former may be lost when the latter is still effective.

(*e*) *Effect of a Constant Battery Current.*—A constant electric current, if allowed to flow through a nerve or muscle, not only alters the irritability, but also the conductivity. The change in the conductivity affects both the strength and rate of the conduction process. Von Bezold[1] found that weak and medium currents have little effect on the conductivity, but that strong currents completely destroy the power of the nerve to transmit the nerve-impulse. As the strength of the current is increased, the first effect is observed at the anode, and shows itself in a slowing of the passage of the exciting impulse. This action is the greater the more of the nerve exposed to the current, the stronger the current, and the longer it is closed. The loss of conduction power is associated with changes at the place where the current enters and where it leaves the nerve rather than with alterations within the intrapolar region. Engelmann, in his experiments on the smooth muscle-fibres of the ureter, saw a decline of power of conduction at the anode by weak currents, which when the strength of the current was increased appeared also at the kathode; the conductivity was wholly lost at both poles when the current was very strong. In the case of a striated muscle, such as the sartorius of the frog, the kathode has been found to become impassable after strong currents have flowed through a muscle for a considerable time. The same is true of nerves.

It is not surprising that a current which can greatly decrease the irritability at the anode, and even inhibit a contraction which may be present when it is applied, should be found to decrease the conductivity as well, but that the conductivity should be decreased at the kathode, where the irritability is greatly increased, was not to be expected. Rutherford[2] found that with weak currents the rate of the conduction power at the kathode was increased rather than diminished, and that it was only when strong currents acted a considerable time that the conduction power lessened at the kathode. Biedermann explains this on the ground that the increased excitability at the kathode leads in the muscle to a condition of latent contraction and therefore to fatigue, and that it is this which lessens the conductivity. The lessened power to conduct continues at the kathode after the removal of the current. There is little doubt that fatigue interferes with the conduction power of muscle, but this explanation would hardly apply to nerves which are not known to fatigue at the point of stimulation, *i. e.* if we limit the term fatigue to changes resulting from physiological activity. Undoubtedly chemical and physical alterations may

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[1] *Untersuchungen über die elektrische Erregung der Nerven und Muskeln*, Leipzig, 1861.

[2] *Journal of Anatomy and Physiology*, 1867, vol. 2, p. 87.

occur in nerves as a result of the passage of an electric current through them, and it would seem as if the loss of conductivity which they show when subjected to strong currents is to be accounted for by such electrolytic changes.

The changes produced in the conductivity of nerves by strong currents explain the failure of the closing of the ascending current and opening of the descending current to irritate the muscle (see Pflüger's law, p. 50). In the former case the anode region of decreased conductivity intervenes between the kathode, where the closing stimulus is developed, and the muscle. In the latter case the irritation developed at the anode, on the opening of the current, is unable to pass the region of decreased conductivity which is formed at the kathode, and which persists after the current is opened.

Practical Application of Alterations produced by Battery Currents.—The alterations produced by strong battery currents in the irritability and conductivity of nerves and muscles may be made use of by the physician. If the effect of only one pole is desired, it may be applied as a small electrode immediately over the region to be influenced, while the other pole may be a large electrode placed over some distant part of the body where there are no important organs. The size of the electrodes used determines the density of the current leaving or entering the body and consequently the intensity of its action. The application of the anode to a region of increased excitability, by decreasing the irritability, may for the time lessen irritation; on the other hand the kathode may heighten the irritability of a region of decreased excitability. The sending of a strong polarizing current through a motor nerve, by lessening the conductivity, may prevent abnormal motor impulses from reaching muscles, and so stop harmful "cramps;" or the sending of such a current through a sensory nerve may, during the flow of the current, keep painful impulses from reaching the central nervous system. In applying a strong battery current to lessen irritability or conductivity it must be remembered that the after-effect of such a current is increased irritability.

(*f*) *Effect of Conduction and Fatigue of Nerves.*—Many experiments have been made in the hope of detecting some form of chemical change as a result of conduction. The nerve has been stimulated for many hours in succession with an electric current, and then been examined with the utmost care to find whether there had been an accumulation of some waste product, as carbon dioxide, or some other acid body. The gray matter of the spinal cord, which is largely composed of nerve-cells, is found to become acid as a result of activity,[1] but this cannot be found to be the case with the white matter of the cord, which is chiefly made up of nerve-fibres, nor has an acid reaction been obtained with certainty in nerve-trunks.[2]

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[1] Funke: *Archiv für Anatomie und Physiologie*, 1859, S. 835. Ranke: *Centralblatt für medicinische Wissenschaft*, 1868 and 1869.

[2] Heidenhain: *Studien aus dem physiologischen Institut zu Breslau*, ix. S. 248; *Centralblatt für Medicin*, 1868, S. 833. Tigerstedt: "Studien über mechanische Nervenreizung," *Acta Societatis Scientiarum Fennicæ*, 1880, tom. xi.

Not only has an attempt to discover this or other waste products which might be supposed to result from chemical changes within the nerve-fibre failed, but observers have been unable to obtain evidence of the liberation of heat, which one would expect to find were the nerve-fibre the seat of chemical changes during the process of conduction.[1] Stewart writes: "Speaking quite roughly, I think we may say that in the nerves of rabbits and dogs there is not even a rise of temperature of the general nerve-sheath of $\frac{1}{2000}$ of a degree during excitation."

Many experiments have been made to ascertain whether a nerve would fatigue if made to conduct for a long time. Most of these have been made upon motor nerves, the amount of contraction of the muscle, in response to a definite stimulus applied to the nerve, being taken as an index of the activity of the nerve. Since the muscle would fatigue if stimulated continuously for a long time, various means have been employed to block the nerve-impulse and prevent it from reaching the muscle, except at the beginning and end of the experiment. This block has been established by passing a continuous current through the nerve near the muscle, thus inducing an electrotonic change and non-conducting area;[2] or the nerve-ends were poisoned with curare (see p. 26), and the nerve excited until the effect of the drug wore off, and the nerve-impulse was able to reach the muscle;[3] or the part of the nerve near the muscle was temporarily deprived of its conducting power by an anæsthetic, such as ether. Another method of experimentation consisted in using the negative variation current of a nerve (see p. 150) as an indication of its activity, the presence of the current being observed with the galvanometer.[4] Other experimenters have examined the vagus nerve, to see if after long-continued stimulation it was still capable of inhibiting the heart, the effect of the stimulation being prevented from acting on the heart muscle during the experiment by atropin,[5] or by cold, applied locally to the nerve.[6] Still another method was to study the effect of long-continued stimulation on the secretory fibres of the chorda tympani, the exciting impulse being kept from the gland-cells by atropin.[7] Most of these experiments have yielded negative results, and it is doubtful whether nerves are fatigued by the process of conduction.

These results, of course, do not show that the nerve-fibres can live and function independently of chemical changes. As has been said, nerves lose their irritability in time if deprived of the normal blood-supply, and undoubtedly they are, like all protoplasmic structures, continually the seat of metabolic

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[1] Helmholtz: *Archiv für Anatomie und Physiologie*, 1848, S. 158. Heidenhain: *op. cit.* Rolleston: *Journal of Physiology*, 1890, vol. xi. p. 208. Stewart: *ibid.*, 1891, vol. xii. p. 424.

[2] Bernstein: *Pflüger's Archiv*, 1877, xv. S. 289. Wedenski: *Centralblatt für die medicinischen Wissenschaften*, 1884.

[3] Bowditch: *Journal of Physiology*, 1885, vi. p. 133.

[4] Wedenski: *loc. cit.* Maschek: *Sitzungsberichte der Wiener Academie*, 1887, Bd. xcv. Abthl. 3.

[5] Szana: *Archiv für Anatomie und Physiologie*, 1891, S. 315.

[6] Howell, Budgett, and Leonard: *Journal of Physiology*, 1894, xvi. p. 312.

[7] Lambert: *Comptes-rendus de la Société de Biologie*, 1894, p. 511.

processes. The normal function of the nerve, however, the conduction of the nerve-impulse, seems to take place without any marked chemical change.

Nature of the Conduction Process.—There have been a great many views as to the nature of the conduction process, one after the other being advanced and combated as physiological facts bearing on the question have been accumulated. It has been suggested that the whole nerve moved like a bell-rope; that the nerve was a tube, and that a biting acid flowed along it; that the nerve contained an elastic fluid which was thrown into oscillations; that it conducted an electric current, like a wire; that it was composed of definitely arranged electro-motor molecules which exerted an electro-dynamic effect on each other; that it was made up of chemical particles, which like the particles of powder in a fuse, underwent an explosive change, each in turn exciting its neighbor; that the irritant caused a chemical change, which produced an alteration of the electrical condition of such a nature as to excite neighboring parts to chemical change and thereby to electrical change, and so alternating chemical and electrical changes progressed along the fibre in the form of a wave; finally, that the molecules of the nerve-substance underwent a form of physical vibration analogous to that assumed for light.

A discussion of these different theories, none of which can be regarded as entirely satisfactory, cannot be entered upon here.

Although the exact nature of the conduction process is not determined, there seems little doubt that it is of the same type in all forms of protoplasm. In all cases it is a property of the living substance of the cell and is lost when the cell dies: the state of activity spreads like a wave in all directions through the living substance, and is markedly altered by physical and chemical influences which change the irritability of the living substance, and in much the same way as this is altered; continuity of protoplasm is absolutely essential to conduction, hence the spread of the excitation change is limited to the one cell, unless the cell is connected by protoplasmic bridges with other cells, or possesses a specially differentiated exciting end-organ.

In its details the conduction process exhibits many peculiarities in different cells and even in the different parts of the same cell. The receiving organs at the extremities of the dendrites of different classes of neurones differ widely in respect to structure, and in their capacity to react to different kinds of stimuli and to transmit the state of excitation to the dendrite. The exciting organs at the extremities of the axones of different classes of neurones are of different types, and behave differently, the discharge of the exciting process upon a muscle, gland, or nerve-cell being adjusted to the capacity for reaction possessed by the organ in question. In each neurone the strands of protoplasm which connect these distant receiving and exciting mechanisms with the cell body, and the body of the cell itself, work each according to its own nature. For example, the time spent by the phase of activity in the body of a ganglion-cell of the posterior spinal root-ganglion, is far longer than that used in a corresponding length of protoplasm in the dendrite of the cell. Although the conduction process differs in its details even in different parts of the same neurone, the condition of activity which spreads through the neurone and which we call the nerve impulse, has the same general characteristics in all forms of nerves whether medullated or non-medullated, motor, sensory, or secretory. The character of a movement or secretion depends on the character of the organ excited, and not on the nature of the change transmitted along the efferent nerve, and the specific character of a special sensation depends on the form of psychic activity developed in the central nervous system, and not on the nature of the process of transmission in the afferent neurone. This view that the nerve impulse is to be regarded merely as an excitatory process, and that it has the same general characteristics in all kinds of nerves, is strengthened by two sets of experiments which have been reported lately.

One of these sets of experiments was reported by Langley.[1] He found that preganglionic sympathetic fibres—*i. e.* fibres between the ganglion and the cord—if cut centrally from the ganglion, after a time regenerate and make new connections with the nerve-cells of the ganglion. In some cases they unite with cells of their own class, and sometimes with other cells; for example, pupillo-dilator fibres were found to have established connection with pilo-motor neurones—*i. e.* with ganglion-cells which send their axones to the erector muscles of the hairs. Further, by section of post-ganglionic fibres—*i. e.* fibres between the ganglion and the periphery—it was found, after regeneration had occurred, that pilo-motor fibres can form nerve-endings in the iris and become pupillo-dilator fibres. Evidently ganglion-cells and muscle-fibres can be excited by nerve impulses developed in other nerves than those normally connected with them.

A still more remarkable result was obtained by Budgett and Green. A description of this experiment is given on page 85. They succeeded in causing sensory fibres of the pneumogastric to grow down a degenerated motor trunk, the hypoglossal, and connect with the muscles of the tongue. In this case excitation of the peripheral part of the afferent nerve caused muscular contractions. If we should think of the nerve which was excited, we would be inclined to say that a sensory impulse was generated; if we should think of the effect on the muscle, we would call it a motor impulse, and the latter would be the proper term. Evidently the condition of activity which can be aroused in a sensory nerve is capable under suitable conditions of exciting muscles, and sensory nerves cannot be considered to be the seat of specific forms of energy different from those generated in motor nerves.

D. CONTRACTILITY.

Contractility is the property of protoplasm by virtue of which the cell is able to change its form when subjected to certain external influences called irritants, or when excited by certain changes occurring within itself. The change of form does not involve a change of size. The contraction is the

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[1] Langley: *Journal of Physiology*, 1897, xxii. p. 215.

result of a change in the position of the more fluid parts of the cell-protoplasm, and the effect is to cause the cell to approach a spherical shape. In the case of an amœba, for instance, excitation causes a drawing in of the pseudopods, and as the material in them flows back into the cell the body of the cell expands and acquires a globular form. In the simpler forms of contractile protoplasm the movement does not appear to be limited to any special direction, but in the case of the highly differentiated forms, such as muscle, both contraction and relaxation occur on definite lines.

When a muscle is excited to action, energy is liberated through chemical change of certain constituents of the muscle-substance, and this energy in some unknown way causes a rearrangement of the finest particles of the muscle-substance, and the consequent change of form peculiar to the contracted state. When the irritation ceases and relaxation takes place, there is a sudden return of the muscle-substance to the position of rest, either because of elastic recoil or of some other force at work within the muscle itself. That the recovery of the elongated form peculiar to the resting muscle is not dependent on external influences is evidenced by the fact that a muscle floating on mercury, and subjected to no extending force, will on the cessation of irritation assume its resting form. The relaxation no less than the contraction must be regarded as an active process, but on account of their flexibility muscle-fibres are incapable of exerting an expansion force, therefore cannot by relaxing do external work.

Both the histological structure and physiological action of the striated muscles which move the bones show them to be the most highly differentiated, the most perfect form of contractile tissue. It is by means of these structures that the higher animals perform all those voluntary movements by which they change their position with reference to external objects, acquire nourishment, protect themselves, and influence their surroundings. An exact knowledge of the method of action of these mechanisms and the influences which affect them is therefore of the greatest importance to us.

1. Simple Muscle-Contractions Studied by the Graphic Method.— When a muscle makes a single contraction, in response to an electric shock or other irritant, the change of form is too rapid to be followed by the eye. To acquire an adequate idea of the character of the movement it is necessary that we should obtain a continuous record of the alterations in shape which it undergoes. This can be done by connecting the muscle with a mechanism which enables it automatically to record its movements.

If one moves a pencil vertically up and down on a piece of paper, a straight line is written; if while the vertical movements are continued the paper be drawn along at a regular rate in a direction at right angles to the movement of the pencil, a curve will be traced. If the paper be moved at a regular rate, the shape of the curve will depend on the rate at which the pencil is moved, and, if the speed of the paper be known, the rate of movement of the pencil can be readily determined. This principle is employed in recording the movements of muscles. The muscle is connected with a mechanism which rises and falls as the muscle contracts and relaxes, and records the movement of the muscle on a surface which passes by the writing-point at a regular speed (see Fig. 38); such a record is called a myogram.

The Myograph.—The writing mechanism, together with the apparatus which moves the surface on which the record of the movement of a contracting muscle is taken is called a myograph. The writing mechanism has usually the form of a light, stiff lever, which moves very easily on a delicate axis; the lever is so connected with the muscle as to magnify its movements. The point of the lever rests very lightly against a glass plate, or surface covered with glazed paper, which is coated with a thin layer of soot. The point of the lever scratches off the soot, and the movements are recorded as a very fine white line. At the close of the experiment the record is made permanent by passing it through a thin alcoholic solution of shellac. The recording surface in some cases is in the form of a plate, in others of a cylinder, and is moved at a regular rate by a spring, pendulum, falling weight, clockwork, electric or other motor.[1]

FIG. 36.—Records of four contractions of a gastrocnemius muscle of a frog: *a*, recording surface at rest; *b*, surface moving slowly; *c*, surface moving more rapidly; *d*, surface moving even faster.

The record which is traced with the myograph lever by the muscle has the form of a curve. From the height of the curve we can readily estimate the amount that the muscle changes its length, but in order to accurately determine the duration of the contraction process and the time relations of different parts of the curve, it is necessary to know the exact rate at which the recording surface is moving. The shape of the curve drawn by the muscle will depend very largely on the rate of the movement of the surface on which the record is taken. This is illustrated by the four records reproduced in Figure 36. These were all taken from the same muscle within a few minutes of each other and under exactly the same conditions, except that in the successive experiments the speed of the drum on which the record was traced was increased.

A glance at these records shows that a knowledge of the rate of movement of the surface on which the record is taken is indispensable to an understanding of the time relations of the different parts of the curve written by the muscle. The rate of movement of the recording surface can be registered by an instrument called a chronograph.

The chronograph (*g*, Fig. 37), consists of one or two coils of wire wound round cores of soft iron, and a little lever bearing a strip of iron, which is attracted to the soft-iron cores whenever they are magnetized by an electric current flowing through the coils of wire about them. When the current ceases to flow and the iron ceases to be magnetized, a spring draws the lever

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[1] See O. Langendorff: *Physiologische Graphik*, Franz Deuticke, Leipzig, 1891; J. S. Brodie: *The Essentials of Experimental Physiology*, London, 1898.

away from the iron. Many of the instruments employed for this purpose are very delicate, and are capable of responding to very rapid interruptions of the current. The electric current is made and broken at regular intervals by a clock, tuning-fork (*b*, Fig. 37), or other interrupting mechanism, and the lever of the chronograph, which has a writing-point at its free end, moves correspondingly and traces an interrupted line on the recording surface of the myograph (see Fig. 38). The space between the succeeding jogs marked by the chronograph lever is a measure of the amount of the surface which passed the point of the chronograph in one second, $\frac{1}{50}$ second, or $\frac{1}{100}$ second, as the case may be.

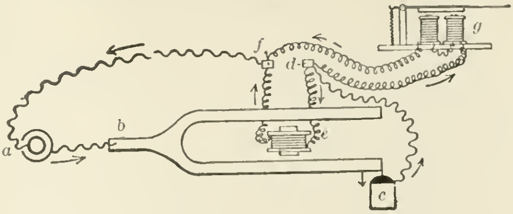

FIG. 37.—Method of interrupting an electric circuit by a tuning-fork, and of recording the interruptions by means of an electro-magnet: *a*, battery; *b*, tuning-fork, with platinum wire at the extremity of one of its arms, which with each vibration of the fork makes and breaks contact with the mercury in the cup below; *c*, mercury cup; *e*, electro-magnet which keeps the fork vibrating; *g*, chronograph. The current from the battery *a*, passes to the fork *b*, then, by way of the platinum wire, to the mercury in cup *c*, then to the binding-post *d*, where it divides, a part going through the coils of wire of the chronograph *g*, and thence to the binding-post *f*, the rest through the coil of wire of electro-magnet *e*, and then to the post *f*, from which the united threads of current flow back to the battery. The electro-magnet *e* keeps the fork in vibration, because when the platinum wire enters the mercury at *c*, the circuit is completed and the electro-magnet magnetizes its soft-iron core, which attracts the arms of the fork, and thus draws the wire out of the mercury and so breaks the circuit. When the current is broken the fork, being released, springs back, dips the wire into the mercury, and by closing the circuit causes the process to be repeated.

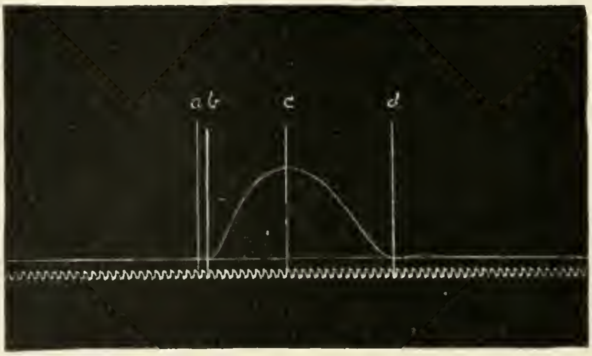

FIG. 38.—Myogram from gastrocnemius muscle of frog; beneath, the time is recorded in 0.005 second: *a*, moment of excitation; *b*, beginning of contraction; *c*, height of contraction; *d*, end of contraction.

Myogram of Simple Muscle-contraction.—The rate of the movement of the muscle during every part of its contraction can be readily determined by comparing the record it has drawn with that of the chronograph.

Figure 38 is the reproduction of a single contraction of a gastrocnemius muscle of a frog. The rise of the curve shows that the contraction began comparatively slowly, soon became very rapid, but toward its close was again gradual; the relaxation began almost immediately, and took a similar course, though occupying a somewhat longer time. The electric current which actuated the chronograph was made and broken by a tuning-fork which made 200 complete vibrations per second, therefore the spaces between the succeeding peaks of the chronograph curve each represents 0.005 second. A comparison of the movements of the muscle with the tuning-fork curve reveals that about $\frac{5}{100}$ second elapsed between the point *b*, at which the muscle curve began to rise, and *c*, the point at which the full height of the contraction was reached, and that about $\frac{7}{100}$ second was occupied by the return of the muscle curve from *c* to point *d*, at the level from which it started. The muscle employed in this experiment was slightly fatigued, and the movements were in consequence a little slower than normal.

Latent Period.—The time that elapses between the moment that a stimulus reaches a muscle and the instant the muscle begins to change its form is called the latent period. In the experiment recorded in Fig. 38 the muscle received the shock at the point *a* on the curve, but the lever did not begin to rise until the point *b* was reached. The latent period as recorded in this experiment was about 0.006 second. The latent period and the time relations of the muscle-curve were first measured by Helmholtz, who introduced the use of the myograph.[1] Helmholtz concluded from his experiments that the latent period for a frog's muscle is about $\frac{1}{100}$ second, that the rise of the curve occupies about $\frac{4}{100}$, and the fall about $\frac{5}{100}$ second, the total time occupying about $\frac{1}{10}$ second. These rates can be considered approximately correct, excepting for the latent period, which has been found by more accurate methods to be considerably shorter. Tigerstedt connected a curarized frog's muscle with a myograph lever, which was so arranged as to break an electric contact at the instant that the muscle made the slightest movement; the break in the electric circuit was recorded on a rapidly revolving drum, by an electro-magnet similar to the chronograph. By this means he found the latent period of a frog's muscle may be as short as 0.004 second. Tigerstedt[2] did not regard this as the true latent period, however; he expressed the belief that the muscle protoplasm must have begun to respond to the excitation much sooner than this. The contraction of the whole muscle is the result of a shortening of each of the myriad of light and dark disks of which each of the muscle-fibres is composed (see Fig. 39). The distance to be traversed by the finest particles of muscle-substance is microscopic, hence the rapidity of the change of form of the whole muscle. Even such a change would require time, however, and it is probable that the muscle protoplasm becomes active before any outward manifestation occurs. That this view is correct has been proved by electrical observations.

When muscle protoplasm passes from a state of rest to one of action it undergoes an alteration in electrical condition. This change can be detected by the galvanometer (Fig. 62, p. 144) or by the capillary electrometer (Fig. 63, p. 146). Burdon Sanderson[3] has found that by the aid of the latter instru-

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[1] *Archiv für Anatomie und Physiologie*, 1850, S. 308.

[2] *Ibid.*, 1885, Suppl. Bd., S. 111.

[3] *Journal of Physiology*, 1898, vol. xxiii. p. 350.

ment an alteration of the electrical condition of the muscle of a frog can be detected less than 0.001 second after the stimulus has been applied to it. Since some slight interval of time must have been lost even by this delicate method, it would seem that muscle protoplasm begins to be active at the instant it is stimulated.

According to this view, muscle-substance has no latent period; nevertheless we can still speak of the latent period of the muscle as a whole. It will be necessary, however, to distinguish between the electrical latent period and the mechanical latent period: by the former we mean the time which elapses between the moment of excitation and the first evidence obtainable of a change in the electrical condition of the muscle; by the latter, the time between excitation and the earliest evidence of movement which can be observed. In the case of the striated muscles of a frog the electrical latent period is less than 0.001 second, and the mechanical about 0.004 second. Mendelssohn[1] estimated the mechanical latent period of the muscles of man to be about 0.008 second. There can be little doubt, however, that this figure is too large.

Bernstein[2] found that if a normal frog's muscle be excited indirectly, by the stimulation of its nerve, the mechanical latent period is somewhat longer than when it is directly excited. Of course a certain length of time is required to transmit the excitation through the length of nerve intervening between the point stimulated and the muscle fibres. If this time be deducted, there still remains a balance of about 0.003 second, which can only be accounted for on the assumption that the motor nerve end-plates require time to excite the muscle-fibres. The motor end-plates are therefore said to have a latent period of 0.002–0.003 second.

The latent period, and the time required for the rise and fall of the myograph curve, are found to be very different not only for the muscles of different animals, but even for the different muscles of the same animal. Moreover, the time relations of the contraction process in each muscle are altered by a great variety of conditions.

Before considering the effect of various influences upon the character of the muscle contraction, let us give a glance at the finer structure of the muscle, and the change of form which the microscopic segments of the muscle-fibre undergo during contraction.

2. Optical Properties of Striated Muscle during Rest and Action.—An ordinary striated muscle is composed of a great number of very long muscle-cells, fibres as they are called, arranged side by side in bundles, the whole being bound together by a fine connective-tissue network. Each muscle-fibre consists of a very delicate elastic sheath, the sarcolemma, which is completely filled with the muscle-substance. Under the microscope the fibres are seen to be striped by alternating light and dark transverse bands, and on focusing, the difference in texture which this suggests is found to extend through

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[1] *Archives de Physiologie*, 1880, 2d series, t. vii. p. 197.

[2] *Untersuchungen über den Erregungsvorgang im Nerven und Muskelsystem*, 1871.

the fibres, *i. e.* the light and dark bands correspond to little disks of substances of different degrees of translucency. More careful study with a high power, shows under certain circumstances other cross markings (see Fig. 39, *A*), the light band is found to be divided in halves by a fine dark line, *Z*, and parallel to it is another faint dark line, *n*, while the dark band, *Q*, is found to have a barely perceptible light line in its centre.

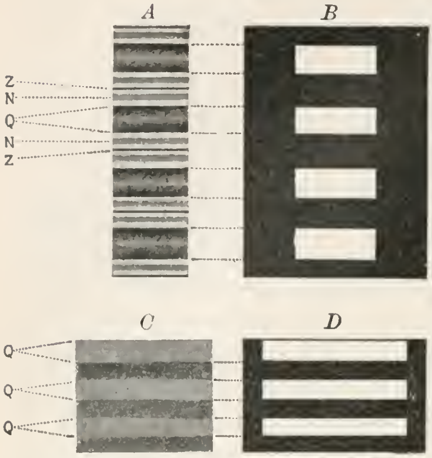

FIG. 39.—Schema of histological structure of muscle-fibre: *A*, resting fibre as seen by ordinary light; *B*, resting fibre seen by polarized light; *C*, contracting fibre by ordinary light; *D*, contracting fibre by polarized light.

The fine dark lines, *Z*, which run through the middle of the light bands, were for a time supposed to be caused by delicate membranes (Krause's membrane), which were thought to stretch through the fibre and to divide it into a series of little compartments, each of which had exactly the same construction. Kuehne chanced to see a minute nematode worm moving along inside a muscle-fibre, and observed that it encountered no obstruction, such as a series of membranes, however delicate, would have caused. As it moved, the particles of muscle-substance closed in behind it, the original structure being completely recovered. This observation did away with the view that the fibre is divided into compartments, but the arrangement shown in Figure 39, *A*, repeats itself throughout the length of the fibre and indicates that it is made up of a vast succession of like parts.

Muscle-substance consists of two materials, which differ in their optical peculiarities and their reaction to stains. If a muscle-fibre be examined by polarized light, it is found that there is a substance in the dark bands which refracts the light doubly, is anisotropic, while the bulk of the substance in the light bands is singly refractive, isotropic (*B*, Fig. 39). The anisotropic substance is found to stain with hæmatoxylin, while the isotropic is not thus stained; on the other hand, the isotropic substance is often colored by chloride of gold, which is not the case with the anisotropic. By means of these reactions it has been possible to ascertain something as to the arrangement of these substances within the muscle-fibre, though the ultimate structure has not been definitely decided. It appears that the isotropic material is the sarcoplasma, which is distributed throughout the fibre and holds imbedded within it the particles of the anisotropic substance, these particles having a definite arrangement. Striated muscle-fibres present not only cross markings, but under favorable conditions longitudinal striations, these being most evident in the dark bands. These longitudinal striations are looked upon with great interest as indicating that the particles of anisotropic material are arranged in long chains as incomplete fibrillæ. According to this view the muscle-fibre is composed of semifluid isotropic substance, in which are the particles of anisotropic material, arranged to form vast numbers of parallel fibrillæ of like structure, and so placed as to give the effect of transverse disks (*Z*, *n*, *Q*, Fig. 39).

When a striated muscle contracts, each of its fibres becomes shorter and thicker, and the same is true of the dark and light disks of which the fibres are composed. If we examine a muscle-fibre which has been fixed by osmic acid at a time when part of it was contracting, we see that in the contracted part the light and dark bands have both become shorter and wider, but that the volume of the dark bands (*Q*, Fig. 39, C) has increased at the expense of the light bands.

Further, the dark bands are seen to be lighter and the light bands darker in the contracted part, while examination with polarized light shows that though the anisotropic substance does not seem to have changed its position, (Fig. 39, *D*), the original dark bands have less and the lighter bands greater refractive power. These appearances would seem to be explained by Engelmann's view that contraction is the result of imbibition of the more fluid part of the sarcoplasm by the anisotropic substance. He has advanced the theory that the cause of the imbibition is the liberation of heat by chemical changes which occur at the instant the muscle is excited. In support of this theory Engelmann[1] showed that dead substance containing anisotropic material, such as a catgut string, can change its form, by imbibition of fluid under the influence of heat, and give a contraction curve in many respects similar to that to be obtained from muscle. This theory of the method of action of the muscle-substance, though attractive, can be accepted only as a working hypothesis, and is not to be regarded as proved. Various other theories have been advanced to explain the connection between the chemical changes which undoubtedly occur during contraction and the alteration of form, but none have been generally accepted. Enough has been said to show that the contraction of the muscle as a whole is the result of a change in the minute elements of the fibrillæ, and that the various conditions which influence the activity of the process of contraction must act chiefly through alterations produced in these little mechanisms.

3. Elasticity of Muscle.—The elasticity and extensibility of muscle are of great importance, for by every form of muscular work the muscle is subjected to a stretching force. Elasticity of muscle is the property by virtue of which it tends to preserve its normal form, and to resist any external force which would act to alter that form. The shape of muscles may be altered by pressure, but the change is one of form and not of bulk; since muscles are largely made up of fluid, their compressibility is inconsiderable. The elasticity of muscles is slight but quite perfect, by which is meant that a muscle yields readily to a stretching force, but on the removal of the force quickly recovers its normal form. Most of the experiments upon muscle elasticity have been made after the muscle had been removed from the body, hence under abnormal

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[1] *Ueber den Ursprung der Muskelkraft*, Leipzig, 1893.

conditions. Under these circumstances it is found that if a number of equal weights be added to a suspended muscle, one after the other, the extension produced is not, like that of an inorganic body such as steel spring, proportional to the weight, but each weight stretches the muscle less than the preceding. If the weights be removed in succession, an elastic recovery is observed, which, although considerable, is incomplete. If the change in the length be recorded by a lever attached to the muscle, the surface being moved along just the same amount after each weight is added or removed, a curve is obtained such as is shown in Fig. 40, *b*. Above this is a record taken in a similar way from a piece of rubber (*a*). The rubber resembles a steel spring in that equal weights stretch it to like amounts, but the elastic recovery, though more complete than that of the muscle, is imperfect.

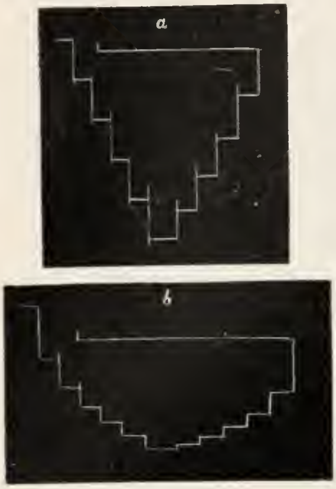

FIG. 40.—*a*, Curve of extensibility and elasticity of a rubber band; *b*, curve of extensibility and elasticity of a sartorius muscle of a frog. The weights employed were 10 grams each. The same length of time was allowed to pass between the adding and subtracting of the weights.

In such an experiment it is found that the full effect of adding the weights, or removing them from the muscle, does not occur immediately, but when a weight is added there is a gradual yielding to the stretching force, and, on the removal of a weight, a gradual recovery of form under the influence of the elasticity. This slow after-action makes it difficult to say just what is to be considered the proper curve of elasticity of muscle, especially as the physiological condition of the muscle is always changing. The elasticity of muscles is dependent on normal physiological conditions, and is altered by death, or by anything which causes a change in the normal constitution of the muscles, as the cutting off of the blood-supply. The dead muscle is less extensible and less elastic than the normal living muscle. Heating, within limits, increases, and cooling decreases the elasticity, possibly by altering the mobility of the semifluid materials of the muscle, and hence changing the internal friction.[1] Contraction is accompanied by increased extensibility, *i. e.* lessened elasticity—and the changes caused by fatigue lessen the elasticity. It is interesting to note in this connection that the elasticity is decreased by weak acid solutions and increased by weak alkaline solutions (Brunton and Cash).[2]

The elasticity of a muscle within the body is generally considered to be more perfect than that of the isolated muscle, but even here one can observe the after-stretching described by Weber and the contraction remainder described by Hermann. Mosso[3] suggests the following experiment on man:

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[1] Blix: *Skandinavisches Archiv für Physiologie*, 1893, iv. S. 392.

[2] *Philosophical Transactions*, 1884, p. 197.

[3] Mosso: *Archives italiennes de Biologie*, 1895, xxv. p. 27.

Place the subject in a sitting position, make the suspended leg immovable by suitable clamps, strap a board to the bottom of the foot, and connect the toe end of the board with a weight by means of a cord passing over a pulley. As the weight is increased or decreased the foot is more or less flexed, and the gastrocnemius muscle is stretched more or less. A pointer fastened to the foot-board moves over a scale and indicates the amount the muscle changes its length when subjected to various weights. Mosso reports that though the curve of elasticity has about the same character as that of isolated frog muscle, the curve of extensibility is different, each of the added weights causing greater amount of stretching. This is probably due to the fact that a muscle within the body is always being influenced by the central nervous system. Its length at any given moment is due not only to its elasticity as compared with that of its antagonist, but also to the strength of the nervous impulses, reflex and voluntary (often unintentional), coming to it. The subject would have to be under an anæsthetic or in very deep sleep for such an experiment to give a true picture of its elasticity. Mosso describes, in fact, movements of the foot accompanying the respirations, due to variations in the tonus impulses coming to the muscles in inspiration and expiration. In spite of the innate difficulties of such an experiment, we can ascertain that in general the conclusions arrived at by studying the isolated muscles of a frog apply to the muscles when in the living body.

The elasticity of a muscle within the normal body suffices to preserve the tension of the muscle under all ordinary conditions. The muscles are attached to the bones under elastic tension, as is shown by the separation of the ends in case a muscle be cut. This elastic tension is very favorable to the action of the muscle, as it takes up the slack and ensures that at the instant the muscle begins to shorten the effect of the change shall be quickly imparted to the bones which it is its function to move. The extensibility of the muscle is a great protection, lessening the danger of rupture of the muscle-fibres and ligaments, and the injury of joints when the muscles contract suddenly and vigorously, or when they are subjected to sudden strains by external forces. The importance of extensibility and elasticity to muscles which act as antagonists is evident. When a muscle suddenly contracts against a resisting force such as the inertia of a heavy weight, the energy of contraction, which puts the muscle on the stretch, is temporarily stored in it as elastic force, and as the weight yields to the strain, is given out again; thus the effect of the contraction force is tempered, the application of the suddenly developed energy being prolonged and softened. Elasticity is very important to the function of the non-striated muscles of the blood-vessels, bladder, intestine, etc. This is especially true of the sphincter muscles, for it is an important factor in securing the continued tension characteristic of their action.

4. Influences which Affect the Activity and Character of the Contraction.—(*a*) *The Character of the Muscle.*—Attention has been called to the fact that irritability and conductivity may be different not only in different kinds of muscle-tissue, and in muscles of different animals, but even in similar kinds of muscle-tissue in the different muscles of the same animal; the same may be said of contractility. Although irritability, conductivity, and contractility are to be regarded as different properties of muscle protoplasm, they are usually found to be developed to a corresponding degree in each muscle. Those forms of muscle which require for their excitation irritants of slow and prolonged action, are found to conduct slowly and to make slow and long-drawn-out contractions, and muscles which are excited by irritants acting rapidly and briefly are noted for the quickness with which they contract and relax.

Differences in the activity of the contraction process are made evident by the duration of single contractions of different forms of muscle-tissue. The duration of the contraction of the striated muscles of different animals differs greatly, *e. g.* of the frog $\frac{1}{10}$ second, of the turtle 1 second, of certain insects only $\frac{1}{300}$ second. Even muscles of apparently the same kind in the same animal exhibit different degrees of activity. Cash[1] reports the following differences in the duration of the contractions of different striated muscles of a frog in fractions of a second: Hyoglossus, 0.205; rectus abdominis, 0.170; gastrocnemius, 0.120; semimembranosus, 0.108; triceps femoris, 0.104. Similar differences are found to exist between different muscles in other animals —in the turtle, for instance, as is shown by the myograms in Fig. 41.

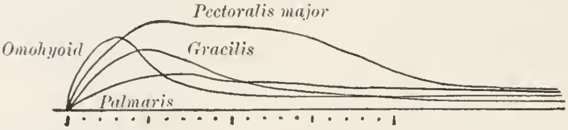

FIG. 41.—Records of maximal isotonic contractions of four different muscles from a turtle, each weighted with 30 grams: Pectoralis major; omohyoid; gracilis; palmaris. The dots mark $\frac{1}{5}$ second, and the longer marks seconds (after Cash).[2]

It is interesting to connect the rate of the contraction process in different muscles with their function. The omohyoid muscle of the turtle is capable of comparatively rapid contractions, and the action of this muscle is to draw back the head beneath the projecting shell; the pectoralis, on the other hand, although strong, contracts slowly; it is a muscle of locomotion and has to move the heavy body of the animal. Unstriated muscles, which are remarkable for the slowness and the duration of their contractions, are found chiefly in the walls of the intestines, blood-vessels, etc., which require to remain in a state of continued contraction for considerable periods and do not need to alter rapidly. It is the business of the heart-muscle to drive fluids often against considerable resistance, and a strong, not too rapid, slightly prolonged contraction, such as is peculiar to it, would be best adapted to its function. The bulk of the muscles of the bodies of warm-blooded animals are capable of rapid contraction and relaxation, but the rate normal to the muscle is found to vary with the form of work to be done. The muscles which control the vocal organs, for instance, have a very rapid rate of relaxation as well as of con-

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[1] *Archiv für Anatomie und Physiologie*, 1880, Suppl. Bd., S. 147.

[2] *Op. cit.*, S. 157.

traction. The muscles which move the bones appear to have different rates of contraction and relaxation according to the weight of the parts to be moved; those which control the lighter parts, as the hand, being capable of rapid contractions, while those which have to overcome the inertia of heavier parts, to which rapidity of action would be a positive disadvantage, react more slowly. In general, where rapid, brief, and vigorous contractions are required, pale striated muscles are found; where more prolonged contractions are needed, red striated muscles occur. The accompanying myograms (Fig. 42) illustrate the difference in the rate of contractions of pale and red striated muscles of the rabbit. Ranvier says the latent period of red muscle of rabbit is four times as long as that of the pale; and Tigerstedt states the latent period of red muscles of the frog to be 0.02 second and of the pale muscles 0.005 second.

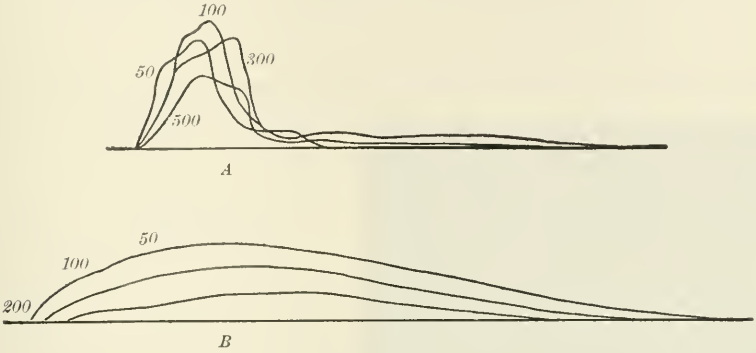

FIG. 42.—*A*, maximal contractions of the gastrocnemius medialis of the rabbit (pale muscle), weighted with 50, 100, 300, and 500 grams; *B*, maximal contractions of the soleus of the rabbit (red muscle), weighted with 50, 100, and 200 grams (after Cash).

Pale and red striated fibres are found united in the same muscle in certain instances, and in these cases it is supposed that the former, which are capable of very rapid and powerful but short-lived contractions, start the movement, while the slower red muscles continue it. Bottazzi[1] would explain many of the peculiarities of muscle contraction on the theory that both the isotropic and anisotropic substances are contractile, and that they react differently under varying conditions. The isotropic substance, the sarcoplasma, is responsible for the slow, prolonged movements of the muscle and the anisotropic substance for the rapid, brief movements. In ordinary contractions they both act, though to different degrees.

(*b*) *Effect of Tension Caused by Weights and Myograph-lever on the Extent and Course of the Contraction.*—As we have seen, the rate of the contraction of an ordinary striated muscle is much too rapid to be followed by the eye, and to study the course of the change in form it is necessary to employ some kind of recording mechanism. Every mechanical device for recording the movements of the muscle has inertia, and, if given motion, acquires momen-

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[1] Bottazzi: *Journal of Physiology*, 1897, xxi. p. 1.

tum. Both of these factors would tend to alter the shape of the record, and the more the greater the weight of the recording apparatus.

A weight, or tension, can be applied to a muscle in various ways, and the form of the contraction will be correspondingly changed. If a muscle is made to work with a considerable weight hanging on it, we speak of it as *loaded;* if the weight be connected with the muscle, but so supported that it does not pull on it until the muscle begins to shorten, the muscle is said to be *after-loaded;* if the weight is the same throughout the contraction, as when the muscle has only to lift a light weight, applied close to the axis of the lever, the contraction is said to be *isotonic;* if on the other hand the contracting muscle is made to work against a strong spring, so that it can shorten very little, *i. e.* has almost the same length throughout the contraction, the contraction is said to be *isometric.*[1] The shape of the myogram recorded as a result of the same stimulus would evidently be very different in these four cases. The effect of a weight to alter the myogram is illustrated in the record given in Figure 43. Increasing the weight prolonged the latent period, and lessened the height and duration of the contractions.

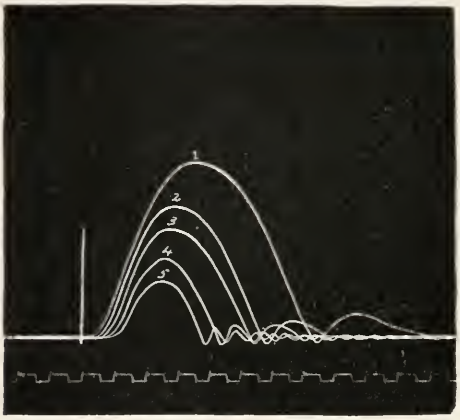

FIG. 43.—Effect of the weight upon the form of the myogram. The gastrocnemius muscle of a frog excited by maximal breaking induction shocks five times, the weight being increased after each contraction, and in the intervals supported at the normal resting length of the muscle; *i. e.* the muscle was after-loaded: 1, muscle weighted only with very light lever; 2, weight five grams; 3, ten grams; 4, twenty-five grams; 5, fifty grams. The perpendicular line marks the moment of excitation. The time is recorded at the bottom of the curve by a chronograph, actuated by a tuning-fork vibrating 50 times per second.

The alterations liable to occur in the form of the myogram by the isotonic method, as a result of the mechanical conditions under which the work is done, are—

(1) *Prolongation of the latent period.* There can be no movement of the lever until the inertia of the weight has been overcome, and the first effect of the contraction is to stretch the muscle, a part of the energy of contraction being changed to elastic force, which on the recoil assists in raising the weight. Thus the myogram may fail to reveal the instant that the contraction process starts. Indeed, inasmuch as tension increases the activity of muscle protoplasm, it is probable that the presence of the weight really hastens the liberation of energy at the same time that it delays the recording of the contraction.

(2) *Alteration in the shape of the ascending limb of the myograph curve.* The weight will either lessen the rate at which the curve rises and decrease the height, or, if the weight be not great, it may acquire a velocity from the energy suddenly imparted to it by the muscle, which will carry the record higher

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[1] Fick: *Mechanische Arbeit und Wärmeentwickelung bei der Muskelthätigkeit,* Leipzig, 1882.

than the absolute contraction of the muscle. The part of the myogram corresponding to the height of the contraction of the muscle can be distinguished from that due to the throw of the lever by a method suggested by Kaiser.[1] If the rising lever strikes a check, it remains in contact with the check as long as the muscle continues to contract, but falls immediately if not held there by the contraction process. By varying the height of the check, the point corresponding to the true contraction height can be ascertained.

(3) *The fall of the curve may be altered.* The weight, suddenly freed by the rapidly relaxing muscle, may acquire a velocity in falling which will stretch the muscle-tissue, carry the record lower than the actual relaxation of the muscle would warrant, and lead to the development of artificial elastic after-oscillations. It must not be supposed, however, that the relaxation of the muscle is merely a passive affair, and that it returns to its original shape because, when it ceases to develop energy, it is stretched by the weight. The relaxation, like the contraction process, is an active event, and it is antagonistic to the contraction process.[2]

These sources of error can be in part overcome by the employment of an exceedingly light, stiff writing-lever, and by bringing the necessary tension on the muscle by placing the extending weight very near the axis of the lever, so that it shall move but little and hence acquire little velocity.

(*c*) *Effect of Rate of Excitation on Height and Form of Muscular Contraction.*—If a muscle be excited a number of times by exactly the same irritant and under the same external conditions, the amount and course of each of the contractions should be exactly the same, provided the condition of the muscle itself remains the same. The condition of the muscle is, however, altered every time it is excited to contraction, and each contraction leaves behind it an after-effect. This altered condition is not permanent; as we have seen, increased katabolism is accompanied by increased anabolism, and, if the excitations do not follow each other too rapidly, the katabolic changes occurring in contraction are compensated for by anabolic changes during the succeeding interval of rest. Normally, a muscle, under the restorative influence of the blood, rapidly recovers from the alterations produced by the contraction process, and, therefore, if not excited too frequently, will give, other things being equal, the same response each time it is called into action. The best illustration of this is the heart, which continues to beat at a regular rate throughout the life of the individual. Tiegel found that one of the skeletal muscles of a frog, while in the normal body, can make more than a thousand contractions in response to artificial stimuli without showing fatigue; finally the effect of the work shows itself in a lessening of the power to contract. Every muscle contains a surplus of energy-holding compounds and also substances capable of neutralizing waste products, and even a muscle which has been separated from the rest of the body retains for a considerable time the ability to recover from the effects of excitation. It is evident that when a

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[1] Kaiser: *Zeitschrift für Biologie*, 1896, xxxiii. S. 157, 360.

[2] Fick, v. Kries, and others.

muscle is excited repeatedly, a certain interval of rest must be permitted between the succeeding excitations if its normal condition is to be maintained, and that the more extensive the chemical changes produced by the excitations the longer must be the periods allowed for recovery. This being the case, the rate of excitation and consequent length of the interval of rest will have a great effect upon the condition of the muscle and its capacity for work.

(1) *Effect of Frequent Excitations on the Height of Separate Muscular Contractions.*—Other things being equal, the height to which a muscle can contract when excited by a given irritant can be taken as an index of its capacity to do work, and if a muscle be excited many times in succession, the effect of action upon the strength of the contraction process, the endurance, and the coming on of fatigue can be estimated from the height of the succeeding contractions. One might expect that every contraction would tend to fatigue and to lessen the power of the muscle, but almost the first effect of action is to increase the irritability and mobility of muscle protoplasm.

Introductory and Staircase Contractions.—The peculiar effect of action to increase muscular activity was first observed by Bowditch,[1] when studying the effect of excitations upon the heart. He found that repeated excitations of equal strength applied to the ventricle of a frog's heart caused a series of contractions each of which was greater than the preceding. If the contractions were recorded on a regularly moving surface, the summits of the successive contractions were seen to rise one above the other like a flight of steps. This peculiar phenomenon received the name of the "staircase contractions" (see Fig. 44).

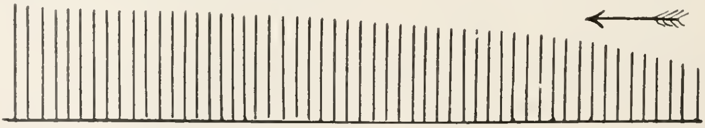

FIG. 44.—Staircase contractions of a frog's ventricle in response to a series of like stimuli, written on a regularly revolving drum by the float of a water manometer connected with the chamber of the ventricle (after Bowditch). The record is to be read from right to left.

This effect of repeated excitations was later observed by Tiegel,[2] on the skeletal muscles of frogs; by Rossbach,[3] on the muscles of warm-blooded animals, and by Romanes[4] on the contractile tissues of Medusæ.

The following series of contractions (Fig. 45), which closely resembles the above, was obtained from the gastrocnemius muscle of a frog, excited at a regular rate by a series of equal breaking induction shocks.

The contractions in Figure 45 did not begin to increase in height immediately; on the contrary, each of the first four contractions was slightly lower than the one which preceded it. A decline in the height of the first three or four contractions is the rule when a normal resting muscle is called into action

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[1] *Berichte der königlichen sächsischen Gesellschaft der Wissenschaft*, 1871. [2] *Ibid.*, 1875.

[3] *Pflüger's Archiv*, 1882, 1884, Bd. xiii., xv.

[4] Romanes: *Jelly-fish and Star-fish*, International Science Series, p. 54.

(see Figs. 46 and 49), and these contractions at the beginning of a series have received the name of the "introductory contractions." The introductory contractions appear to indicate that the first effect of action is to lessen irritability, or that anabolic changes are too slow to compensate for katabolic changes, and each of the first few contractions leaves behind it a fatigue effect. It is not long, however, before the influence of activity to heighten anabolism and increase irritability shows itself in the growth of the height of the succeeding contractions, and the "staircase contractions" are observed. This growth of the height of contractions must necessarily reach a limit, and the amount of increase is found to gradually lessen until the succeeding contractions have the same height. Sometimes the full height of the staircase is not reached before more than a hundred contractions have been made. These maximal contractions may be repeated many times; sooner or later, however, an antagonistic effect of the work manifests itself and the height of the contractions begins to lessen.

Effect of Fatigue.—A decline in the height of the contractions is an evidence of fatigue, and indicates that anabolism is failing to keep pace with katabolism, or that the waste products which result from the work are collecting faster than they can be removed or neutralized and are exerting a paralyzing influence on the muscle protoplasm (see p. 70). From this time on, the height of the succeeding contractions continually lessens, and often with great regularity, so that a line drawn so as to connect the summits of the declining contractions, the "curve of fatigue," as it is called, may be a straight line. In the experiment, parts of the record of which are reproduced in Figure 46, an isolated gastrocnemius muscle of a frog was excited with maximal breaking induction shocks at the rate of 25 times a minute for about one and one-half hours; the contractions were isotonic, and the total weight of lever and load did not exceed 20 grams; the records of the succeeding contractions were recorded on a slowly moving cylinder. The experiment consisted of two parts—in the first 66 contractions, in the second over 1700 contractions were made; an interval of rest of five minutes was permitted between the two series.

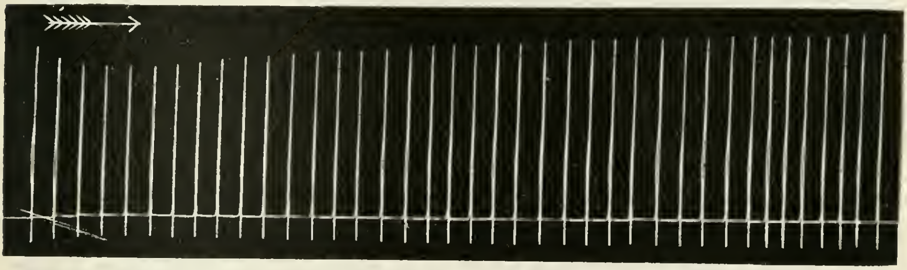

FIG. 45.—Staircase contractions of gastrocnemius muscle of a frog, excited once every two seconds by strong breaking induction shocks.

In the first part of the experiment there was a decline in the height of the contractions for the first five contractions, the "introductory contractions," then during the next sixty-one contractions a gradual rise in the height of the contractions, the "staircase contractions." These phenomena repeat themselves in the second part of the experiment, that following the interval of rest. The contractions at the beginning of the second series were not so high as those at the end of the first series, though somewhat higher than those seen at the beginning of the first series; the rest of five minutes was not sufficient to entirely do away with the stimulating influence of the preceding work. The contractions of the second series took the following course: The first four introductory contractions gradually declined, then came the staircase contractions, which continued to rise until the 100th contraction, when a gradual lessening of the height of the contractions began. This decline continued throughout the long series of more than 1700 contractions given in the record, and, had the experiment been continued, would have undoubtedly gone on until the power was completely lost. The curve of fatigue was not a straight line, but fell somewhat more rapidly during the early part of the work than toward the end.

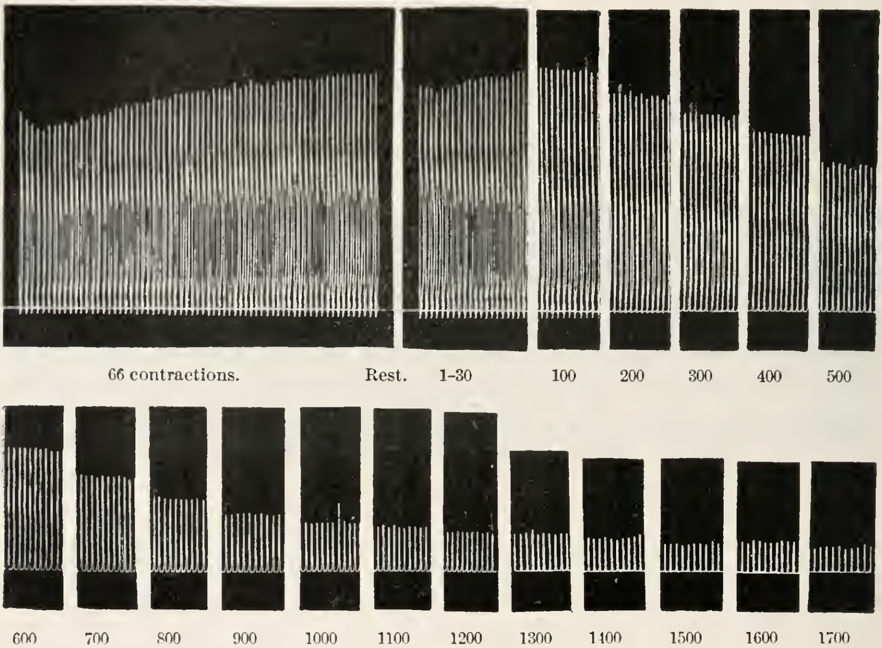

Fig. 46.—Effect of fatigue on the height of muscular contractions. The figure is a reproduction of parts of a record of over 1700 contractions made by an isolated gastrocnemius muscle of a frog. The contractions were isotonic, the weight being about 20 grams. The stimuli were maximal breaking induction shocks, and were applied directly to the muscle, at the rate of 25 per minute. Between the first group of 66 contractions and the following groups a rest of five minutes was given; after this rest the work was continued without interruption for about one and a half hours. The second group of contractions, that immediately following the period of rest, contains the first twenty contractions of the new series; the next group the 100th to the 110th; the next the 200th to the 210th, and so on.

That the peculiar changes in the height of the contractions which occur in the early part of an experiment such as that which we have described are not abnormal, and the result of the artificial conditions under which the work is done, is shown not only by the fact that they are observed when a muscle which has its normal blood-supply is rhythmically excited to a large number of contractions, but by the personal experience of every one accustomed to violent muscular exercise. Everyone is conscious that he cannot put out the greatest muscular effort until he has "warmed up to the work." The runner precedes the race by a short run; the oarsman takes a short pull before going to the line; in all the sports one sees the contestants making movements to "limber up" before they enter upon the work of the game. These preliminary movements are performed not only to put the muscles in better condition for action, but to ensure more accurate co-ordination—that is to say, the facts ascertained for the muscle can be carried over to the central nervous system. The finely adjusted activities of the nerve-cells which control the muscles reach their perfection only after repeated action.

In such experiments as that recorded in Figure 46 the record shows to a remarkable degree the fact that at any given time the muscle has a definite capacity for work. A suitable explanation of this is lacking. The correspondence in the height of the contractions of the same group, and the difference in the height of different groups of contractions, must be attributed to the existence within the muscle-cell of some automatic mechanism which regulates the liberation of energy and which has its activity greatly influenced by the alterations which result from action. Whether this supposed automatic regulatory mechanism controls both the preparation of the final material from which the energy displayed by the muscle is liberated, and the amount of the explosive change which results from the application of the irritant, cannot be definitely said.

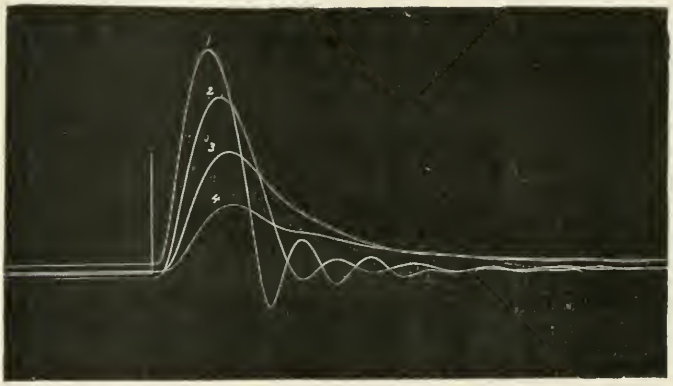

FIG. 47.—Effect of excitation upon the form of separate contractions. In this experiment the records of the muscular contractions were taken upon a rapidly revolving drum. The muscle was the gastrocnemius of the frog; the contractions were isotonic; the weight was very light, about 10 grams; the stimuli were maximal breaking induction shocks; and the rate of stimulation was twenty-three per minute. 1 marks the first contraction; 2, the 100th; 3, the 200th; 4, the 300th. The muscle was excited automatically by an arrangement carried by the drum, and the excitation was always given when a definite part of the surface of the drum was opposite the point of the lever which recorded the contractions.

(2) *Effect of Frequent Excitations upon the Form of Separate Contractions.*—The effect of activity is not only observable in the change in the height

of the muscular contractions, but in the length of the latent period, in the rate at which the muscle shortens, and in the rate at which the muscle relaxes. The effect of a large number of separate contractions, made in quick succession, upon the rate at which the muscle changes its form during contraction, is illustrated in the myograms reproduced in Figure 47.

In Figure 47 only the 1st, 100th, 200th, and 300th contractions were recorded. The perpendicular line marks the point at which the stimulus was given. In this experiment the latent period for each of the succeeding contractions is seen to be longer; the height is lessened; the rise of the curve of contraction is slowed and the curve of relaxation is even more prolonged. These and certain other changes are to be observed in the records of Figure 48, which were taken in an experiment made under the same conditions as the last, except that the rate of excitation was 80 per minute, instead of 23, as in the preceding experiment, and the record of every 50th contraction was recorded.

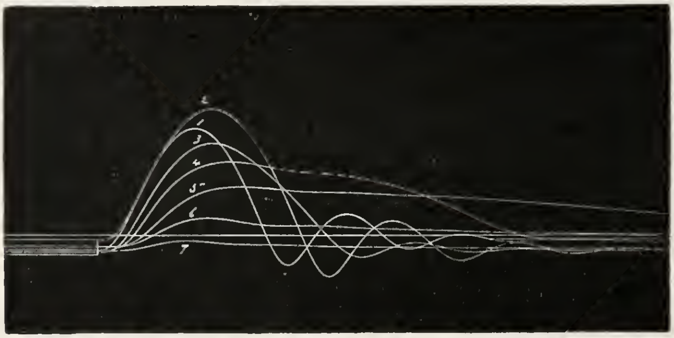

FIG. 48.—Effect of frequent excitation on the form of separate contractions. The method employed to obtain this record is the same as in the preceding experiment, except that the drum is revolving more rapidly, and every 50th contraction is recorded: 1 marks the first contraction; 2, the 50th: 3, the 100th; 4, the 150th; 5, the 200th; 6, the 250th; 7, the 300th.

A comparison of the first with the 50th contraction gives a number of points of interest. The stimulating effect of action upon the contraction process is shown by the fact that the latent period of the 50th (2 of Fig. 48) is shorter than that of the first, the rise of the curve is somewhat steeper, and the height is considerably greater. It is noticeable, however, that the crest is prolonged, and consequently the total length of the contraction is increased. Such a prolongation of the contraction is known as "Contracture." In considering the greater activity of the contraction process of this 50th contraction as compared with the first, we must recall that it represents one of a series of staircase contractions, such as we noticed in Figure 46. If we examine the 100th contraction (3 of Fig. 48), we see the evidences of the beginning of fatigue; although the latent period is nearly as quick as in the first, the rise of the curve is less rapid, the height is less, and rate of relaxation is very much slowed. These changes are to be seen in a more marked degree in the 150th contraction (4 of Fig. 48), and the prolongation of the crest of the contraction and the decreased rate of relaxation are particularly noticeable. The same sort of differences is to be observed in the later contractions. By still more rapid rates of excitation these alterations in the contraction curve are not only exaggerated, but develop more quickly, and play a very important part in producing the peculiar form of continued contraction known as tetanus.

Lee[1] states that the slowing of the contraction process, which is comparatively slight in the muscles of the frog, is very marked in the muscles of the turtle, but practically absent from the white muscles of the cat. Moreover, the prolongation of the relaxation which is very noticeable in the case of the muscles of frogs and turtles, is very slight in those of the cat. Contracture effects have, however, been seen on both the red and pale muscles of the rabbit and on the muscles of man. Although the muscles of different animals show certain peculiarities, the facts illustrated in the above experiments can be considered as in general true of most striated muscles.

(3) *Effect of Frequent Excitations to Produce Tetanus.*—As we have seen, the normal muscle the first time that it is excited relaxes almost as quickly as it contracts, but if it be excited rhythmically a number of times a minute, gradually loses its power of rapid relaxation. The tendency to remain contracted begins to show itself in a prolongation of the crest of the contraction curve, even before fatigue comes on, and increases for a considerable time in spite of the effect of fatigue in lessening the height of the contractions. If a skeletal muscle of a frog be excited many times, at a rate of about once every two seconds, the gradual increase in the duration of the contractions will have the effect of preventing the muscle from returning to its normal length in the intervals between the succeeding stimuli, for contraction will be excited before relaxation is complete. As is shown in the record of the experiment reproduced in Figure 49, there will come a time in the work when the base-line connecting the lower extremities of the succeeding myograms will be seen to rise in the form of a curve, the change being at first gradual, then more and more rapid, and then again gradual (see *b*, Fig. 49). The effect of the change in the power to relax is to make it appear as if the muscle were the seat of two contraction processes, the one acting continuously, the other intermittently in response to the successive excitations. Such a condition as that exhibited in section *c*, Figure 49, is spoken of as an incomplete tetanus, complete tetanus being a condition of continuous contraction caused by rhythmical excitations, in which none of the separate contraction movements are visible. In complete tetanus the muscle writes an unbroken curve.

The slowing of the relaxation of the muscle and consequent state of continued shortening which is to be seen in the latter part of the above experiment is the result of the developing contracture. The amount of contracture increases, within limits, with the increase in the strength and rate of excitation. The intensity and rate of stimulation required for the production of this condition depend very largely upon the character of the muscle and its condition at the time. In the experiment recorded in Figure 50 the development of the condition of contracture was more marked than in the

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[1] Lee: *American Journal of Physiology*, 1899, ii. 3, p. 11.

above experiment, and the resulting condition of continued contraction caused first incomplete and finally complete tetanus.

Although frequent excitations appear to be essential to the development of contracture, it is not to be considered a fatigue effect, since the contracted state which it produces may be increasing at the time that fatigue is lessening the height of the ordinary contraction movements, and since the form of contraction peculiar to contracture is itself seen to lessen as fatigue becomes excessive. Both of these facts are illustrated in Figure 50, but are more strikingly shown in Figure 51, in which a more rapid rate of excitation was used. The effect of fatigue to prolong muscular contractions and the relation of contracture to fatigue effects will be considered later (see p. 130).

The record in Figure 51 shows many points of interest: *a* to *b*, a rapidly developing *staircase*, which is accompanied by a rising of the base line, which indicates that contracture began to make itself felt from the moment the work began; *b* to *c*, a rapid and then a gradual fall in the height of contractions due to *fatigue effects; c* to *d*, a rise in the top of the curve in spite of the lessening height of the contractions, due to the increasing *contracture; d* to *e*,

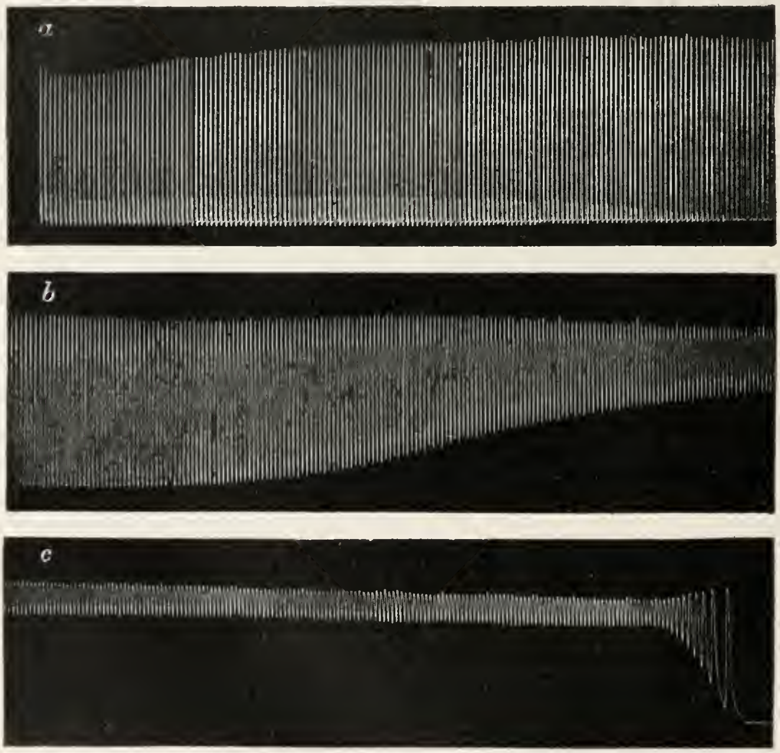

Fig. 49.—Effect of frequent stimuli to gradually produce incomplete tetanus. Series of isotonic contractions of a gastrocnemius muscle of a frog, excited once every two seconds by strong breaking induction shocks. Only a part of the record is shown, 70 contractions have been omitted between the end of the section marked *a* and the beginning of section *b*, and 200 contractions between the end of section *b* and the beginning of *c*. The increase in the extent of the relaxations seen at the close of the record was due to the slowing of the rate of excitations at that time.

a gradual fall of the curve of incomplete tetanus, due to the effect of *fatigue* on the contracture; *e*, complete tetanus, but continued gradual *decline* in the height of the curve under the influence of fatigue.

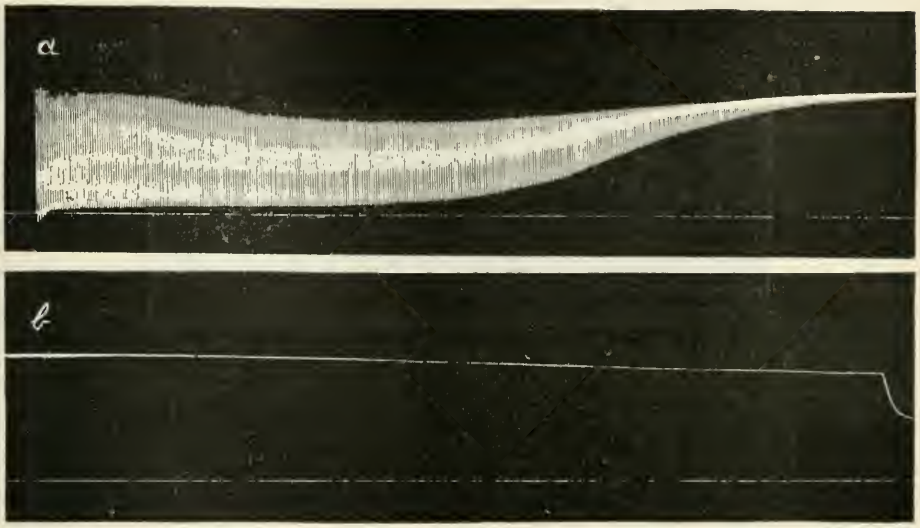

FIG. 50.—Effect of frequent excitations to gradually produce tetanus. Experiment on a gastrocnemius muscle of a frog, similar to the last. The weight was only 10 grams. The rate of excitation was 100 per minute. This muscle had been worked a short time before this series of contractions was taken, and, as a result, the introductory and staircase contractions were absent and contracture began much sooner than in the experiment recorded in Figure 48. The record in section *b* is a continuation of that in section *a*.

The following experiment, Figure 52, differs from those which have preceded it, in that the muscle, instead of being directly excited, was stimulated indirectly by irritation of its nerve. Each shock applied to the nerve was represented by a separate contraction process in the muscle. The experiment illustrates well the combined effect of the *staircase* and the *contracture* to raise the height of the contractions. On account of the more rapid rate of excitation, the contracture came on more quickly than in the preceding experiments; it did

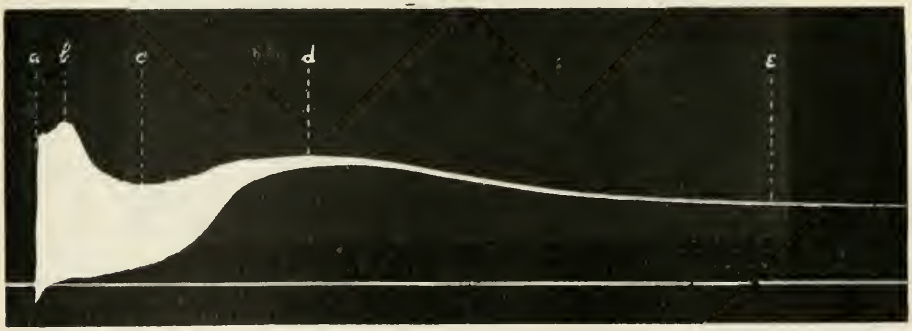

FIG. 51.—Development and fatigue of contracture. Experiment on a gastrocnemius muscle of a frog. The weight was 10 grams. As in the preceding experiments strong maximal breaking induction shocks were used to excite. The rate of excitation was 5 per second. The record appears as a silhouette for the reason that the drum was moving very slowly.

not become sufficient during the few seconds that this experiment lasted to prevent the separate relaxations from being seen, and an incomplete tetanus was the result.

In the experiment the record of which is given in Figure 53, the muscle was directly stimulated, and the rate of excitation was rapid, 33 per second. Not even this rate sufficed to cause complete tetanus, and the crest of the curve shows fine waves, which represent the separate contractions the combined effect of which resulted in the almost unbroken curve seen in the record. Had the rate been a little more rapid, no waves could have been detected and the tetanus would have been complete from the start. The effects of the staircase and contracture are merged into one another, and a very rapid high rise of the curve of contraction is the result. It is noticeable that the summit of the curve is rising throughout the experiment, owing to the increasing contracture.

FIG. 52.—Development of incomplete tetanus and contracture, by indirect stimulation. A gastrocnemius muscle of a frog was indirectly stimulated by breaking induction shocks, of medium strength, applied to the sciatic nerve. The rate was about 8 per second, as shown by comparison of the seconds traced at the bottom of the figure with the oscillations caused by the separate contractions. The weight was somewhat heavier than in the preceding experiment. The drum was revolving much faster than in the other experiments, hence the difference in the apparent duration of the contractions.

It is evident that the condition of contracture which is developed in a rapidly stimulated muscle will tend to maintain a condition of continuous contraction, there being no opportunity for the muscle to relax in the intervals between the succeeding excitations.

FIG. 53.—Effect of rapid excitations to produce tetanus. Experiment with a gastrocnemius muscle of a frog, excited directly, with breaking induction shocks of medium strength, at the rate of 33 per second. The weight was about 15 grams. The drum was moving much more slowly than in the preceding experiment. The time record gives fiftieths of a second.

4. *Explanation of the Great Height of Tetanic Contractions.*—We have now to seek an explanation of the fact that a muscle when tetanized will con-

tract much higher than it will as a result of a single excitation. As we have seen, repeated excitations cause, in the case of a fresh muscle, a gradual increase in irritability and consequently a gradual rise in the height of the succeeding contractions, but the staircase sooner or later reaches its upper limit, and will not alone account for the great shortening which occurs in tetanus.

Effect of Two Rapidly Following Excitations.—Helmholtz was the first to investigate the effect of rate of excitation on the height of combined contractions. For the sake of simplicity, he excited a muscle with only two breaking induction shocks, of the same strength, and observed the effect of varying the interval between these two excitations. He concluded that if the second stimulus is given during the latent period of the first contraction, the effect is the same as if the muscle has received but one shock; if the second shock be applied at some time during the contraction excited by the first, the second contraction behaves as if the amount of contraction present when it begins were the resting state of the muscle, *i. e.* the condition of activity caused by the first shock has no influence on the amount of activity caused by the second, but the height of the second contraction is simply added to the amount of the first contraction present. Were this rule correct, as a result of this summation, if the second contraction occurred when the first was at its height, the sum of the two contractions would be double the height of either contraction taken by itself.

Helmholtz' conclusion, that the condition of activity awakened by the first excitation has no effect upon that caused by the second excitation, has not been substantiated by later observers. Von Kries[1] has found that the presence of the first contraction hastens the development of the contraction process resulting from the second excitation; and Von Frey[2] has ascertained that Helmholtz's rule of summation applies only to weighted muscles. In the case of unweighted muscles the summation effect is greatest when the second contraction starts during the period of developing energy caused by the first excitation, *i. e.* during the rise of the first contraction. If the second contraction starts during the period of relaxation of the first, the second may be not even as high as when occurring alone (see Fig. 54).

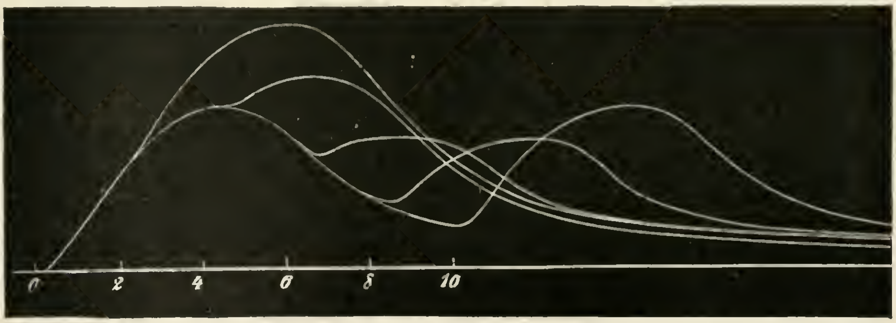

FIG. 54.—A schema of the effect of double excitations upon the gracilis muscle of a frog, by different intervals of excitation. To obtain this figure, the results of different experiments were superimposed (after Von Frey).

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[1] *Archiv für Anatomie und Physiologie*, 1888.

[2] *Ibid.*, S. 213.

The fact that the second contraction is higher if it starts during the ascent of the first, may be explained as due to a summation of the condition of excitation awakened by the two irritants, and hence the liberation of a greater amount of energy. Nevertheless, the increased irritability, indicated by staircase contractions, and the summation of excitation effects which occur by rapidly repeated excitations, shown by the above experiment, do not suffice to wholly explain the great shortening of the muscle seen in tetanus. Helmholtz' idea, that there is a support afforded by the first contraction to the second, must also play an important part, and we must turn to this for the completion of the explanation of the great height acquired by the tetanus curve.

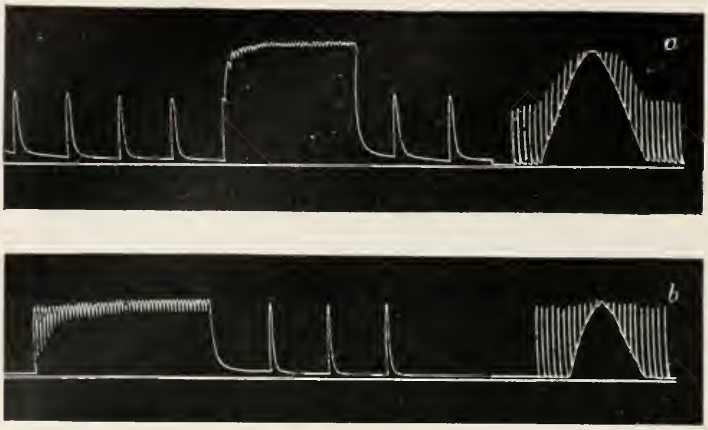

Fig. 55.—Effect of support on height of contractions (after Von Frey): *a*, gastrocnemius muscle of a frog, separate contractions, tetanus, separate contractions, aud group of supported contractions; weight 10.5 grams; *b*, the same, by weight of 0.5 grams.

Effect of Support on the Height of Contractions.—Von Kries[1] and Von Frey[2] found that, in general, the shorter the distance the muscle has to raise a weight, the higher it can contract, and that if a muscle be excited at a regular rate, and the support for the weight be raised between each of the succeeding contractions, at a certain height of the support the contractions may be as high as during tetanus (see Fig. 55) This effect can be got with a fresh muscle when the interval between the excitations is such that there can be no summation in Helmholtz' sense.

The importance of this discovery to our understanding of tetanus is very great, for it has been found that if an unsupported muscle be rapidly excited, effects are observed which closely resemble those obtained by the aid of a support; this we have seen in the experiments recorded in Figures 50, 51, p. 119. After a certain amount of excitation, a change occurs in the condition of a muscle, owing to which it acts as if it had received an upward push, and as if a new force had been developed within it, which aids the ordinary contraction process in raising the weight. The new aid to high contraction is the support afforded by the developing condition of contracture. That con-

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[1] *Archiv für Anatomie und Physiologie*, 1886.

[2] *Ibid.*, 1887.

tracture offers an internal support to the muscle, and raises the total height of the contraction curve just as von Frey found an external support to do, can be seen in Figure 57.

5. *Effect of Gradually Increasing the Rate of Excitation.*—One of the most instructive methods of exciting tetanus is to send into the muscle a series of breaking induction shocks of medium intensity, at a gradually increasing rate. The record of such an experiment has been reproduced in Figure 56.

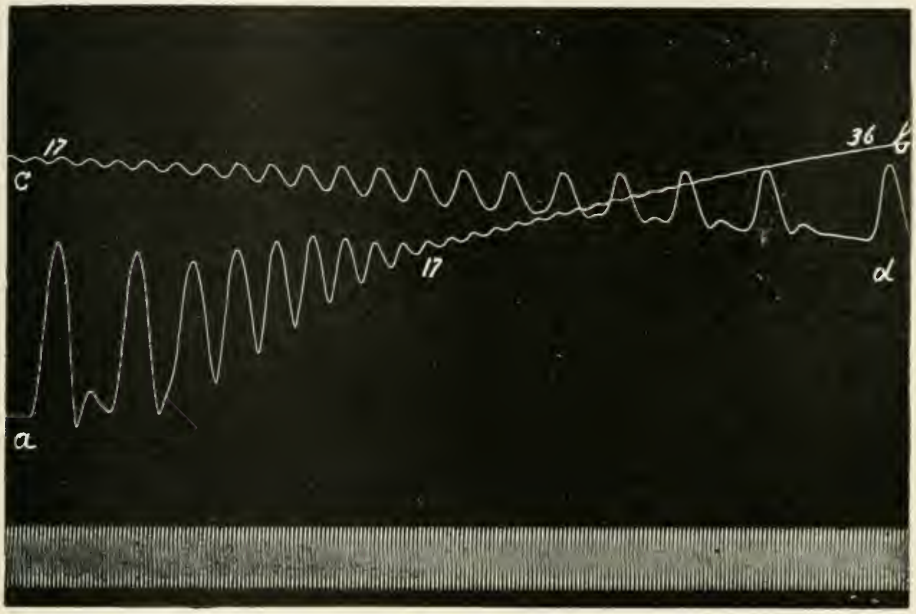

FIG. 56.—Effect of a gradually increasing rate of excitation. Excitation of a gastrocnemius muscle of a frog with breaking induction shocks of medium strength. The time was recorded directly, by a tuning-fork making 100 vibrations per second. The rate of excitation was gradually increased, and then gradually decreased. The ascending curve, *a–b*, shows the effect of increasing, and the descending curve, *c–d*, of decreasing the rate of stimulation. Excitation was given by means of a special mechanism for interrupting the primary circuit of an induction apparatus and at the same time short-circuiting the making shocks. This interrupter was run by an electric motor which was allowed to speed up slowly, and was slowed down gradually.

At the beginning of the experiment, *a*, one complete contraction with a wave of elastic after-vibration was recorded; this was followed by two contractions of less height, "introductory contractions;" then came three contractions each of which was higher than the preceding, "staircase contractions;" these were followed by three contractions, which, in spite of the developing contracture, were of less height, "fatigue effect." The rate of excitation at this place was about 17 per second. From this point on, the developing contracture supported the muscle more and more and the contraction waves became less and less, until finally, when the rate had become 36 a second, the effect of the separate stimuli could scarcely be detected, although the curve continued to rise. This is as far as the record shows, but the rate was increased still further, and the contraction curve continued to rise, although less and less, until finally an almost straight, unbroken line was drawn. After a little time this was seen to begin to fall, the contracture yielding to the effect of fatigue.

As the drum had nearly revolved to the place at which the experiment had been begun, the rate of excitation was then slowly decreased. With the lessening rate, the curve fell more and more rapidly, and oscillations began to show themselves. The character of the record during the rest of the experiment is shown in the curve *c–d*, Figure 56. At *c* the rate was about 17, and at *d* it was so slow that separate contractions were recorded, nevertheless the curve as a whole kept up. Indeed, even after the excitation had altogether ceased, the muscle maintained a partially contracted state for a considerable time, on account of the contracture effect, which only gradually passed off.

6. *Summary of the Effects of Rapid Excitation which produce Tetanus.*—Muscle-tetanus is the result of the combined action of a great many different factors, but the essential condition is that the muscle shall be excited at short intervals, so that the effect of each excitation shall have an influence on the one to follow it. This influence is exerted in several different ways: 1. Increase of irritability resulting from action, and leading to the production of staircase contractions; 2. Summation of excitation effects, as when each of the succeeding stimuli begins to act before the contraction process excited by its predecessor has ceased; 3. Support given by the contracting muscle to itself, especially the support offered by contracture.

The experiment, the record of which is reproduced in Figure 57, was made on the gastrocnemius muscle of a frog during the latter part of the winter, and when the muscle had begun to show the effects of spring irritability. A light weight was used. The muscle was first tested with four separate breaking induction shocks given at intervals of two seconds; it was then subjected for nine seconds to a tetanizing current; and in order that the condition of the muscle during this period might be ascertained, the tetanizing current was shut off from the muscle by a short-circuiting mechanism for a brief period every two seconds. Finally, at the close of the tetanus, the condition of the muscle was again tested by single-breaking shocks of the same intensity as those used before the tetanus. The curve reveals many points of interest.

a. The first four single contractions show the "introductory" effect and the beginning of a "staircase" effect such as is usually observed by serial excitations.

b. Each of the short tetani starts with a sharp rise of the curve, making what has been called the "introductory peak." These introductory peaks, which are caused by the throw of the recording lever, give an evidence of the intensity of the summation effects at these times. It is interesting to observe that the first is high, the second low, and the third, fourth, and fifth show a staircase-like growth, which is indication of the fact that excitation increases the activity of the contraction processes.

c. The amount that the curve falls in the short interval separating the succeeding periods of tetanus reveals the extent of the contracture present at these times.

d. The height of the base-line after the tetanus shows the persistence of the contracture condition.

e. The height of the separate contractions following the period of tetanic excitation was 22 mm., while the height of the first of the single contractions preceding the tetani was 14 mm., which well illustrates how excitation may increase irritability.

f. The total height to which the curve was carried by the separate shocks after the period of tetanic excitation exhibits the effect of the support offered by the contracture to increase the total height of contraction, and corroborates von Frey's statement that supported single contractions may carry the curve as high as tetanus.

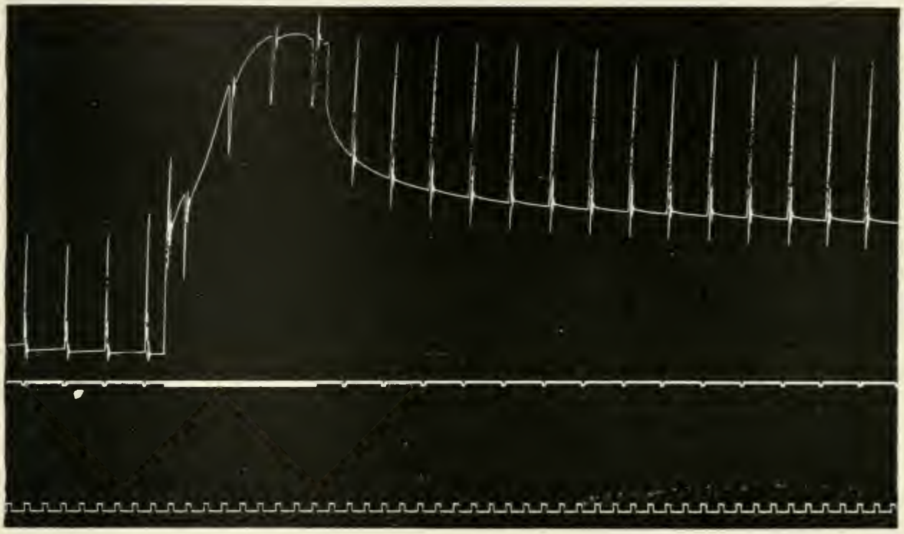

Fig. 57.—Effect of tetanizing excitations to increase the irritability of a muscle and at the same time to produce a condition of contracture. The gastrocnemius muscle of a winter frog, connected with a very light lever and a small weight, was arranged to write isotonic contractions on a slowly moving kymograph drum. The time was recorded in seconds at the bottom of the record, and above this the movement of the interrupter of the induction apparatus was written by an electric signal. The muscle was excited four times by breaking induction shocks at intervals of two seconds; then it was subjected to a tetanizing current, this being short-circuited for brief periods at intervals of two seconds; finally it was again excited at two second intervals with breaking induction shocks of the same strength as those used at the beginning of the experiment.

g. The rapid growth in the height of the crests of succeeding short tetani, taken in connection with the lessening amount of relaxation during the interval when the tetanizing current was shut off, and the curve of contraction seen at the close of the tetani, all go to show how contracture may aid summation and staircase effects to give the great height to the tetanus curve. Finally, it may be stated that the elasticity of the muscle gradually increases as a result of tetanic excitations, and this may aid in the support of the weight during long-continued tetanic contractions.

7. *Number of Excitations required to Tetanize.*—The number of stimuli per second required to tetanize a muscle depends largely on the nature of the

muscle, for this decides the character of the separate contractions, and, through them, the effect of their combined action.

The duration of the separate contractions, and the tendency of the muscle to enter into contracture, are the predominant factors in determining the result. Complete tetanus can only be obtained in the case of a fresh muscle, when the interval between succeeding stimuli is shorter than is required for the muscle to reach its maximal contraction by a single stimulus. Thus the prolonged contractions of smooth muscles permit of the development of a form of tetanus by successive closures of the galvanic current at intervals of several seconds. The non-striated muscle of the bladder of the cat can be tetanized by induction shocks given at a rate of a little less than one in two seconds.[1] The contraction of some of the muscles of the turtle may last nearly a second, and two or three excitations a second suffice to tetanize. The muscles of marmots during the winter sleep can be tetanized by 5 excitations per second (Patrizi). Tetanus of the red (slowly contracting) striated muscles of the rabbit can be obtained by 10 excitations per second, while 20–30 per second are required to tetanize the pale (active) striated muscles (Kronecker and Sterling); 100 stimuli per second are needed to tetanize the muscles of some birds (Richet), and over 300 per second would be required to tetanize the muscles of some insects (Marey). Any influence that will prolong the contraction process will lessen the rate of excitation required to tetanize.

8. *Effect of Exceedingly Rapid Excitations.*—The question arises, Is there an upper limit to the rate of excitation to which muscles will respond by tetanus? There is no doubt that this is the case, but there is a difference of opinion as to what the limit is, and how it shall be explained.

Striated muscles and nerves can be excited by rates at which our most delicate chronographs fail to act. The muscle ceases to be tetanized by direct excitation at a rate by which it can still be indirectly excited through its nerve. The highest rate for the nerve has been placed at from 3000 to 22,000 by different observers,[2] and this wide difference is probably attributable to the methods of excitation employed. That such different results should have been reached is not strange, if we recall the many conditions upon which the exciting power of the irritant depends. That tetanus should be obtained by such high rates does not show that the nerve responds to each of the separate shocks. As a rule, when the rate of excitation is so high that tetanus fails a contraction is observed when the current is thrown into the nerve, and often another when it is withdrawn from the nerve—that is, the muscle behaves as if it were subjected to a continuous battery current. A satisfactory explanation for this, as well as for the failure of the tetanus, is at present lacking.

9. *Relative Intensity of Tetanus and Single Contractions.*—The amount that a muscle is capacle of shortening, when tetanized by maximal excitations, and

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[1] C. C. Stewart: *American Journal of Physiology*, 1900, iii. p. 25.

[2] Kronecker and Sterling: *Archiv für Anatomie und Physiologie*, 1878, and *Journal of Physiology*, 1880, vol. i. Von Frey und Wiedermann: *Berichte der sächsischen Gesellschaft der Wissenschaft*, 1885. Roth: *Pflüger's Archiv*, 1888.

the strength of the tetanic contraction, depends very largely on the kind of muscle. For example, pale striated muscles, although capable of higher and more rapid single contractions than the red striated, do not show as great an increase in the height and strength of contractions when tetanized as do the red; the latter, which are very rich in sarcoplasma, have likewise the greater endurance. Gruetzner has called them "tetanus muscles," since they seem to be particularly adapted to this form of contraction. Fick found that human muscles when tetanized develop ten times the amount of tension, by isometric contractions, that they give by single contractions; and in this respect they can be said to resemble red striated muscles. The following relations have been found to exist between the strength of separate contractions and tetanus in certain muscles: triceps and gastrocnemius of the frog, 1 : 2 or 3; the corresponding muscles of the turtle, 1 : 5; hyoglossus and rectus abdominalis of the frog, 1 : 8 or 9.[1] It is evident that no just estimate of the part played by different groups of muscles in the movement of the body can be reached without a careful analysis of the nature of the contractions peculiar to each of the muscles participating in the movement.

Both the height and strength of the tetanus is controlled by the intensity of the stimulus. A strong stimulus not only causes the separate contractions of which the tetanus is composed to be higher, but is favorable to the development of all the other factors which have been described as entering into the production of tetanus. All normal physiological contractions are supposed to be tetani, and everyone is conscious of the wonderful accuracy with which he can grade the extent and strength of his voluntary movements. The remarkable shading of the intensity of action observable in co-ordinated movements must find its explanation in the adjustment of protoplasmic activity in the nerve-cells of the central nervous system.

10. *Continuous Contractions and Contractures.*—Under ordinary circumstances a striated muscle, if excited by a single stimulus, gives a rapid contraction, followed almost immediately by a nearly equally rapid relaxation. The duration and character of the period of relaxation are, however, subject to great variation. In certain conditions the muscle may remain in a state of continuous contraction for a considerable time, and then relax either slowly or quite suddenly; or it may begin to relax quickly and then suddenly stop, as if the relaxation process had received a sudden check; or, after relaxing quite rapidly for a short time, it may, without having received any visible stimulus, contract again for a short distance and remain so contracted for a considerable time. In any case when the relaxation period is unusually long, the condition of prolonged contraction is termed "contracture." The form of contracture which we are considering at present originates in the muscle itself, and is to be sharply distinguished from a form of pathological contracture, which originates in the central nervous system and in which the muscle is kept continuously contracted by impulses coming from the spinal cord.

There are a great variety of conditions under which muscles respond to

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[1] Biedermann: *Elektrophysiologie*, S. 109.

excitation by prolonged contractions. If a muscle be excited by frequent induction shocks, even at a rate insufficient to produce tetanus, after a time it will take on a condition of continuous contraction, which may be maintained for some time after the excitations have ceased (see Fig. 50). If the muscle be very irritable, the contraction caused by a single irritation may be long drawn out. A muscle poisoned by veratria—and the same is true of some other drugs (see p. 137)—may show a remarkable degree of contracture as a result of a single excitation. The contractions of fatigued muscles tend to be greatly prolonged; and this is very markedly the case with a dying muscle, which gives well-defined, long-continued contractions, localized at the point excited, called by Schiff the "idio-muscular contraction." The contractions caused by the making and breaking of a strong battery current applied to a muscle may likewise be followed by localized contractions which last a considerable time.

In this connection one must bear in mind that the length of muscles varies with their elasticity (see p. 105), and that this changes not a little under varying conditions. Finally, it is necessary to recall that muscles when entering into rigor mortis or rigor caloris take on a condition of contraction which may last for days (see p. 159).

Contracture in Normal Muscles following Frequent Excitations.—The condition of prolonged after-contraction which results from frequent excitations was first studied with care on the muscles of the frog, by Tiegel,[1] who gave it the name of "contracture."

Richet found that the claw-muscles of the crab are particularly subject to this form of contraction, Rossbach observed it in the muscles of the cat, and Mosso[2] saw it in the muscles of man when vigorously excited either voluntarily or electrically. Mosso finds a teleological reason for its existence in that it appears most marked under conditions when prolonged contractions are desirable, and might offer a certain economy in the innervation of muscle by lessening the work of the nerve-cell. Richet[3] writes that normal contracture is not to be confused with the prolonged relaxation of fatigued and dying muscles, nor with the contraction of muscle substance in rigor mortis; it is best seen on muscles which are fresh and excitable. Although most readily called out by strong direct electrical excitation of the muscle, it is not due to the effect of the current as such, because it may be produced by exciting the muscle indirectly through its nerve, and by voluntary muscular contractions of man. On the other hand, the presence of the nerve is not essential, for curarized muscles may exhibit contracture.

That a condition of increased excitability is favorable to the development of contracture is made evident by the curve reproduced in Figure 57. In this experiment the muscle was subjected to a tetanizing induction current for nine seconds, the stimulation being interrupted for an instant every two

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[1] Tiegel: *Pflüger's Archiv*, 1876, xiii. S. 71-84.

[2] Mosso: *Archives italiennes de Biologie*, 1890, xiii. pp. 165-179.

[3] Richet: *Dictionnaire de Physiologie*, 1899, t. iv. pp. 391-393.

seconds, to permit the contracture which was present at these times to show itself. The effect was to increase the excitability of the muscle, as shown by the increased height of the contractions recorded after the tetanus, and to produce a marked contracture, as was shown by the fact that the muscle only partially relaxed after the tetanizing current had ceased, and kept partially contracted in the intervals between the succeeding separate contractions. The fact that contracture can develop hand in hand with increasing excitability shows that it may occur in the absence of fatigue. It is interesting to note that the muscle made contraction and relaxation movements at the same time that it remained continually, although incompletely, contracted; and finally, that the contracture offered a firm, elastic support to the separate contraction movements, and that the relaxation movements following these separate contractions were rapid, as is made evident by the character of the elastic oscillations resulting from the rapid fall of the lever.

The fact that a muscle can remain continuously, though incompletely, contracted, at the same time that it makes rapid contraction and relaxation movements, suggests that it may at the same time be the seat of two independent contraction processes. The observation recalls the action of the heart muscle, for the ventricle maintains a condition of greater or less tonus, at the same time that it makes separate beats; it is therefore in harmony with a well-known physiological process.

Contracture following Single Excitations.—An examination of the contracture effects sometimes seen to follow single excitations of irritable muscles throws some light on the nature of the process. Richet observed on the closing-muscle of the claw of the crab that a single excitation caused a rapid contraction, which was followed by a rapid relaxation, and this in turn by a second contraction movement which lasted a considerable time.

A similar curve may be obtained from the striated muscle of a frog incompletely poisoned with veratria; if a single shock be given, the curve rises suddenly, and this quick rise is followed by an immediate fall, which is interrupted by a second and slower rise, which is continued as a prolonged contraction. In both cases the curve suggests that the single excitation called out two contraction movements, the first a rapid, short-lived contraction, the second a slower, prolonged contraction. It has been suggested that the muscle contains two kinds of muscle-fibres, which, like the pale (rapidly contracting radialis externus) and red (slowly contracting radialis internus) muscles of the rabbit, have two different rates of contraction.[1] This explanation is not very satisfactory, because it has been found that both the pale and the red muscles of the rabbit can give typical veratria contracture curves.[2] Moreover, both heart-muscle and non-striated muscles show independent tonus and contraction movements though containing only one kind of muscle-fibre.[3]

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[1] Grützner: *Pflüger's Archiv*, 1887, Bd. 41, S. 256.

[2] Carvallo and Weiss: *Journal de Physiologie et Pathologie générale*, 1899, t. i. p. 1. Bucannan: *Journal of Physiology*, 1899, vol. xxv. p. 145.

[3] Bottazzi: *Journal of Physiology*, 1897, vol. xxi. p. 1

It is hard to think of one and the same kind of muscle substance contracting and relaxing quickly at the same time that it is continuously contracted, and the attempt has been made to explain the phenomenon on the assumption that every muscle-fibre contains two kinds of contractile substance, and that the anisotropic fibrillary structures of the fibre are capable of rapid contractions and the isotropic sarcoplasma of slow contractions. According to this, the first quick rise of the contraction of the veratrinized muscle, etc., is due to the anisotropic substance, and the prolonged after-contraction to the sarcoplasma. This explanation offers much that is satisfactory, but can scarcely be accepted until we are sure that anisotropic and isotropic substances are capable of independent contractions.

The prolonged contraction of a muscle treated by veratria is an active process, and not merely the result of a change in its physical condition, such as an increase in elasticity. This is shown by the fact that during the stage of contracture the muscle liberates more heat than when at rest. The heat developed during a single veratria contraction may be as much as is given off by a normal muscle excited to tetanus for two seconds.[1] The fact that the prolonged contraction of the veratrinized muscle disappears on etherization, and returns as the effect of the ether passes off, also favors the view that it is dependent on physiological activity of the muscle protoplasm.[2]

This conclusion is likewise indicated by the observation that the prolongation of the contraction is most marked at a moderate temperature, and fails at very low or very high temperatures.[3] It has sometimes been thought that it was an expression of fatigue, but this can hardly be the case, because it is seen when the rate of the rise and the height of the curve of contraction are normal, and it ceases in the case of the veratrinized muscle if the muscle is worked for a time, and reappears when it has become rested. Moreover, veratria in small doses strengthens the contractions of fatigued muscle and increases its irritability, so that it responds to smaller stimuli by more work. It would appear that we may conclude that the contracture of the veratrinized muscle, like that of the normal muscle, is a true contraction process, but that we must await further evidence before deciding as to the exact nature of the contracture.

Effect of Fatigue.—If a muscle be excited to contraction by frequent excitations, its irritability for a time will be increased, the contractions will become stronger, higher, and more prolonged. If a muscle be excited to contraction at too slow a rate to cause an increase of irritability, it will gradually fatigue, and, as it does so, its contractions will become weaker, lower, and more prolonged. The prolongation of the contractions seen in these two cases is probably due to quite different causes.

In the first experiment it was a true contraction process; in the second it

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[1] Fick and Boehm: *Verhand. der physikal.-med. Gesellschaft in Würzburg*, 1872, Bd. iii., N. F., S. 198.

[2] Locke: *Journal of Experimental Medicine*, 1896, vol. i. p. 630.

[3] Brunton and Cash: *Journal of Physiology*, 1883, vol. iv. p. 237.

was the result of inability to relax. Relaxation as well as contraction is to be regarded as an active process, and in fatigue the power both to contract and relax is lessened.

The prolonged contraction of the fatigued muscle is chiefly caused by the injurious effects of the waste products produced within it as a result of the chemical changes accompanying its activity. One of these waste products, sarcolactic acid, is known to have the effect to prolong muscular contractions,[1] and it is not unlikely that others may exert a similar influence.

In case the muscle be excited frequently and for a considerable time, the contraction effect and the decreased power of relaxation due to fatigue, toward the end of the experiment, may both be present at the same time, and both act to prolong the curve of contraction. This was probably the case in the experiments the records of which are given in Figures 47 and 48, and many of the figures employed to illustrate the development of tetanus.

An example of this is to be seen in the effect of certain chemical substances on the muscle. For example, the withdrawal of water by drying, by the application of glycerin, or by a strong solution of sodium chloride, may, by rapidly altering the constitution of the protoplasm, cause an increase of excitability which may pass over to a state of excitation, which will be manifested by irregular but more or less continuous contractions. Such contractions are of the type of an incomplete tetanus.

Effect of Constant Battery Current.—Attention has already been called to the fact that under certain circumstances a form of continuous contraction may be excited by a continuous constant electric current. If the current be very strong, the short closing contraction may be followed by a more or less continuous contraction—the closing (or Wundt's) tetanus ; and the short opening contraction may be followed by another continuous contraction, which only gradually passes off—the opening (or Ritter's) tetanus. This form of contraction is quite readily excited in normal human muscles by both direct and indirect excitation. The term "galvanotonus" is sometimes employed for the continuous contraction of human muscles excited by the continuous flow of a constant current.

Although a continuous contraction caused by the constant current is spoken of as tetanus, it is a matter of doubt whether it is a true tetanic condition, for the term tetanus is limited to a form of contraction which, though apparently continuous, is really an interrupted process, and results from many frequently repeated stimuli. Von Frey[2] expresses the view that the continuous contraction which follows the closing of the continuous constant current is a form of tetanus. It is certainly true that the closing tetanus often shows irregular oscillations, suggestive of a more or less intermittent excitation which might be explained on the supposition that the flow of the current produces electrolytic decompositions within the tissue, and that the liberated ions exciting the protoplasm of the different fibres irregularly lead

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[1] Lee: *American Journal of Physiology*, 1899, vol. ii. p. 11.

[2] *Archiv für Anatomie und Physiologie*, 1885, S. 55.

to irregular contractions of the separate fibres, the combined action of which produces more or less regular continued contraction. Another view would be that contracture might be produced under the influence of the changes caused by the electric current, and a condition result similar to that which causes the prolonged contractions characteristic of poisoning with veratria, etc.

Effect of Death Processes.—If a muscle be dying, it responds to excitations by very slow, weak, and prolonged contractions, definitely localized at the place excited. Such a form of contraction is often classed as contracture, in spite of the fact that the irritability is greatly lessened. This form of contraction may be seen toward the end of prolonged wasting diseases in the case of the muscles of men. They respond to mechanical stimulations by localized, slowly developing contractions.

Pathological Contracture of Central Nervous Origin.—In certain pathological conditions there may be contractures which do not depend upon the condition of the muscle, but which originate in the central nervous system. In these cases the muscles are in continuous receipt of nerve impulses from the spinal cord cells, and are kept in continuous contraction, which varies in degree from the amount observed during ordinary reflex muscle tonus to a state of intense rigidity. The peculiarity of the condition is its endurance. The muscle does not appear to fatigue; moreover, it is said that it does not develop the large amount of heat (Brissand et Regnard) which is always formed as a result of the chemical changes which take place during the ordinary contractions.

For these reasons, Richet[1] considers the shortening of the muscle to be not a true contraction, but the result of an increase of elasticity. It is possible that some pathological contractions may be of different nature from those which we have been considering, but they have not been studied sufficiently to enable us to draw definite conclusions from them.

(*d*) *Normal Physiological Contractions.*—All normal physiological contractions of muscles are regarded as tetani. Even the shortest possible voluntary or reflex movements are considered to be too long to be single contractions. Inasmuch as we can artificially excite normal muscles to continuous contraction only by means of a series of rapidly following stimuli, we find it hard to explain continuous physiological contractions on any other basis, and hence the view that the excitation sent by the nerve-cells to muscles has always a rhythmic character, and that the normal motor-nerve impulse is a discontinuous rather than continuous form of excitation. The view is probably correct, but cannot be considered as proved. The evidence in favor of it is as follows:

Muscle-sounds, Tremors, etc.—During voluntary muscular contractions the muscle gives out a sound, which would imply that its finest particles are not in a state of equilibrium, but vibrating. By delicate mechanisms it has been possible to obtain records of voluntary and reflex contractions which showed oscillations, although the contraction of the muscle appeared to the eye to be

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[1] *Dictionnaire de Physiologie,* 1899, iv. p. 393.

continuous. If the surface of a muscle be exposed and be wet and glistening, the light reflected from it during continued contractions is seen to flicker, as if the surface were shaken by fine oscillations. In fatigue the muscle passes from apparently continuous contraction to one exhibiting tremors, and muscular tremors are observed under a variety of pathological conditions.

With these facts in mind, a number of observers have endeavored to discover the rate at which the muscle is normally stimulated. Experiments in which muscles have been excited to incomplete tetanic contractions by induced currents, interrupted at different rates, have shown that the muscle follows the rate of excitation with a corresponding number of vibrations, and does not show a rate of vibration peculiar to itself. Further, it has been ascertained that the sound given out by a muscle excited to complete tetanus, *i. e.* an apparently continuous contraction, corresponds to the rate at which it is excited. Apparently, any rate of oscillations detected in a muscle during normal physiological excitation would be an indication of the rate of discharge of impulses from the central nerve-cells.

Wollaston was the first to observe that a muscle gives a low dull sound when it is voluntarily contracted, and that this sound corresponds to a rate of vibration of 36 to 40 per second. It may be heard with a stethoscope placed over the contracting biceps muscle, for instance, or if, when all is still and the ears are stopped, one vigorously contracts his masseter muscles. Helmholtz placed vibrating reeds consisting of little strips of paper, etc., on the muscle, and found that only those which had a rate of vibration of 18 to 20 per second were thrown into oscillation when the muscle was voluntarily contracted. This observation indicated that the muscle had a rate of vibration of 18 to 20 per second, a rate too slow to be recognized as a tone. He concluded that the tone heard from the voluntarily contracted muscle was the overtone, instead of the true muscle-tone. The consideration that the resonance tone of the ear itself corresponds to 36 to 40 vibrations per second, makes it questionable whether the muscle-sound should be accepted as evidence of the rate of normal physiological excitation; nevertheless, the experiments with the vibrating reeds remain to indicate 18 to 20 per second to be the normal rate.

Within the last few years a number of researches bearing upon this question have been published, and the results of these point to a still slower rate of voluntary excitation, varying from 8 to 12 per second according to the muscle on which the experiment is made. Lovén[1] discovered in the tetanus excited in frogs poisoned with strychnia, and in voluntary contractions, both by mechanical methods and by recording the electrical changes occurring during action with the capillary electrometer, rates of 7 to 9 per second. Horsley and Schafer[2] excited the brain cortex and motor tracts in the corona radiata and the spinal cord of mammals by induction shocks, at widely differing rates, and recorded the resulting muscular contractions by tambours placed over the muscles. They observed oscillations in the myograms obtained which had a

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[1] *Centralblatt für die medicinischen Wissenschaften*, 1881.

[2] *Journal of Physiology*, 1886, vii. p. 96.

rate of 8 to 12 per second, the average being 10. The rate of oscillations was quite independent of the rate of excitation, and oscillations of the same rate were seen by voluntary and by reflex contractions. Tunstall[1] found by the use of tambours, in experiments on voluntary contractions of men, a rate of 8 to 13 per second, with an average of 10. Griffiths[2] likewise used the tambour method, and studied the effect of tension on the rate of oscillations in voluntarily contracted human muscles. He observed rates varying from 8 to 19, the rate being increased with an increase of weight up to a certain point, and beyond this decreased. The oscillations became more extensive as fatigue developed. Von Kries by a similar method found rates varying with different muscles, but averaging about 10.

It is not easy to harmonize the view that 8 to 13 excitations per second can cause voluntary tetani, when it is possible for the expert pianist to make as many as 10 or 11 separate movements of the finger in a second. It is, indeed, a common observation that a muscle can be slightly and continuously voluntarily contracted, and, at the same time, be capable of making additional short rapid movements. Von Kries would explain this as due to a peculiar method of innervation, while Biedermann favors Gruetzner's[3] view that the muscle may contain two forms of muscle-substance, one of which is slow to react, resembling red muscle-tissue, and maintains the continuous contraction, the other, of more rapid action, being responsible for the quicker movements. Although the evidence is, on the whole, in favor of the view that all normal contractions of voluntary muscles are tetanic in character, there is a great deal which remains to be explained.

Effect of Artificial compared with Normal Stimulation.—Experiment shows that, with the same strength of irritant, a muscle contracts more vigorously when irritated indirectly, through its nerve, than when it is directly stimulated. Rosenthal describes the following experiment: If the nerve of muscle A be allowed to rest on a curarized muscle B, and an electric shock be applied in such a way as to excite nerve A and muscle B to the same amount, muscle A will be found to contract more than muscle B.

Further, it has been found that muscles respond more vigorously to voluntary excitations than to any artificial stimulus which can be applied to either the nerve or muscle. This shows itself, not only in the fact that a muscle can by voluntary stimulation lift much larger weights than by electrical excitation, but that after a human muscle has been fatigued by electrical excitations it can still respond vigorously to the will. An illustration of this is given in Figure 58.

Fatigue of Voluntary Muscular Contractions.—Mosso and his pupils have done a large amount of work upon the fatigue of human muscles when excited by voluntary and artificial stimuli under varying conditions (see p. 72). The results at which they arrived all favor the view that human muscles differ but little from those of warm-blooded animals, and that the facts which have

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[1] *Journal of Physiology*, 1886, vii. p. 114.

[2] *Journal of Physiology*, 1888, ix p. 39.

[3] *Pflüger's Archiv*, 1887, Bd. 41, S. 277.

been ascertained by experiments upon cold-blooded animals, such as the frog, can be accepted with but slight modifications for the muscles of man. In the experiment recorded in Figure 58 we see the effect of repeated tetanic contractions, excited by electricity, to fatigue a human muscle. Normal voluntary contractions, if frequently repeated, provided the muscle has to raise a considerable weight, likewise cause fatigue. This was illustrated in the experiment recorded in Figure 59.

FIG. 58.—Voluntary excitations are more effective than electrical. The flexor muscles of the second finger of the left hand of a man were excited first voluntarily, *a*, then electrically, *a-b*, and then voluntarily, *b*. The electrical excitation consisted of series of induction shocks, which were applied once every two seconds, during about half a second, the spring interrupter of the induction coil vibrating 23 times per second. Each time the muscle contracted it raised a weight of one kilogram. Each of the contractions recorded, whether the result of electrical or voluntary excitation, was a short tetanus.

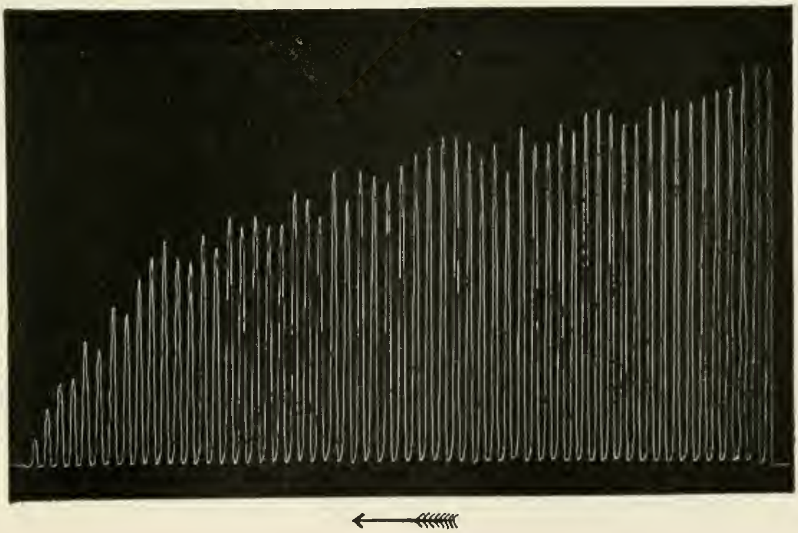

FIG. 59.—Effect of fatigue on voluntary muscular contractions. The flexor muscles of the second finger of left hand were voluntarily contracted once every two seconds, and always with the utmost force. The weight raised was four kilograms.

It is doubtful whether, in an experiment such as is shown in Figure 59, the loss of the power to raise the weight is due to fatigue of the muscles. It is more likely that the decline in power is due to fatigue of the central nerve-cells by which the muscles are excited to action during the voluntary muscular work.[1] This fact, that the nerve-cells give out before the muscles, explains the apparent contradiction, that a muscle fatigued by electric excitations can be voluntarily contracted, and when the power to voluntarily contract the muscles has been stopped by fatiguing voluntary work the muscles will respond to electrical excitation. It is undoubtedly of advantage to the body that the nerve-cells should fatigue before the muscles, for the muscles are thereby protected from the injurious effects of overwork, and are always ready to serve the brain.[2] It may be added that nerve-cells not only fatigue more quickly, but recover from fatigue more rapidly than the muscles.

(*e*) *Effect of Temperature upon Muscular Contraction.*—Heat, within certain limits, increases the irritability and conductivity of muscle-tissue, and at the same time has a favoring influence upon those forms of chemical change which liberate energy. The effect of a rise of temperature, as shown by the myogram, is a shortening of the latent period, an increase in the height of contraction, and a quickening of the contraction and relaxation, the whole curve being shortened. Of course there is an upper limit to this favoring action, since, at a certain temperature, about 45° C. for frog's muscle and about 50° C. for the striated muscles of warm-blooded animals, 53°–58° C. for the non-striated muscles of the bladder of the cat,[3] heat-rigor begins, and this change is accompanied by a loss of all vital properties. Cold can be said, in general, to produce effects the opposite of those of heat; as the muscle is cooled, the latent period, the contraction, and the relaxation are all prolonged.

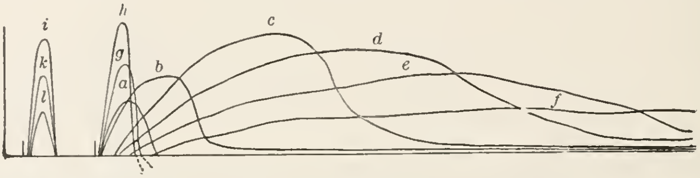

FIG. 60.—Schema of effect of temperature on height and form of contraction curve: *a*, contraction at 19° C.; *b*, *c*, *d*, *e*, *f*, contractions made at intervals, each one at a lower temperature; *g*, *h*, contractions at higher temperatures than 19° C., *h* being made when the temperature was 30° C.; *i*, *k*, *l*, show a different series of contractions, made as the temperature was increased from 30° C. toward the point at which the muscle-substance coagulates (after Gad and Heymans).

Nevertheless, the effect of temperature is not a simple one (see Fig. 60). If during the cooling process a striated muscle of a frog be irritated from time to time with single induction shocks, the height of the contractions does not continually grow less as one would expect.[4] The maximal height is obtained at 30° C., the height above this point being somewhat less, the irritability lessening as the coagulation-point is approached; from 30° C. to 19° C. the height continually decreases, but from 19° to 0° C. the height increases, while

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[1] Lombard: *Archives italiennes de Biologie*, xiii. p. 1; or *American Journal of Psychology*, 1890, p. 1; *Journal of Physiology*, 1892, p. 1; 1893, p. 97.

[2] Waller: *Brain*, 1891, p. 179.

[3] C. C. Stewart· *American Journal of Physiology*, 1900, iii. p. 25.

[4] Gad und Heymans: *Archiv für Anatomie und Physiologie*, 1890, S. 73.

below 0° C. it again becomes less, until at the freezing-point of muscle no contraction is obtained. The cause of these peculiar phenomena is not definitely understood.

(*f*) *Effect of Drugs and Chemicals upon Muscular Contraction.*—Certain drugs and chemicals have a marked effect upon the irritability (see p. 58) and conductivity (see p. 93) of muscles, and these effects must necessarily find expression in the amount of contraction which would be excited by a given irritant. In addition to this, it is worthy of notice that the character of the contraction may be altered.

The drug which has the most striking effect upon the form of contraction is veratria. A few drops of a 1 per cent. solution of the acetate of veratria, injected into the dorsal lymph sac of a frog whose brain has first been destroyed, in a few minutes alter completely the character of the reflex movements: the muscles are still capable of rapidly contracting, but the contractions are cramp-like, the power to relax being greatly lessened. The poison acts upon the muscle-substance, and even a very small dose applied directly to the muscle for a few hours—*e. g.*, a solution containing 1 part to 100,000 of 0.6 per cent. solution of sodium chloride—suffices to greatly alter the character of the contraction called out by various irritants.[1] If a muscle poisoned with veratria be isolated and connected with a myograph, a contraction excited by a single induction shock will show a rise as rapid, as high, and as strong as normal, but the fall of the curve will be greatly prolonged (see Fig. 61). Often the crest of the curve will exhibit a notch, which shows that relaxation may begin and be checked by a second contraction process which carries the curve up again and holds it there for a considerable time. In the above experiment the contracture effect followed the primary contraction immediately. The nature of the contracture of a muscle poisoned with veratria has been considered (see p. 130).

FIG. 61.—Myogram of muscle poisoned with veratria and that of a normal muscle: *a*, myogram from a normal gastrocnemius muscle of a frog—the waves at the close are due to the recoil of the recording lever; *b*, myogram from a gastrocnemius muscle poisoned with veratria, recorded at the same part of the drum.

There are a number of drugs which have an action on muscle-tissue similar to that of veratria—*e. g.*, cornutine[2] produces a similar effect on striated muscles; digitaline increases the tonus of heart muscle and of the smooth

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[1] Bucannan: *Journal of Physiology*, 1899, xxv. p. 137.

[2] Cushny: *Pharmacology and Therapeutics*, 1899.

muscle-tissue of the walls of the blood-vessels; epinephrin,[1] the active principle of the extracts obtained from the medullary part of the suprarenal capsules, may be mentioned here, and is of especial interest because derived from the animal body. If injected into the blood, it increases the strength and prolongs the contraction of the muscles generally, and causes through its effect on the muscle of the heart and the non-striated muscles of the blood-vessels a marked rise of blood-pressure.[2]

Barium salts, and to a less degree calcium and strontium, act similarly to veratria to prolong the relaxation of the muscle, without lessening the rapidity and height of contraction.

Potassium and ammonium salts and a large number of other chemical substances and drugs act to kill the muscle, and as the death process develops excitation produces prolonged localized contractions. This effect seems to be quite different from that of veratria, for it is accompanied by a rapid lessening of the muscular power.

5. Liberation of Energy by the Contracting Muscle.—The law of conservation of energy applies no less to the living body than to the inanimate world in which it dwells. Every manifestation of life is the result of the liberation of energy which was stored in the body in the form of chemical compounds. When a muscle is excited to action it undergoes chemical changes, which are accompanied by the conversion of potential into kinetic energy. This active energy leaves the muscle in part as thermal energy, in part as mechanical energy, and, to a slight extent, under certain conditions, as electrical energy. In general, the sum of the liberated energy is given off as heat or motion. The proportion in which these two forms of energy shall be produced by a muscle may vary within wide limits, according to the state of the muscle and the conditions under which the work is done. Fick[3] states that if the muscle works against a very heavy weight, possibly one-fourth of the liberated energy may be obtained as mechanical work; but if the weight be light not more than one-twentieth of the chemical energy is given off in this form, the muscle working no more economically than a steam engine. Zuntz[4] studied the work that the body as a whole could accomplish, and found that somewhat more than one-third of the energy liberated can be obtained as external mechanical work. The fact that always a part, and often the whole, of the mechanical energy developed by the muscle is converted to thermal energy within the muscle, and leaves it as heat, makes it the more difficult to determine in what proportion these two forms of energy were originally produced. Moreover, if Engelmann's view be correct, that the change of form exhibited by the muscle is the result of the imbibition of the fluid of the isotropic substance by the anisotropic material, this change being brought about by the heat which is liberated within the muscle, we must consider potential energy to be set free first as heat, a part of which is afterward

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[1] Abel: *Zeitschrift für physiologische Chemie*, 1899, Bd. xxviii. S. 354.

[2] Oliver and Schäfer: *Journal of Physiology*, 1895, xviii. pp. 230–276.

[3] Fick: *Pflüger's Archiv*, 1878, xvi. S. 85.

[4] *Ibid.*, 1897, Bd. lxviii., S. 191.

changed to mechanical energy, which in part, at least, is again changed to heat.

Liberation of Mechanical Energy.—The amount of work which a muscle can do depends on the following conditions:

(*a*) *The kind of muscle.* The muscles of warm-blooded animals are stronger than those of cold-blooded animals; a human muscle can do twice the amount of work of an equal amount of frog's muscle. The muscles of certain insects have even greater strength.[1] Within the same animal there are great differences in the capacity of different forms of muscle tissue (see p. 107). Pale striated muscle tissue, although more capable of rapid liberation of energy, has not the endurance or the strength of the red striated muscle tissue; and different forms of non-striated muscle differ among themselves as well as from striated in their capacity for work.

(*b*) *The condition of the muscle.* Any of the influences which lessen the irritability of the muscle—lack of blood, fatigue, cold, etc.—decreases the power to liberate energy, and any influence which heightens the irritability is favorable to the work. The effect of tension to heighten irritability has already been referred to and is of especial interest in this connection, since the very resistance of the weight is, within limits, a condition favorable to the liberation of the energy required to overcome the resistance. This will be referred to again.

(*c*) *The strength and character of the stimulus.* The liberation of energy is, up to a certain point, the greater, the stronger the excitation. Furthermore, rapidly repeated excitations are much more effective than single excitations, because a series of rapidly following stimuli, both by altering the irritability and by inducing the form of contraction known as tetanus, act to produce powerful and high contractions. Bernstein states that the energy developed by the muscle increases with the increase of the rate of excitation from 10 to 50 per second, at which rate the contraction power may be double that called out by a single excitation.

(*d*) *The method of contraction and the mechanical conditions under which the work is done.* In estimating the amount of mechanical energy liberated by a muscle, we observe the amount of external work which it accomplishes, *i. e.* the amount of mechanical energy which it imparts to external objects. If a muscle by contracting raises a weight, it gives energy to the weight, the amount being exactly that which the weight in falling through the distance which it was raised by the muscle can impart as motion, heat, etc., to the objects with which it comes in contact. The measure of the mechanical work done by the contracting muscle is the product of the weight into the height to which it is lifted. For example, if a muscle raises a weight of 5 grams 10 millimeters, it does 50 grammillimeters of work. An unweighted muscle in contracting does no external work; a muscle, however vigorously it may contract, if it be prevented from shortening, does no external work; finally, a muscle which raises a weight and then lowers it again when it relaxes, does not alter its surroundings as the total result of its activity, and

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[1] Hermann: *Handbuch der Physiologie*, 1879, Bd. i. S. 64.

hence does no external work. Although no external work is accomplished under these circumstances, internal work is being done, as is evidenced by the heat evolved by the muscle and the fatigue produced. Unquestionably mechanical energy is developed within the muscle in all these cases, but it is all converted to heat before it leaves the muscle.

The amount of weight is an important factor in determining the extent to which a muscle will shorten when excited by a given stimulus, and, therefore, the quantity of work which it will accomplish. If a muscle be after-loaded, *i. e.* if the weight be supported at the normal resting length of the muscle, and the muscle be excited to a series of maximal contractions, the weight being increased to a like amount before each of the succeeding excitations, there is, in general, a gradual lessening in the height of the contractions, but the decrease in height is not proportional to the increase of the weight. The decrease in the height of contractions is, as a rule, more rapid at the beginning of the series than later, though at times an opposite tendency may show itself and the increasing weights temporarily increase the irritability and therefore increase the amount of shortening. The effect of tension to increase the activity of the contraction process is seen if a muscle which is connected with a strong spring or heavy weight be excited to isometric contractions and in the midst of a contraction be suddenly released; the muscle under such circumstances is found to contract higher than when excited by the same stimulus without being subjected to tension.[1] The effect of tension on the activity of muscular contractions is to be clearly seen in the case of the heart muscle. A rise of pressure of the fluid within the isolated heart of a frog increases the strength as well as the rate of the beat.

If the weight be gradually increased, although the height of the contractions is lessened, the work will for a time increase, and a curve of work (constructed by raising ordinates of a length corresponding to the work done, from points on an abscissa at distances proportional to the weights employed), will be seen to rise. After the weight has been increased to a certain amount the decline in the height of contractions will be so great that the product of the weight into the height will begin to decrease, and the curve of work will fall, until finally a weight will be reached which the contracting muscle can just support at, but not raise above, its normal resting length This weight will be a measure of the absolute muscular force.

Example.

Load (grams).	Height of lift (millimeters).	Work (grammillimeters).
0	13	0
30	11	330
60	9	540
90	7	630
120	5	600
150	3	450
180	2	360
210	0	0

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[1] Fick: *Mechanische Arbeit*, etc., S. 132. Santesson: *Skandinavisches Archiv für Physiologie*, 1889, i. S. 56.

In the above experiment 30 grams were added to the muscle after each contraction; as the weight was increased up to 90 grams the amount of work was increased, with greater weights the amount of work was lessened.

It is evident that the absolute force of a muscle of a given type will depend not only on the quantity, but also on the arrangement of the microscopic elements of which the muscle is composed. Each element of a fibre has to stand the strain of the whole fibre; so the force to be developed depends not on the length of the fibres, but on the number of muscle elements which are arranged side by side, *i. e.* the absolute force of a muscle will be proportionate to the number of fibres. This can be stated for a muscle with parallel fibres in terms of the cross section of the muscle. In the case of a muscle like the gastrocnemius, where the fibres take an oblique course and are inserted into a common tendon in the middle, the "physiological cross-section" has to be estimated, *i. e.* the total section taken at right angles to the fibres. Such a muscle is very strong in proportion to its thickness. Rosenthal estimated the absolute force of striated muscles of the frog to be about 3 kilograms per square centimeter, and Hermann[1] found the absolute force of striated muscle of man to be 6.24 kilograms per square centimeter.

The physiological work of which a muscle is capable, on the other hand, is dependent not only on the weight which it can lift, but also the height to which the weight can be lifted. All the muscle elements, whether arranged side by side or in chains, influence the result, and for purposes of comparison one can state the capacity of the muscle for work in terms of the unit of bulk, the cubic centimeter, or the unit of weight, the gram. Thus, Fick states the maximal amount of external work of which frog's muscle is capable, as one grammeter per gram of muscle substance.

From what has been said it is evident that the amount of muscle substance determines the amount of work of which the muscle is capable, while the arrangement of the muscle substance decides the character of the work which it is best fitted to perform. Muscles with long parallel fibres, even though of small sectional area, such as the sartorius, are specially fitted to produce extensive movements of the parts to which they are attached; and muscles which have a large number of fibres, even though these be short, as in the case of the gastrocnemius, are adapted to move great weights.

Carvallo and Weiss[2] state that the gastrocnemius muscle of the frog when at rest tears if subjected to a weight of 2 kilos. Its contraction power is estimated to be half a kilo, and when it is contracting its resistance is correspondingly increased, so that a weight of 2½ kilos is required to rupture it. The increased resistance can be best explained on the idea that, as Pflüger thinks, a new chemical attraction force is developed in contraction.

Liberation of Thermal Energy.—Energy leaves the body as mechanical energy only when by its movements the body imparts energy to surrounding objects. Most of the energy liberated within the body leaves it as heat;

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[1] *Pflüger's Archiv,* 1898, Bd. 73, S. 429.

[2] Carvallo and Weiss: *Comptes rendus Société de Biologie,* 1899, p. 122.

even during violent muscular exercise five times more energy may be expended as heat than as mechanical energy, and the disproportion may be even greater than this. Rosenthal says that at the most not more than 30 per cent. of the energy developed in the muscle by oxidation and splitting processes is to be got as available mechanical energy. So great is the production of heat during exercise that, in spite of the great amount leaving the body, the temperature of an oarsman has been found to be increased, during a race of 2000 meters, from 37.5° C. to 39° or 40° C.[1]

It is exceedingly difficult to ascertain with accuracy on the warm-blooded animal the exact relation of heat-produccion to muscular contraction. The best results have been obtained by experiments on isolated muscles of cold-blooded animals. Helmholtz observed the temperature of a muscle of a frog to be increased by tetanus lasting a couple of minutes 0.14° to 0.18° C.; Heidenhain saw a change of 0.005° C. result from a single contraction; and Fick ascertained that a fresh, isolated muscle of a frog can by a single contraction produce per gram of muscle-substance enough heat to raise 3 milligrams of water 1° C.[2] To obtain evidence of the slight changes of temperature which occur in such small masses of muscle-tissue it is necessary to employ a very delicate instrument, such as a thermopile or a bolometer.

The thermopile consists of strips of two dissimilar metals, united at their extremities, so as to form a series of thermo-electric junctions. If there be a difference of temperature at two such junctions, a difference of electric potential is developed, which causes the flow of an electric current. If the current be passed through the coils of wire of a galvanometer its amount can be measured, and the extent of the change in temperature at one of the junctions, the other remaining constant, can be estimated. In the more sensitive instruments, several thermo-electric junctions are used. The amount of current depends largely on the metals employed, antimony and bismuth being a very sensitive combination.

The action of the bolometer is based on the fact that the resistance of a wire to the passage of an electric current changes with its temperature.

The amount of heat developed within the muscle by direct conversion of potential to thermal energy, and the amount formed indirectly, through conversion of mechanical to thermal energy, has been made a subject of careful study by Heidenhain,[3] Fick and his pupils,[4] and others, the experiments being made chiefly with isolated muscles of frogs.

In general, the stronger the stimulus and the greater the irritability of the muscle—in other words, the more extensive the chemical changes excited in the muscle—the greater the amount, not only of mechanical, but of thermal energy liberated. Increase of tension, which is very favorable to muscular

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[1] George Kolb: *Physiology of Sport*, translated from the German, second edition, London, 1892.

[2] Fick: *Pflüger's Archiv*, 1878, xvi. S. 89.

[3] *Mechanische Leistung, Wärmeentwicklung und Stoffumsatz bei der Muskelthätigkeit*, Leipzig, 1864.

[4] *Myothermische Untersuchungen aus den physiologischen Laboratorium zu Zurich und Wurzburg*, Wiesbaden, 1889.

activity, greatly increases the heat-production. For this reason isometric contractions, that is, those in which the muscle works against a resistance which is sufficient to prevent it from shortening, are accompanied by a greater liberation of heat than isotonic contractions, in which the contracting muscle raises a constant weight. As the weight is increased, both the amount of heat developed and the work are increased, but the liberation of heat reaches its maximum and begins to decline sooner than the amount of work—*i. e.*, with large weights the muscle works more economically; similarly, as the muscle is weakened by fatigue the heat-production lessens sooner than the work.

Muscle-tonus and Chemical Tonus.—During waking hours, the cells of the central nervous system are continually under the influence of a shower of weak nervous impulses, coming from the sensory organs all over the body;[1] moreover, activity of brain-cells, especially emotional forms of activity, leads to an overflow of nervous impulses to the spinal cord and an increased irritability, or, if stronger, excitation of motor nerve-cells. If, when one is quietly sitting and reading, he turns his attention to the sensory impressions which are coming at every moment from all over the body to the brain, notes the temperature of different parts of the skin, the pressure of the clothes, etc., upon different parts, the light reflected from neighboring objects, and the slight sounds about him, he will recognize that the central nervous system is all the time subject to a vast number of excitations, which, because of their very repetition, are ordinarily disregarded by the mind, but which are, nevertheless, all the time influencing the nerve-cells. The effect of this multitude of afferent stimuli, in spite of their feebleness, is to cause the motor cells of the cord to continually send delicate motor stimuli to the muscles. These cause the muscle to keep in the state of slight but continued contraction which gives the tension peculiar to waking hours, and which is called *muscle-tonus.* That such a tension exists is made evident by the change in attitude which occurs when the relaxation accompanying sleep comes on. The effect of brain activity to cause muscular tension is, likewise, most easily recognized by observing the relaxation of the muscles which occurs when mental excitement ceases.

Muscle-tonus, like every form of muscular contraction, is the result of chemical change, and the liberation of energy. But little of this energy leaves the body as mechanical energy, most of it being given off as heat.

This view is by no means universally accepted, and many physiologists believe in a production of heat by the muscles, as a result of nervous influences, independent of contraction. It is thought that a condition of slight but continuous chemical activity resulting in the production of heat may be maintained in the muscles by intermittent but frequent reflex excitations, a condition which has been called *chemical tonus.*[2] That the chemical activity of muscles is kept

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[1] Brondgeest: *Archiv für Anatomie und Physiologie,* 1860, S. 703; Hermann, *Ibid.*, 1861, S. 350.

[2] Roehrig und Zuntz: *Pflüger's Archiv,* 1871, Bd. iv; Pflüger: *Pflüger's Archiv,* 1878, xviii. S. 247.

up by small stimuli from the spinal cord is shown by the fact that if the nerves be severed, or the nerve-ends be poisoned by curare, the muscle absorbs less oxygen and gives off less carbon dioxide than when at rest under normal conditions.[1]

The theory of a reflex chemical tonus independent of contraction implies the existence of special nervous mechanisms for the exciting of chemical changes in the muscles which shall result in the liberation of energy as heat, independent of the change of form of the muscle. The question of the existence of special nervous mechanisms controlling heat-production—heat-centres, as they are called—will be considered in another part of this book.

E. Electrical Phenomena in Muscle and Nerve.[2]

The active muscle liberates three forms of energy: mechanical work, heat, and electricity. The active nerve makes no visible movements, gives off no recognizable quantity of heat, but exhibits changes in electrical condition quite comparable to those observed in the active muscle. The electrical changes in nerves are the only evidence of activity which we can observe, aside from the effect of the nerve on the organ which it excites; they are therefore of great interest to us.

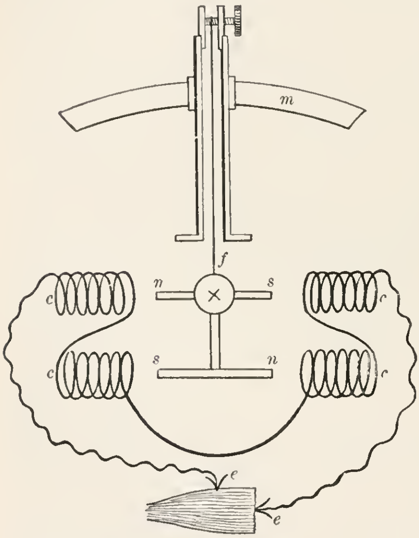

Fig. 62.—Schema of galvanometer: *n*, *s*, north and south poles of astatic pair of magnets; *m*, compensating magnet, held by friction on the staff, and capable of being approached to, or rotated with reference to, the suspended magnet; ×, mirror; *f*, fibre supporting the magnets; *c*, *c*, *c*, *c*, coils of wire to carry the electric current near to the magnets, the upper coils being wound in the opposite direction to the lower; *e*, *e*, non-polarizable electrodes applied to the longitudinal surface and cross section of a muscle.

Electrical energy, like all forms of active energy, is the result of a transformation of potential or some form of kinetic energy. In the case of the muscle, as of an electric battery, we find electricity to be associated with chemical change, and believe it to be liberated from stored potential energy. In the case of nerves no chemical change can be detected during action, and hence we are at a loss to explain the development of electricity. We can only say that it is the result of some chemical or physical process which we have as yet failed to discover.

Although activity of nerve and muscle is found to be associated with electrical change, we must not suppose functional activity to be in any sense an electrical process. The movements

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[1] Zuntz: *Pflüger's Archiv*, 1876, xii. 522; Colasanti, *Ibid.*, 1878, xvi. S. 57.

[2] Biedermann: *Electrophysiologie*, Jena, 1895, Bd. ii.; translation by F. A. Welby, 1898; Waller: *Lectures on Animal Electricity*, London, 1897.

of a man may be interpreted from the movements of his shadow, but they are very different phenomena; the activity of the nerve and muscle is indicated by the electrical changes accompanying it, but they may be independent processes. Certainly the irritating change which is transmitted along the nerve and which excites the muscle to action, although accompanied by electrical changes, is not itself an electric current.

Electrical energy is exhibited not only by active nerve and muscle, but during the activity of a great variety of forms of living matter. It may be detected in gland-cells, in the cells of many of the lower animal organisms, and even in plant-cells. The amount of electrical energy developed in animal tissues may be far from trivial. Although delicate instruments are necessary to observe the electrical changes in nerve and muscle, as the great internal resistance of the tissues causes the currents to be small, we find in certain fish special electric organs, which appear to be modified muscle tissue, and which are capable of discharging a great amount of electrical energy when excited through their nerves. So intense is the action of this electrical apparatus that it can be used as a weapon of defence and offence. Gotch and Burch state that the electric organ of the malapterurus electricus can give a shock having an electric potential of 200 volts.[1]

1. **Methods of Ascertaining the Electrical Condition of a Muscle or a Nerve.**—If the electric tension of any two parts of an object differs, the instant they are joined an electric current will flow from the point where the tension is greater to that where it is less. The presence, direction of flow, and strength of an electric current can be detected by an instrument called a galvanometer. If any two parts of a muscle or nerve, as *e*, *e*, Figure 62, be connected by suitable conductors with the coils, *c*, *c*, of a galvanometer, and if there be a difference in the electric potential of the two parts examined, an electric current will be indicated by the instrument. In such tests all extra sources of electricity are to be avoided, therefore the electrodes applied to the muscle must be non-polarizable.

The Galvanometer—An ordinary form of galvanometer consists of a magnet suspended by an exceedingly delicate fibre of silk, or quartz, and one or more coils, composed of many windings of pure copper wire, placed vertically near the magnet and in the plane of the magnetic meridian. If an electric current be allowed to flow through the wire, it influences the magnetic field about it, and, if the coils be close to the suspended magnet, causes the magnet to deviate from the plane of the magnetic meridian in one or the other direction, according to the direction of the flow of the current. In the more delicate instruments the influence of the earth's magnetism is lessened by the use of two magnets of as nearly as possible the same strength, placed so as to point in opposite directions, and fastened at the extremities of a light rod. As each magnet tends to point toward the north, they mutually oppose each other, and therefore the effect of the earth's magnetism is partly compensated. Still another magnet may be brought near this "astatic" combination, and by opposing the action of the earth's magnetism make the arrangement even more delicate. In the Thompson galvanometer, the rod connecting the needles bears a slightly concave mirror, from which a beam of light can be reflected on a scale. Or a scale may be placed so that its image falls on the mirror, and the slightest movement of the magnet may be read in the mirror by a telescope.

The ordinary galvanometer is influenced by changes in the magnetism of the earth, and by earth currents which may be due to an escape of electricity from neighboring street-car circuits, etc. These disturbances may interfere with the use of the instrument,

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[1] *Proceedings of the Royal Society*, 1900, vol. lxv. p. 442.

because they may lead to uncontrollable movements of the magnet, and a consequent shifting of the 0 point. There are other forms of instruments, such as the Deprez-d'Arsonval mirror galvanometer,[1] which are not affected by such influences.

The galvanometer is very sensitive to the presence of electric currents. Another apparatus which is even more responsive to changes in electric potential of short duration is the capillary electrometer.

The capillary electrometer (Fig. 63) consists of a glass tube (a) drawn out to form a very fine capillary, the end of which dips into a glass cup with parallel sides (f) containing a 10 per cent. solution of sulphuric acid. The upper part of the tube is connected by a thick-walled rubber tube with a pressure-bulb containing mercury (c). As the pressure-bulb is raised, the mercury is driven into the capillary, the flow being opposed by the capillary resistance. By a sufficiently great pressure, mercury may be driven to the extremity of the capillary and all the air expelled. When the pressure is relieved the mercury rises again in the tube, drawing the sulphuric acid after it. The column of mercury will come to rest at a point where the pressure and the capillary force just balance. Seen through the microscope (e), the end of the column of mercury, where it is in contact with the sulphuric acid appears as a convex meniscus (d). Any alteration of the surface tension of the meniscus causes the mercury to move with great rapidity in one direction or the other along the tube; and a very slight difference of electric potential suffices to cause a change in surface tension of the mercury-sulphuric acid meniscus. A platinum wire fused into the glass tube (a), and another dipped into a little mercury at the bottom of the cup holding the acid, permit the mercury in the capillary and the acid to be connected with the body the electric condition of which is to be examined. If the mercury and acid be connected with two points of different electric potential, as g and h of muscle M, the mercury will instantly move from the direction of greater to that of lesser tension, descending deeper into the tube if the tension be raised on the mercury side, or lowered on the acid side, and *vice versa*. As seen through the microscope the picture is reversed (d), and the movements of the mercury appear to be in the opposite direction to that stated. The extent of the movements of the mercury column can be estimated by a scale in the eyepiece. Moreover, the movement of the mercury can be recorded photographically, by placing a strong light behind the column of mercury, and letting its shadow fall through a slit in the wall of a dark chamber, upon a sheet of sensitized paper stretched over the surface of a revolving drum or a sensitized plate moved by clockwork or other suitable mechanism. This instrument, of which there are a number of different forms besides that originally devised by Lippmann, is very delicate, recording exceedingly slight differences in electrical potential.

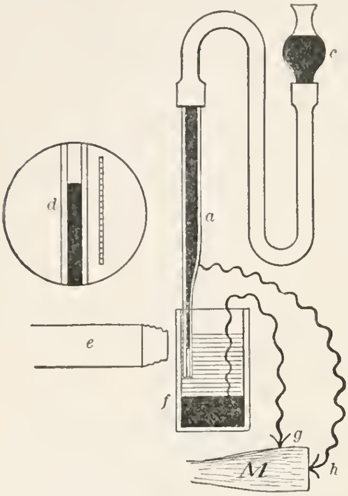

FIG. 63.—Schema of capillary electrometer.

The movements of a galvanometer may be recorded photographically by letting the beam of light reflected from the mirror fall through a horizontal slit on a photographic plate. If the plate be arranged to descend at a regular rate in a dark chamber behind the screen holding the slit, the movements of the galvanometer magnet will be pictured as black lines on a white ground.

The movements of the mercury column of a capillary electrometer may be recorded in a similar manner, by placing the instrument in front of a vertical slit behind which a photographic plate or sheet of sensitized paper moves horizontally. If a strong light falls on

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[1] Bernstein: *Pflüger's Archiv*, 1898, Bd. lxxiii. S. 376.

the slit, it will influence the sensitized surface except where the mercury column intervenes; the movements of the mercury will be photographed as a silhouette.

2. **Currents of Rest.**—A normal resting nerve or muscle presents no differences in electric tension and gives no evidence of electric currents, wherefore we say it is iso-electric. If any part of the structure be injured, its electrical condition is forthwith changed, and if the injured portion and some normal part be connected with a galvanometer, an electric current is observed to flow from the normal region to the point of injury. These muscle-currents were discovered at about the same time by Matteucci and Du Bois-Reymond, and the latter wrote a now celebrated treatise upon the electrical phenomena to be observed in the nerve and muscle under varying conditions.[1]

Directions of Currents of Rest.—If a striated muscle, with long parallel fibres, such as the sartorius or the semimembranosus of a frog, be prepared with care not to injure the surface, and then be given a cylindrical shape by cutting off the two ends at right angles to the long axis, the piece will present two cross sections of injured tissue and a normal longitudinal surface (see Fig. 64). If non-polarizable electrodes, connected with the coils of wire of a galvanometer, be applied to various parts of such a piece of muscle, it will be found that all points on the longitudinal surfaces are positive in relation to all points on the cross sections, but that the differences of tension will differ according to the points which are compared. Suppose that the cylinder be divided into equal halves by a plane parallel to the cut ends. Points on the line bounding this plane, the equator, show the greatest positive tension, and the farther other points on the longitudinal surface are from the equator the less their tension. Points on the cross section show a negative tension, and this lessens from the centre to the periphery of the cross section. Points on the cross section equidistant from the centre, or on the longitudinal surface equidistant from the equator, have the same potential and give no current, while points placed unsymmetrically give a current. Splitting the cylinder by separation of the parallel fibres gives pieces of muscle which show the same electrical peculiarities, and without doubt the same would be true of separate muscle-fibres or pieces of fibres.

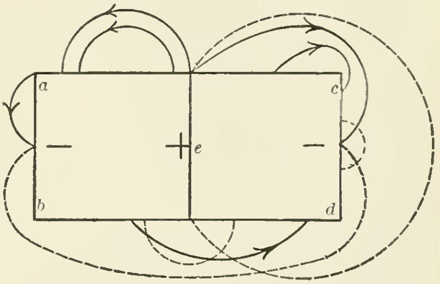

FIG. 64.—Schema to show the direction of currents to be obtained from muscle. The schema represents a cylindrical piece of muscle with normal longitudinal surface (*a*, *c* and *b*, *d*), and two artificial cross sections (*a*, *b* and *e*, *d*). The position of the equator is shown by line *c*. The unbroken lines connect points of different potential, and the arrows show the direction which the currents would take were these points connected with a galvanometer. The broken lines connect points of equal potential from which no current would be obtained.

Samjloff[2] says that the electro-motive force of the currents ordinarily

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[1] *Untersuchungen über thierische Elektricität*, Berlin, 1849.

[2] Samjloff: *Pflüger's Archiv*, 1899, Bd. lxxviii. S. 1.

obtainable from muscle, 0.06–0.08 volt, represents only about 80 per cent. of the true electro-motive force of the muscle-currents, because only a part of the current is led off to the galvanometer, the rest being short-circuited through the fluids surrounding the muscle-fibres, and in the sheath of the muscle.

The fact that there is a difference in electrical potential between the normal longitudinal surface and the injured cross section of the muscle can be ascertained by the use of the "physiological rheoscope," as the nerve-muscle preparation is called. If the nerve of a fresh nerve-muscle preparation be allowed to fall so as to suddenly close a circuit between these two parts of the muscle, an electric current will flow through it, it will be excited, and the muscle will contract. A muscle can even be made to stimulate itself by its demarcation current, if some point on the equator be suddenly connected with a fresh cross section by a good conductor.

Theories as to Cause of Currents of Rest.—Du Bois-Reymond,[1] impressed by the facts which he had ascertained as to the direction of action of the electromotive forces exhibited by the muscle, tried to explain the difference in electrical tension of the surface and cross section on the supposition that the muscle was composed of electro-motive molecules which presented differences in electric tension similar to those shown by the smallest particles of muscle which it is possible to study experimentally. Further, he considered these differences in tension, and the consequent electric currents, to exist within the normal muscle—the longitudinal surface and normal cross section, *i. e.* the point where the muscle-fibre joins the tendon, having the same sort of difference in electric potential as the normal longitudinal surface and the artificial cross section. When the muscle is injured the balance of the electro-motive forces within is lost, and they are revealed. It is difficult to refute such a theory by experiment, because our instruments only record differences in tension at points on the surface of the muscle to which we can apply the electrodes. We cannot say that there is an absence of electric tension or lack of electric currents within the normal resting muscle; we can only say that there is no direct experimental evidence of the existence of such currents.

Another theory of the electrical phenomena observed in muscle, and one which has found many adherents, was advanced by Hermann.[2] According to Hermann's view there are no differences in electric potential and no electric currents within the normal muscle; the "current of rest" is a "current of injury," a "demarcation current," *i. e.* it is due to chemical changes occurring in the dying muscle-tissue at the border line between the injured and living muscle-tissue.

Although the greatest differences in potential are observed when many muscle-fibres are injured, as when a cut is made completely through a muscle, injury to any part causes that part to become negative as compared with the rest. Even an injury to a tendon causes a difference in potential. It is exceedingly

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[1] Du Bois-Reymond: *Gesammelte Abhandlungen*, 1877, Bd. ii. S. 319.

[2] Hermann: *Handbuch der Physiologie*, 1879, Bd. i. S. 235.

difficult, therefore, to expose a muscle without injuring it; but this can be done in the case of the heart ventricle, and Engelmann showed that this gives no current when at rest, although a current is found as soon as any part is hurt, the part becoming immediately negative in relation to other uninjured parts. In experiments on isolated, long, parallel-fibred muscles, the current which is caused by the injury of one extremity is found to fade away only very gradually (it may last forty-eight hours or more), and this current can be strengthened but little by new injuries. In the case of the heart-muscle the current caused by cutting off a piece of the ventricle soon disappears, but another current of equal strength is got if a new section be made by cutting off the tissue injured by the first cut. In the case of the long-fibred muscles the death process gradually progresses the length of the injured fibres, while in the case of the heart-muscle, in which the cells are very short, the death processes are limited to the injured cells, and on their death the current disappears; when a new cut is made other cells are injured and again a strong current is obtained.

Dead tissue gives no current; normal resting living tissue gives no current; dying tissue is electrically negative as compared with normal living tissue.

Hering[1] has carried Hermann's view that electrical change is the result of chemical action still further. He considers that the condition of negativity is an evidence of katabolic (breaking-down) chemical processes and that anabolic (building-up) chemical processes are accompanied by a positive electrical change. Like Du Bois-Reymond, he believes that the normal resting muscle may be the seat of electro-motive forces which do not manifest themselves as long as the different parts are in like condition.

Current of Rest of a Nerve.—Nerves like muscles show no electric currents if normal and resting, but give a demarcation current if injured, the dying portion being negative to normal parts, and the direction of the currents is the same as injured muscle. The current of injury of a nerve lasts only a short time. The death process which is the immediate result of the injury proceeds along the nerve only a short distance, perhaps to the first node of Ranvier, and when it has ceased to advance the current fails; a new injury of the nerve causes another demarcation current as strong as the first. Gotch and Horsley[2] ascertained the electro-motive force in the nerve of a cat to be 0.01 of a Daniell cell and of an ape only 0.005, while in the spinal nerve-roots of the cat it was 0.025, and in the tracts of the spinal cord of the cat 0.046, and of the ape 0.029. Larger currents are obtained from non-medullated nerves, probably because a non-medullated nerve contains a larger number of axis-cylinders than a medullated nerve of the same size. The olfactory nerve of the pike may give a current of 0.0215 to 0.0105 Daniell, while a piece of a frog's sciatic of equal diameter would give a current of only 0.006 Daniell.[3]

Hering found that an irritable nerve, like a muscle, could be excited by

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[1] Hering: *Lotos*, 1888, Bd. ix.; translation in *Brain*, 1897.

[2] *Philosophical Transactions*, 1891, B., vol. 182, pp. 267–526.

[3] Kuehne and Steiner: *Heidelberger Untersuchungen*, 1880, iii. S. 149–169.

its own current, provided the longitudinal and fresh cross section were united suddenly by a good conductor.

3. **Currents of Action in Muscle.**—Just as the dying tissue of nerves and muscles is electrically negative as compared with normal tissue, so active nerve- and muscle-tissue is electrically negative as compared with resting tissue.

Du Bois-Reymond discovered that if the normal longitudinal surface and injured cut end of a muscle were connected with a galvanometer and the muscle were tetanized, the magnet swung back in the opposite direction to the deflection which it had received from the current of rest. This backward swing of the magnet was not due to a lessening of the current of rest, for if the effect of the current of rest on the galvanometer were compensated for by a battery current of equal strength and of opposite direction, so that the needle stood at 0, and the muscle were then tetanized, there was a deviation of the needle in the opposite direction to that given it by the current of rest. Du Bois-Reymond called this current of action the negative variation current. This negative variation current was found to last as long as the muscle continued in tetanus. On the cessation of the stimulus the current subsided more or less rapidly and the needle returned more or less completely to the position given it by the current of rest before the excitation. The return was rarely complete, and by repeated excitations there was a gradual lessening of the current of rest, the amount varying with the extent of the preceding irritation. The strength of the current of action is influenced greatly by the condition of the muscle, the temperature, etc. It increases with increasing strength of excitation, in the same way as the strength of the contraction.[1]

Secondary Tetanus.—Matteucci and Du Bois-Reymond (1842) both discovered the phenomenon which Du Bois-Reymond called secondary tetanus. If two nerve-muscle preparations be made, and the nerve of preparation *B* be laid on the muscle of preparation *A*, when the nerve of *A* is stimulated, not only the muscle of *A* but the muscle of *B* will twitch (see Fig. 65).

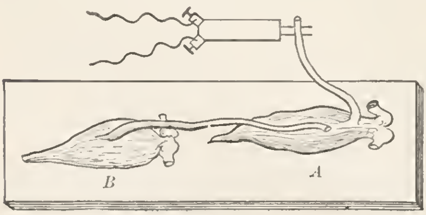

FIG. 65.—Secondary tetanus.

If nerve *A* be excited by many rapidly following induction shocks so that muscle *A* enters into tetanus, muscle *B* will also be tetanized. The phenomenon is not due to a spread of the irritating electric current through nerve and muscle *A* to nerve *B*, for the tetanus of both muscles stops if nerve *A* be ligated; moreover, a secondary tetanus is obtained in case tetanus of muscle *A* is called out by mechanical stimuli, such as a series of rapid light blows, applied to nerve *A*.

Du Bois-Reymond considered "secondary tetanus" a proof of the discontinuity of the apparently continuous contraction of tetanus, for muscle *B* could only have been excited to tetanus by rhythmic excitations from *A*. Each of

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[1] Burdon-Sanderson: *Journal of Physiology*, 1898, xxiii. p. 323.

the rapidly following excitations applied to *A* was the cause of a separate contraction process and a separate current of action in *B*; the separate contractions combined to produce the tetanus of *B*, but the separate currents of action did not fuse, although they caused a continuous negative variation of the slowly moving magnet of the galvanometer.

The correctness of this view has been shown by experiments with the capillary electrometer, which approaches the "physiological rheoscope," as the nerve-muscle preparation is called, in its sensitiveness to rapid changes in electrical potential.

Burdon Sanderson [1] has obtained, by photographically recording the movements of the column of mercury of the capillary electrometer (see Fig. 63, p. 146), beautiful records of the changes of electric potential which occur when an injured muscle is tetanized.

The record in Figure 66 shows, first, a series of negative changes resulting from the separate stimuli. It is these which cause secondary tetanus and which produced the negative variation current disclosed by the galvanometer in the experiments of Du Bois-Reymond. Second, there is a more permanent negative change, likewise opposed to and lessening the effect of the negative change at the part where the tissue is dying, and called by Sanderson "the diminutional effect." The continuous negative change is possibly attributable to the presence of a continuous contraction process, perhaps the contracture which we observed in studying the tetanus curve (see Fig. 52). This "diminutional effect" is only to be observed upon an injured muscle, since it represents a difference in potential between the normally contracting and the injured, imperfectly contracting muscle-substance. When all parts of the muscle are normal and contracting to an equal amount, the electrical forces would be everywhere of the same nature, balance one another, and give no external evidence. Although the diminutional effect is only to be observed upon the injured muscle, the temporary negative changes which follow each excitation

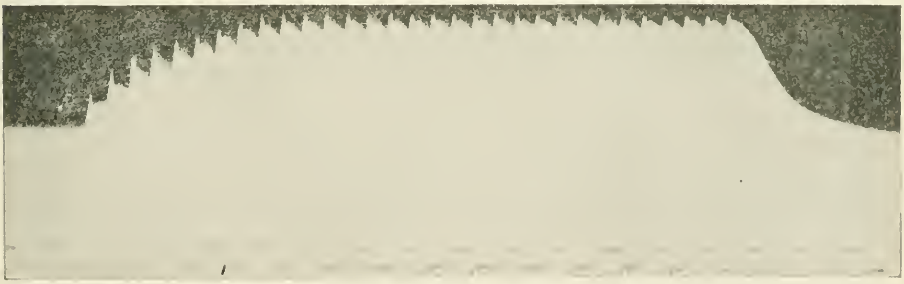

FIG. 66.—Record of changes in electric potential in a tetanized injured muscle of a frog. The leading-off non-polarizable electrodes connected with the capillary electrometer touched the normal longitudinal and injured cut surface of the muscle. The muscle was tetanized by an induction current applied to its nerve, the rate of interruptions being 210 per second. A rise of the curve indicates an electrical change of opposite direction to that caused by the injury. The diminution of the current of injury, which was less than in some other experiments, was 0.008 volt. The time record at the bottom of the curve was obtained from a tuning fork making 500 double vibrations per second (after Burdon Sanderson).

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[1] *Journal of Physiology*, 1895, vol. xviii. p. 717.

are to be observed on the normal muscle. To understand this we must consider the diphasic current of action.

Diphasic Current of Action.—If a normal muscle be locally stimulated by a single irritation, either directly or indirectly through its nerve, the part excited will be the first to become active and electrically negative, and this condition will be taken on later by other parts. Our methods only permit us to observe the relative condition of the parts of the muscle to which the electrodes are applied, the changes in the intermediate tissue failing to show themselves. If an electrode be applied near the place where the uninjured muscle is stimulated, *A*, and another at some distant point, *B*, and these electrodes be connected with a capillary electrometer, a diphasic electrical change will be observed to follow each stimulation. At the instant the irritant is applied the muscle-substance at *A* will become suddenly negative with respect to that at *B;* when the spreading irritation wave has reached *B*, that part too will tend to be negative, and an electrical equality will be temporarily established; finally, *B* continuing to be active after *A* has ceased to act, *B* will be negative in respect to *A*. Since the wave of excitation spreads along the fibres in both directions from the point irritated, each excitation will cause diphasic electrical changes to either side of the place to which the irritant is applied.

If the muscle has been injured at *B*, the dying fibres there will react but poorly to the stimulus, and therefore the antagonistic influence of the negative change at *B* will incompletely compensate for the negativity at *A*, and hence only a single phase due to the condition of negativity at *A* will be seen.

The normally beating heart ventricle shows diphasic currents of action: in the first phase the base, where the contraction process starts, is negative to the apex, and in the second phase the apex is negative to the base. In case the heart be injured, the negative change corresponding to action fails at the injured part, and therefore a single and because not antagonized more prolonged negative change is observed. Under certain conditions a triphasic change is observed, which need not be discussed here. Waller[1] has succeeded in recording the electrical changes which accompany the beat of the human heart.

These diphasic changes of the electric condition are sufficiently strong and rapid in the mammalian heart to excite the nerve of a nerve-muscle preparation, and the muscle will be seen to give one, or, if the heart is uninjured, sometimes two, contractions every time the heart beats.

Bernstein[2] found the time between the two portions of diphasic change to be proportional to the distance between the leading-off electrodes, and to correspond to a rate of transmission the same as that of the wave of excitation, as revealed by the spread of the contraction process (in the muscle of the frog 3 meters per second). Hermann,[3] by using cord electrodes on the human fore-

[1] *Archiv für Anatomie und Physiologie*, 1890; physiol. Abtheil., S. 187.

[2] *Untersuchungen über den Erregungsvorgang im Nerven- und Muskel-system*, 1871.

[3] *Handbuch der Physiologie*, 1879, i. 1, S. 224.

arm, found the rate of spread of the active process by the voluntary contraction of human muscle to be from 10 to 13 meters per second. Du Bois-Reymond dipped a finger of each hand into fluid contained in cups connected with a galvanometer. If the muscles of one arm were vigorously contracted, a deflection of the magnet was seen. This was probably due to electric currents from the glands of the skin and not from the contracting muscles.

Relation of the Negative Variation Current to the Contraction.—Bernstein observed the negative variation of the demarcation current of the muscle almost at the instant that the muscle was excited and before the contraction began to be recorded—*i. e.*, during the mechanical latent period of the muscle—and concluded that it is associated with the excitation rather than the contraction process. This view is supported by others,[1] who find that the highest point of the negative change is generally passed before the contraction shows itself.

On the other hand, it is reported that the negative state may continue throughout the contraction. Sanderson and Page[2] saw the diphasic change which accompanies the beat of the heart to last throughout the systole; and Lee[3] found the diphasic change which occurs when a skeletal muscle of a frog is excited by a single stimulus, to continue as long as the muscle remains active, including the period of relaxation; in some cases it lasted from 0.05 to 0.06 second. Sanderson, as we have seen (see Fig. 66), tetanized injured skeletal muscles of the frog, and found not only a series of negative variations corresponding to the contraction processes which resulted from the separate excitations, but also a continuous negative variation, the diminutional effect, which developed comparatively slowly and lasted after the irritant had ceased to act.

Still other observers, who claim that the electrical state of the muscle is closely related to the contraction process, find sometimes a negative and sometimes a positive change, according as the contractions are isometric or isotonic.

A further consideration of this subject would be out of place here. Suffice it to say that there can be no doubt that the change which occurs in muscle substance when it is excited is associated with a change in its electrical condition; whether the subsequent activity of the muscle protoplasm, manifested in the change of form, has also an electrical change associated with it, must be left an open question.

4. **Currents of Action in Nerves.**—In general, the facts which have been stated with regard to the current of action in muscles apply to nerves. When a normal nerve is excited a negative change is forthwith developed at the stimulated point and passes thence in both directions along the nerve at the same rate as the nerve-impulse. This change is diphasic, first the part excited and later distant parts showing the negative change. If the nerve

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[1] Jensen: *Pflüger's Archiv*, 1899, Bd. lxxvii. S. 107.

[2] *Journal of Physiology*, 1879, vol. ii. p. 396.

[3] *Archiv für Anatomie und Physiologie*, 1887, S. 204.

be injured, and the normal surface be compared with the dying or dead cross section, the second phase is absent. If the nerve be frequently excited, each excitation awakens a separate current of action.

Although nerves are excited most readily by electric currents, negative variations of the demarcation current may be called out by various chemicals —*e. g.*, salt or glycerin[1]—and by mechanical excitation, such as a sharp cut with the shears.[2] It is a physiological phenomenon, for a negative change may be observed to accompany a nerve impulse which has been caused by the spread of excitation from central neurones along their peripheral axones.

Du Bois-Reymond observed with the galvanometer a lessening ("negative variation") of the demarcation current ("current of rest") when in strychnia-poisoning the spinal motor neurones were sending vigorous impulses along their axones and causing cramp-like tetanic muscular contractions. Gotch and Horsley[3] applied electrodes connected with a capillary electrometer to peripheral nerves, spinal nerve-roots, and tracts of motor fibres within the spinal cord, and discovered that if the cortical brain-cells in the motor zones were excited, the nerves showed currents of action corresponding in rate to the discharge of motor impulses from these brain-cells—*e. g.*, if the epileptiform convulsions were occurring at the time, the capillary electrometer revealed changes of potential of like rate in the nerves.

Macdonald and Reed[4] observed currents of action in the phrenic nerve of mammals which corresponded in time with the respiratory movements. These were due to the normal discharge of nerve impulses from the respiratory centers. When a condition of apnœa was established and the respiratory movements ceased, the electrical change failed to appear; when the respiratory movements were quickened in dyspnœa, the rhythmic movements of the galvanometer were quickened to correspond; when during asphyxia the respirations were of the Cheyne-Stokes type, the currents of action showed a like rhythm.

Even physiological sensory nerve-impulses have been found to produce negative variation currents. Steinach[5] observed currents of action to be caused by mechanical pressure on the skin of the frog. If the pressure was continued, the negative change gradually decreased, and a new negative variation was seen if the pressure was suddenly removed.

Light falling on the retina of the eye of a frog has been seen to cause a negative variation of the current of rest of the optic nerve.

The electrical change which we call the current of action can be thought to sweep over the nerve as a wave, having in the medullated nerves of the frog a length of 18 mm., and travelling at the rate of 28 meters per second. The duration of the negative variation is different in different kinds of nerves

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[1] Kühne und Steiner: *Untersuchungen aus der physiologischen Laboratorium in Heidelberg*, 1880, Bd. iii. S. 149.

[2] Hering: *Lotos*, Neue Folge, 1888, Bd. 9, S. 35.

[3] *Physiological Transactions*, 1891, vol. 182, pp. 267–526.

[4] Macdonald and Reed: *Journal of Physiology*, 1898, vol. xxiii. p. 100.

[5] Steinach: *Pflüger's Archiv*, 1896, Bd. lxiii. S. 495.

and in the same nerve under different conditions. In the medullated nerves of the frog it lasts 0.008 to 0.024 second;[1] in the non-medullated nerves of the pike the rise of negativity requires 0.08–0.029 second and the fall 0.40–1.2 second.[2] The rate of conduction is slowed by cold, and this at the same time lengthens the accompanying electrical change. This fact has been made use of to ascertain that in the uninjured nerve, as in the muscle, there is a diphasic current of action spreading in both directions from the point of excitation.

The strength of the electrical change which takes place in a nerve when it is excited is the best evidence which we have of the activity of the nerve. The physiological structures which the nerve normally excites obey laws peculiar to themselves, and are liable to give results which are open to misinterpretation. For example, if a nerve be stimulated in the middle, the condition of activity aroused spreads in both directions, and causes at the one end a contraction of the muscle, and at the other a negative variation of the current of rest, which may be observed with a galvanometer. If the nerve be excited many times in succession, the height of the muscular contractions is seen to decrease while the electrical changes show no sign of fatigue. The decrease in the height of the contractions is really due to the fatigue of the nerve ends and the muscle, and the constancy of the electrical changes is the truer expression of the state of the nerve.

A difficulty presents itself here, however: the negative variation currents observed in such an experiment may be so very regular as to suggest that they are physical rather than physiological phenomena. That they are not purely physical can be ascertained by subjecting the nerve to influences of a type to alter the physiological activity of the protoplasm, without permanently, or indeed markedly, altering its chemical and physical structure. A study of the effect of anæsthetics on the nerve is especially instructive. In general, anæsthetics are found first to heighten, later to lower, and finally to destroy the irritability.

If the anæsthesia is not carried too far, the nerve may completely recover its function on the removal of the drug. Waller[3] describes the following experiment: A fresh nerve is placed on two pairs of non-polarizable electrodes in a moist chamber. One pair is connected with the galvanometer which is to record the current of action, the other pair is connected with an induction apparatus, and brings the exciting current to the nerve. Induction shocks of equal strength are sent into the nerve at regular intervals, and the extent of the currents of action awakened is noted. After the electrical response of the nerve has been tested, fumes of ether (diethyl oxide) are blown through the chamber. At first the electrical response is found to be increased, later it decreases, and at the end of three or four minutes it is altogether lost. If air be now allowed to enter the chamber, the current of action reappears,

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[1] Biedermann: *Electrophysiology*, translation by F. A. Welby, 1898, vol. ii. p. 260.

[2] Gärtner: *Pflüger's Archiv*, 1899, Bd. lxxvii. S. 498.

[3] Waller: *Lectures on Animal Electricity*, 1897, Lecture II.

and at the end of from five to ten minutes may be even stronger than it was at the start. Chloroform, likewise, inhibits the activity of the nerve; but it is even more vigorous in its action and the nerve is less likely to recover. The vapor of ethyl alcohol, after a preliminary exhilarating effect, paralyzes the nerve; under favorable conditions the nerve recovers in a few hours. The action of CO_2 is particularly interesting, since this is one of the normal waste products of the body. In small doses it is found to increase the strength of the current of action, while in large doses it has an anæsthetic effect. The nerve is so sensitive to CO_2 that even a fiftieth of a milligram suffices to change its irritability: the amount that is contained in the expired air, 4 per cent., suffices to do away with the current of action in three minutes.

In general, whatever increases the irritability of the nerve increases the negative variation currents which result from its excitation. For instance, if a nerve be excited at regular short intervals with induction shocks of equal strength, there is a staircase-like increase in the negative variation current; moreover, if it be subjected for a short period to tetanic excitation, the current of action called out by a single shock is found to be increased.[1] Indeed if one photographically records the movements of the galvanometer magnet in such experiments, he obtains a curve closely resembling that obtained by records of muscular contractions when the muscle is so excited (see Fig. 57). Waller suggests that the effect of excitation to increase the irritability of the nerve may be due to the production of CO_2 by the nerve, and a consequent internal stimulation. The fact that the nerve does not fatigue he would explain as the result of rapid restoration of the protoplasm and a rapid neutralization of waste products.

Apparently the strength of the current of action can be taken as a fair index of the activity of the nerve, and consequently of the strength of the nerve impulse. This view corresponds with the fact that there is a close relation between the strength of the current of action of the muscle and the height of the contraction. Waller[2] and Green[3] found experimentally that a current of action can be detected with difficulty with subminimal irritants; but as the strength of the current is raised above the threshold intensity the strength of the electrical change increases proportionally to the strength of the excitation, until a point is reached which is far beyond what is needed to excite maximal muscular contractions. After this the increase is less and less, until finally a maximal current of action is reached. This occurs with a strength of excitation much stronger than is required to call out a maximal muscular contraction, and probably beyond the limit of functional action. It is doubtful whether the nerve-cell could excite such a condition in a nerve.

On account of the great resistance of the nerve, and the short-circuiting

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[1] Waller: *Lectures on Animal Electricity*, 1897, p. 59.

[2] Waller: *Brain*, xvii. p. 200.

[3] Green: *American Journal of Physiology*, 1898, p. 104.

of a part of the current by the lymph, etc., the currents which may be obtained are usually small. Under especially favorable conditions the current may be twice as great as the current of rest, and Gotch and Burch state that they have found it in the sciatic nerve of the frog to have the excitatory effect of 0.033 volt.[1] Hering[2] has shown that it may suffice to excite another nerve in close contact with it, the experiment being of the same type as that described as secondary tetanus, p. 150.

The fact that a negative variation of the demarcation current of a bundle of nerve-fibres may excite other fibres lying beside them in the same nerve, is the explanation of the so-called "paradoxical contraction." This may be seen under the following conditions: Take a frog that has been kept in the cold so that its nerves are very irritable; dissect out the branches of the sciatic nerve at the knee, ligature, divide below the ligatures, and then dissect up the nerve as far as the branches given off to the muscles of the thigh; expose the nervous plexus at the back of the abdominal cavity, and divide close to the spinal cord; remove all extra fluid, and avoid wetting the nerves with salt solution. Raise up the knee end of the nerve, and place on electrodes connected with the secondary coil of an induction apparatus: excite with weak tetanizing current close to the end of the nerve, and see the thigh muscles contract. As the fibres excited at the knee have no anatomical or physiological connection with the fibres of the branches of the nerve distributed to the thigh muscles, the nerve impulse which passes up the nerve could not reach these fibres, and the contraction could not occur were it not for the spread of the current of action under these abnormal conditions. To make sure that the contraction is not due to a spread of the exciting current or to unipolar stimulation effects, one can ligature the nerve above the excited point. This would stop the progress of the nerve impulse and the accompanying current of action, and prevent the "paradoxical contraction." There is still another possible source of error that has to be guarded against: the exciting current, through electrolytic effects, may cause electrotonic currents (see p. 62) to be developed in the nerve, and these may spread sufficiently to excite branches of the thigh muscles. A ligature will stop the spread of these currents, but their presence can be recognized from the fact that the contractions will be the stronger the nearer the electrodes are brought to the part of the nerve from which the branches to the thigh muscles are given off. A contraction called out in this way is called the "electrotonic twitch." A spread of the current of action to neighboring fibres never occurs when the nerve is intact, the rule of isolated conduction by nerve-fibres holding good.

Relation of the Electrical Phenomena of the Nerve to Physiological Processes.—Certain writers of the extreme mechanical school would explain all the forms of functional activity of the nerve as purely physical processes, which result from chemical change occurring within it. This point of view

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[1] *Proceedings of the Royal Society*, 1900, vol. lxv. p. 441.

[2] Hering: *Sitzungsberichte der Wiener Akadamie*, 1882, lxxxv. 3, S. 237.

is largely based on the remarkable results which have been obtained by the study of artificial models of nerves, called core-conductors. These were first carefully studied by Hermann,[1] and since then by Boruttau,[2] Waller,[3] and others. Such a model can be made by placing a platinum wire in a glass tube, and surrounding it with a 0.6 per cent. salt solution. The wire represents the axis-cylinder of the nerve, and the salt solution the medullary sheath. In other models both core and sheath have been made of fluid electrolytes. With such a core-conductor, one can observe electrical phenomena so closely resembling those manifested by the normal nerve that the statement has been made that all the electrical phenomena of the living nerve can be explained if one will look upon it as a core-conductor.[4] According to this idea, conduction in nerve depends on the transmission of an electrical phase caused by local differences in potential, resulting from chemical changes and consequent polarization effects produced when the nerve is excited.

This extreme view is accepted by few physiologists.[5] The electrical effects which follow excitation are exhibited not only by nerves, but also by a great variety of protoplasmic structures; they are stopped by anæsthetics, which do not alter the core-conductor-like structure of the nerve, and are greatly modified by all influences which are capable of changing the irritability of living protoplasm, even though they are too feeble to produce any recognizable change in dead matter; finally, they are called forth, not only by electric currents, but by every form of stimulus capable of exciting living protoplasm to action.

It is very easy to be led astray by the similarity of processes observable on very different structures, and think to see the whole truth in what is only a partial truth. As Engelmann has shown, the anisotropic substance in a piece of catgut suspended in water will cause it to shorten and then lengthen if quickly heated and then cooled, and if a lever be connected with it, to write a curve strikingly like that of the contracting muscle. In muscle there is anisotropic material surrounded by fluid, and heat is produced at the instant of contraction; it is doubtful, however, whether the physiological contraction process is of the same type as that of the piece of catgut. Within the body we have oxidation processes going on, and heat is liberated as it is outside of the body in combustion, but the two sets of changes giving this result are not identical. Similarly we may say that the heart is a pump, and the eye a camera, but the behavior of these living organs is very different from that of lifeless machines.

All physiological phenomena are to be regarded as of chemico-physical nature, but many of them differ so widely from the chemical and physical processes associated with dead matter that a sharp distinction should be

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[1] *Pflüger's Archiv*, 1872, Bd. v., vi., vii.; also *Handbuch der Physiologie*, 1879, Bd. ii. S. 17.

[2] *Pflüger's Archiv*, 1894–1897, Bd. lviii., lix., lxiii., lxv., lxvi., lxix.

[3] *Lectures on Animal Electricity*, London, 1897.

[4] Boruttau: *Pflüger's Archiv*, 1894, Bd. lviii. S. 64.

[5] Biedermann: *Electrophysiology*, translated by F. A. Welby, 1898, vol. ii. p. 303.

made. Purely physiological phenomena are such as can be exhibited only by a mechanism which has the chemical and physical structure of living protoplasm, and such as cease with the life of the protoplasm.

The electrical phenomena of nerve are capable of being divided into two classes, the one, purely chemico-physical, resulting from the core-conductor-like structure, and the other, physiological, intimately dependent on the reactions of the living protoplasm. The medullated nerve is not merely a core-conductor.

It is too soon to try to separate these two classes of phenomena; we must wait not only for more work to be done on nerves, but on other irritable forms of protoplasm, for many of these, although of entirely different structure from the nerve, exhibit very similar electrical reactions.

F. Chemistry of Muscle and Nerve.

1. Chemistry of Muscle.

Muscles consist of muscle-fibres bound together by connective tissue. Between the fibres we find nerves, blood-vessels, and lymphatics. Fat-cells containing considerable fat may also be found in the midst of the connective-tissue network. Each fibre consists of a sheath, the sarcolemma, which resembles elastin in its constitution, and within this the muscle-substance proper, together with certain substances of nutritive value and waste products.

Muscle which has been freed as far as possible from blood, connective tissue, and fat, has a mean specific gravity of 1.060; the extreme variations found for the muscles of different animals being 1.053–1.074.[1] When it is fresh the reaction is slightly alkaline.

It contains about 75 parts of water and 25 parts of solids; nearly 20 parts of the solids are proteids, the remaining 5 parts consisting of fats, extractives, and salts.

Little is known concerning the chemistry of living muscle; the instability of the complex molecules which makes possible the rapid development of energy peculiar to muscles renders exact analysis impossible. The manipulations essential to chemical analysis necessarily alter and kill the muscle protoplasm.

Death of the muscle is ordinarily associated with a peculiar chemical change known as *rigor mortis*. To understand the chemical composition of muscle it is necessary that we should consider the nature of this change.

1. **Rigor Mortis.**—*Rigor mortis,* the rigidity of death, is the result of a chemical change in the substance of a muscle by which it is permanently altered, its irritability and other vital properties being irretrievably lost. The change is manifested by a loss of translucency, the muscle becoming opaque, and by a gradual contraction, accompanied by a development of heat and acidity, and resulting in the muscle being stiff and firm to the touch, less elastic, and less extensible. Whenever muscle dies it undergoes this change.

[1] Carvallo and Weiss: *Journal de Physiologie,* 1899, i. p. 204.

Conditions which Influence the Development of Rigor.—Ordinarily on the death of the body the muscle enters into rigor slowly—the muscle-fibres are involved one after the other, and through the gradual contraction and hardening of the antagonistic muscles the joints become fixed and the body acquires the rigidity which we associate with death. Rigor usually affects the different parts of the body in a regular order, from above downward, the jaw, neck, trunk, arms, and legs being influenced one after the other. The position taken by the body is generally determined by the weight of the parts and the relative strength of the contractions of the muscles.

The time required for the appearance of rigor is very variable. It is determined in part by the nature of the muscle, its condition at the moment of death, and the temperature to which it is subjected. The muscles of warm-blooded animals enter into rigor more quickly than those of cold-blooded animals; of the warm-blooded animals, pale muscles more quickly than red, and the flexors before the extensors; of the cold-blooded animals, frog's muscles more quickly than those of the turtle. In general, the more active the muscle protoplasm, the more rapid are the chemical changes which it undergoes, and amongst these the coagulation of rigor mortis.

The condition of the muscle plays a very important part in determining the onset of rigor. If the muscles are strong and vigorous and death of the body has come suddenly, rigor develops slowly; if the muscles have been enfeebled by disease or fatigued by great exertion shortly before death, it comes rapidly. In the case of wasting diseases rigor comes quickly, is poorly developed, and passes off quickly; when the muscles are fatigued at the time of death, as in the case of a hunted animal, it comes quickly. We hear of soldiers found dead on the field of battle grasping the sword, as if the muscular contractions of life had been continued by the contractions of death. In the case of certain diseases of the spinal cord and brain, too, rigor may come so rapidly that the limbs may maintain the position which they had at the time of death, "cataleptic rigor," as it has been called. The coming on of rigor is particularly striking in the case of diseases which, like cholera, are accompanied by violent muscular cramps and lead to a rapid death. It is not uncommon, in such cases, for the contractions of rigor to cause movements which may mislead a watcher into supposing the dead man to be still alive. This idea is favored by the fact that the body may remain warm, owing to the heat which is produced in the muscles as a result of the chemical changes occurring during rigor. The post-mortem muscular contractions and the rise of temperature observed in such cases are only excessive manifestations of what always occurs on the death of the muscle. The movements are probably due, in part, to the rapidity with which the muscles contract in rigor, and in part to the fact that the antagonistic muscles are not affected at the same time to the same degree. Whether the contractions are partly excited by changes accompanying the death of the motor nerve-cells in the central nervous system is uncertain, but not impossible. Muscles are still able to respond by contractions to stimuli coming to them through the nerve, even after rigor has become quite pronounced, probably because the coagulation process attacks the different fibres at different rates, and certain of the fibres are still alive and irritable after the others are dead and coagulated.

Many observers favor the view that the central nervous system influences muscles after the death of the body as a whole, and by weak stimuli resulting from the changes in the nerve-cells excites chemical changes in the muscles which favor the coming on of rigor.[1] In proof of this it is stated that curarized muscles enter into rigor more slowly than non-curarized. Undoubtedly stimulation of the nerve, or, indeed, anything which would excite a muscle to action, tends to put it in a condition favorable to the coming on of rigor; whether the influence exerted by the central nervous system is more than this is very questionable.

Temperature has a marked influence on the development of rigor mortis. Cold delays and warmth favors, 38°–40° C. being most favorable. Since rigor is the result of a chemical change, these effects of temperature are what one would have expected. Other forms of chemical change which are attributable to ferment action are found to be the most vigorous at a temperature of about 40° C.

In general, it may be said that rigor in warm-blooded animals comes on in from ten minutes to seven hours after death, although some state that it may come as late as eighteen hours. It lasts anywhere from one to six days. The sooner it comes on, the sooner it goes off. The stiffness can be broken up artificially by forced movements of the parts, and when thus destroyed does not return, provided the rigor was complete at the time.

The Cause and Nature of the Contraction of Rigor Mortis.—The most likely explanation of the contraction of the dying muscle is that it is the result of the coagulation of a part of the semi-fluid muscle-substance within the sarcolemma. This was suggested by Bruecke, and Kuehne proved that such a coagulation change takes place, by showing that the semi-fluid muscle-substance, "the muscle-plasma," if expressed from the frozen muscle, coagulates on being warmed. The coagulation is the result of a chemical change, by which two proteids of the plasma, paramyosinogen and myosinogen, are converted into the coagulated proteid myosin, this change being produced by the action of a ferment, the myosin ferment, which is thought to be formed at the death of the muscle.

Another, though less generally accepted view, is that the contraction of the muscle seen in rigor is of the same nature as ordinary muscular contractions.[2] Prolonged muscle contractions are observed under a great variety of conditions (see p. 127), and there are many points of resemblance between the contraction of normal and dying muscle—viz., the change of form, the production of heat, the formation of sarcolactic acid, the using up of oxygen and the production of carbon dioxide, and the fact that the dying and presumably coagulating muscle is, like normal contracting muscle, electrically negative

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[1] Brown-Séquard: *Archives de Physiologie*, 1889, p. 675.

[2] Hermann: *Handbuch der Physiologie*, 1879, Bd. i. S. 146.

as compared with normal resting muscle. To this may be added that, as has been said, the muscle continues to be irritable even when rigor is quite advanced, and that it enters into rigor more quickly if left in connection with the central nervous system.

On the other hand, one cannot fail to be impressed with the differences between the two forms of contraction.

Normal Contracting Muscle.	*Muscle contracting by Rigor Mortis.*
Contains uncoagulated proteids.	Contains coagulated myosin.
Is translucent.	Is opaque.
Is soft and flexible.	Is firm and stiff.
Is no less elastic than in repose.	Is less elastic than before.
Is more extensible than in repose.	Is less extensible than before.
Contracts rapidly.	Contracts very slowly, as a rule.
Fatigues rapidly and relaxes.	Remains contracted a long time.

Furthermore, it may be added that normal contractions only occur when the irritable muscle is stimulated, while a muscle can enter into rigor when its irritability has been taken away by subjecting it to oxalate solutions,[1] also, when it has been curarized and so shut out from all nervous influences.[2]

Rigor is not confined to the voluntary muscles, though it is less easily observed in the case of most involuntary muscles. The heart enters rapidly into rigor, with the formation of sarcolactic acid. The non-striated muscle of the stomach and ureters, too, has been seen to undergo this change.

The passing off of rigor mortis is usually accompanied by beginning decomposition, and, indeed, it has been thought that the decomposition is the cause of softening of the muscle. This is denied by certain observers, and it is stated that rigor may pass off when the presence of putrefactive organisms is excluded by special aseptic precautions. Another explanation is that a process of intramuscular digestion goes on. Pepsin, a proteolytic ferment, has been found in small amounts in the muscle; and acid, which is necessary to the action of this digestive ferment, is formed in the muscle when it coagulates. The presence of these substances would make the digestion of proteid material possible, and the fact that proteoses and peptone, products of such digestion, are to be found in the muscle after death, though not present during life, favors the view. It cannot be considered, however, to be definitely established.

The rigidity of muscles in rigor can be readily broken up by stretching and massaging the muscles, and when this has been done it does not return.

The Chemical Changes which accompany the Development of Rigor.—Rigor mortis is characterized by the coagulation of a part of the muscle-substance; this can be prevented by a temperature a little below 0° C. Cold, although temporarily depriving the muscle of its irritability, does not, unless extreme and long-continued, kill the muscle protoplasm. Frogs can be frozen stiff and recover their activity when they thaw out. Indeed, this probably happens not

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[1] Howell: *Journal of Physiology*, 1893, vol. xiv. p. 476.

[2] Nagel: *Pflüger's Archiv*, Bd. lviii. S. 279.

infrequently to the frogs hibernating in holes in the banks of ponds. Since cold prevents coagulation without destroying the life of the muscle protoplasm, we can by its aid isolate the living muscle-substance from the nerves, blood-vessels, connective tissue, and sarcolemma of the muscle, but as soon as we begin to analyze it it loses its living structure. This method of obtaining muscle-plasma was introduced by Kuehne[1] in the study of the muscles of frogs, and was later employed with slight modifications by Halliburton[2] for the muscles of warm-blooded animals. The blood was washed out of the vessels with a stream of 0.6 per cent. sodium-chloride solution at 5° C.; the irritable muscles were then quickly cut out and frozen in a mixture of ice and salt. The frozen muscle was then cut up fine in the cold, and a yellowish, somewhat viscid, and faintly alkaline muscle-plasma was squeezed out. This fluid was found to coagulate in twenty to thirty minutes at a temperature of 40° C.; if the temperature were lower the coagulation was slower. The clot, which was jelly-like and translucent, contracted slowly and in a few hours squeezed out a few drops of serum. The coagulated material formed in the clot is called myosin. It dissolves readily in dilute neutral saline solutions, as a 10 per cent. solution of sodium chloride or a 5 per cent. solution of magnesium sulphate, and its saline solutions are precipitated in an excess of water or by saturation with sodium chloride, magnesium sulphate, or ammonium sulphate; it has, in short, the characteristics of a globulin. Chittenden and Cummins state that it has the following composition: C 52.82, H 7.11, N 16.17, S 1.27, O 22.03.

Halliburton, in studying the coagulation of muscle, followed for the sake of comparison the methods which have been employed in the study of coagulation of blood. He found that muscle-plasma, like blood-plasma, is prevented from coagulating not only by cold, but by neutral salts, such as magnesium sulphate, sodium chloride, and sodium sulphate; and further, that the salted plasma if diluted coagulates.

The points of resemblance between the coagulation of myosin in the muscle and fibrin in the blood suggest a similar cause, and Halliburton succeeded in obtaining from muscles coagulated by long standing in alcohol a watery extract, which greatly hastened the coagulation of muscle-plasma. He called the substance thus obtained myosin ferment. The extract obtained contained an albumose which was either the ferment or held it in close combination. The pure ferment has not been isolated. In the case of coagulation of the blood, a proteid of the plasma, fibrinogen, is changed by coagulation to fibrin, this change being brought about by the action of the fibrin ferment, for the formation of which calcium is necessary. The calcium does not enter into the chemical change independently, and it can go on in the absence of calcium provided the ferment has been already formed. In the case of coagulation of muscle, two proteids of the muscle plasma, paramyosinogen and myosinogen, are changed by coagulation to myosin, or,

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[1] *Untersuchungen über das Protoplasma*, Leipzig, 1864.

[2] *Journal of Physiology*, 1887, vol. viii. pp. 133–202.

as Fürth says, to myogen-fibrin and myosin-fibrin[1] by the action of myosin ferment. The change can go on in the absence of calcium, but whether this is essential to the formation of the ferment is not yet known. The myosin ferment is not the same as fibrin ferment, since neither can do the work of the other. Moreover, fibrin ferment is destroyed at 75°–80° C. and myosin ferment is not destroyed till 100° C.

The chemical change which results in the formation of myosin is different from that which produces fibrin. The clotting of muscle-plasma and the formation of myosins are accompanied or closely followed by the production of an acid, while no such change occurs during the coagulation of blood-plasma. In the earlier stages of clotting the acidity may be due in part to acid potassium phosphate, but the final acidity is chiefly due to lactic acid. The source of the lactic acid has not been definitely made out. The view that it comes from glycogen is made questionable by Böhm's[2] observation that the amount of glycogen is not lessened in rigor; besides, the muscles of starving animals become acid when entering into rigor, although, as Bernard found, they contain no glycogen. Böhm concluded that the sarcolactic acid may be formed from the proteids. Probably both glycogen and proteids can yield lactic acid.

Some writers have thought that the coagulation of the muscle was due to the formation of an acid by the dying muscle. This is unlikely, although the presence of acid, like that of many other substances, quinine, caffein, digitalin, veratrin, hydrocyanic acid, ether, chloroform, etc., which lead to alterations in the conditions of the normal muscle-substance, may hasten the process. Apparently, anything which causes a deterioration of the muscle-substance, chemical reagents, drugs, or the products of fatiguing work, hastens the coming on of rigor. On the other hand, anything which helps maintain the normal constitution of the muscle appears to postpone the change. Thus Latimer[3] reports that the circulation of dextrose through fatigued muscle largely does away with the effect of fatigue to hasten rigor mortis. Nor is this because fatigue products are washed out of the muscle, for the circulation of other fluids through the muscle, whether neutral, acid, or alkaline, fails to have the effect.

Rigor Caloris.—If a muscle be heated beyond its normal temperature, its irritability is increased, and it undergoes rapid katabolic changes which lead to its death. These changes, if sufficiently rapid, may bring about a contraction of the muscle, and this contraction, involving the different fibres of the muscle to different degrees, may be continued without break by the contraction that is peculiar to rigor mortis; in addition to this, if the temperature is raised sufficiently, there will be a heat precipitation of the various proteids of the muscle, which will lead to a still further shortening, the contraction

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[1] Furth: *Archiv für experimentelle Pathologie und Pharmakologie*, 1895, xxvi. 231; and 1896, xxxvii. 389.

[2] *Pflüger's Archiv*, 1880, Bd. xxiii. S. 44.

[3] Latimer: *American Journal of Physiology*, 1899, ii. p. 29.

of rigor caloris. The heated muscle may, therefore, be the seat of three different kinds of processes, each of which leads to a shortening. If frog's muscle be gradually heated, it shows three separate contraction movements at three separate temperatures, at about 34°, 47°, 58° C. The last two contractions are due to heat coagulation of paramyosinogen (myosin of v. Furth) at 47° C., and myosinogen (myogen of v. Furth) at 58° C. These are undoubted effects of heat rigor. There is a difference of opinion as to the nature of the first contraction. It has been generally attributed to the coming on of rigor mortis—*i. e.*, to a post-mortem coagulation of paramyosinogen and myosinogen. In case a muscle be rubbed between the fingers, so that its anatomical condition is altered, although the chemical structure remain the same, this form of shortening does not occur, and it is not until the temperatures at which paramyosinogen and myosinogen are coagulated by heat are reached that the muscle begins to shorten.[1] Probably the rigor-mortis change occurs, but on account of the physical change in the fibre it does not reveal itself. This suggests the well-known fact, that when the rigidity of a muscle in rigor has been broken up by mechanical means it does not return. The condition of the muscle has an important influence on the temperature at which it will enter into rigor when heated. Latimer[2] reports that a fatigued muscle will go into rigor at a temperature 10 degrees lower than a fresh muscle will. Probably both fatigue and high temperature are favorable to the formation of the myosin ferment, and heat hastens the fermentation process, resulting in coagulation. Another view of the nature of the first form of contraction has been advanced lately. According to Brodie and Richardson,[3] this contraction in the case of frog's muscle may be very considerable, and is due to heat coagulation of soluble myogen fibrin, a form of proteid which v. Furth found to be formed from myosinogen (what he termed myogen) at 30° C. Mammalian muscles do not show any marked contraction at this temperature, and have not been found to contain myogen fibrin. This form of shortening is seen only by light loads, for the coagulation of the proteids of the muscle causes increased extensibility, in addition to the tendency to contract.[4] The change of form in rigor caloris is more in voluntary than in involuntary muscles, as much as 60 per cent. in the former and 10 per cent. in the latter. The beginning of heat-rigor comes at very different temperatures in the different muscles of different animals. Mammalian muscle can stand several degrees higher than the muscles of cold-blooded animals, heart-muscle can be heated two or three degrees higher than the skeletal muscles, and skeletal muscles differ, *e. g.*, the semimembranosus of the frog enters into rigor sooner than the gastrocnemius.[5] These facts are brought out in experiments in which the temperature of the muscle

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[1] Stewart and Sollmann: 1899, xxiv. p. 428.

[2] Latimer: *American Journal of Physiology*, 1899, ii. p. 29.

[3] *Philosophical Transactions of the Royal Society of London*, 1899, Series B., vol. cxci. p. 353.

[4] Gotschlich: *Journal of Physiology*, 1897, vol. xxi. p. 353.

[5] Ward, H. C.: Unpublished experiments at the University of Michigan.

is more or less rapidly raised, at the same time that the changes in the length of the muscle are recorded on a slowly moving surface. Halliburton[1] gives the following precipitation temperatures for muscle proteids.

	Name.	Temperature of coagulation.
Proteids obtained from the dissolved clot . .	Paramyosinogen	47° C
	Myosinogen	56° C.
Proteids obtained from muscle-serum . . .	Myoglobulin	63° C.
	Myo-albumin	73° C.
	Myo-albumose	(not coagulated by heat).

Constituents of Muscle-serum.—*Proteids.*—The fluid which can be expressed from the coagulated fresh muscle is called muscle-plasma. This undergoes a change in the process of coagulation, two of the globulins present, the para-myosinogen and the myosinogen, being precipitated in the form of myosin, which makes the substance of the clot. The fluid which can be expressed from the clotted muscle, the muscle-serum, therefore lacks at least two of the proteid constituents of the normal muscle. The proteids of the muscle-serum are: myoglobulin, myo-albumin, and myo-albumose.

The myoglobulin resembles serum-globulin, although precipitated at 63° C. instead of 73° C. The myo-albumin is apparently identical with serum-albumin.

To these proteids we must add the pigment hæmoglobin. Another pigment, myohæmatin, is also found. It is not unlikely that these pigments have here as elsewhere a respiratory function.

Although the proteids form the larger part of the solids of the muscle-substance, but little is known as to the form in which they exist in the living muscle or the part that they play in its activity. They seem to have a two-fold function, they are at once the machine and the fuel.[2] Under normal conditions they probably supply but a small part of the energy set free by the muscle during ordinary work. In excessive muscular work they undergo katabolic change, as is shown by the increased excretion of nitrogen and sulphur in the urine. In the case of an individual not in training it would appear that during excessive muscular exercise, as in starvation, other parts of the body may give up their proteids to the muscles, for under such circumstances uric acid and phosphorus-holding extractives, the waste products of nuclein, appear in the urine, and the muscle contains but little nuclein.[3] This is much less the case if the individual is in training, from which it would appear that through training muscles acquire the capacity of storing more proteid or of utilizing their stock to better advantage. In any case if a large amount of muscular work is to be done the amount of proteid in the food should be increased.

Nitrogenous Extractives.—The chief nitrogenous extractive is creatin; in

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[1] Halliburton: *Physiological Chemistry*, p. 414.

[2] Pflüger: *Pflüger's Archiv*, 1899, Bd. lxxvii. S. 425.

[3] Dunlop, Paton, Stockman, Maccadam: *Journal of Physiology*, 1897, xxii. p. 67.

addition to this we find small amounts of creatinin and of various xanthin bodies, as xanthin, hypoxanthin, carnin, carnic acid, and sometimes traces of urea, uric acid, taurin, and glycocoll. The chemical nature of these bodies need not be considered here. Physiologically they may be regarded as waste products which result from the partial oxidation of the proteids of muscle during the katabolic processes which are continually occurring even in the resting muscle protoplasm. Monari has shown that the amount of creatin and creatinin is increased by the wear and tear of muscular work, although the proteids of the well-fed muscle probably supply but little of the energy which is set free.

The *non-nitrogenous constituents* of muscle are fats, glycogen, inosit, dextrose, and lactic acid.

Fats are usually found in intermuscular connective tissue, and there is some within the normal fibre. It is doubtful whether fat plays a direct part in the ordinary metabolic processes involved in the action of muscles, although it is probable that if more available sources of energy are lacking it may, like the proteids, be altered and employed. Bogdanow[1] states that the fat which is within the muscle-fibre is of different constitution from that between the fibres; the extracts contain more free fatty acid. He further found that the fat within the fibre is used up during the work of the muscle, and is continually renewed from the blood. If a muscle of a frog be removed from the circulation and tetanized, it stains much less with osmic acid than one with its circulation unimpaired; while a muscle which is curarized, and so does no work, if it has a good blood-supply, stains much darker than ordinary muscle. Under pathological conditions large amounts of fat may be found inside the sarcolemma; in phosphorus-poisoning the degenerated muscle-protoplasm may be replaced by fat in the form of fine globules.

Glycogen is found in very variable amounts in different muscles. The work of many observers has shown that it is here, as in the liver, a store of carbohydrate material, and is employed by the muscle, either directly or after conversion into some other body, as a source of energy. The quantity, which is rarely more than $\frac{1}{2}$ per cent., lessens rapidly during starvation and muscle work.

When it is required, it is changed to dextrose, and is finally oxidized to CO_2 and H_2O. If the action of the muscle is prevented by the cutting of the nerve or of the tendon, the glycogen is found to accumulate.

Sugar is found in muscles in small quantities only; nevertheless it probably plays an important part, for Chauveau and Kaufmann, by studying the levator labii superioris of the horse, found that the muscles take sugar from the blood, and that they take more during action than rest. The sugar which the muscle takes during rest is for the most part stored as glycogen.[2] Although sugar is considered a source of muscle-energy, the exact way in which it is employed is doubtful.

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[1] *Archiv für Anatomie und Physiologie*, 1897, S. 149.

[2] *Comptes rendus de la Société de Biologie*, 1886, civ.

Ergographic experiments on the human subject have proved that muscles which have been fatigued by long-continued voluntary work recover much more rapidly if sugar be eaten. Curiously enough, Waller and Miss Sowton observed that the endurance of an isolated frog's nerve was increased, or at least its capacity to develop strong currents of action was enhanced, if it was put for a time in a 0.6 per cent. solution of sodium chloride containing dextrose.

Lactic Acid.—This is formed in the muscle during work and during coagulation. It has the form of para-lactic acid or sarco-lactic acid, though it is doubtful whether it exists in a free state. It is a decomposition product of the carbohydrates and perhaps of proteid or some complex muscle-substance of which proteid forms a part. It is only partly responsible for acidity of the muscle which has been worked. The acidity may well be in part caused by acid potassium phosphate produced from alkaline phosphates as a result of the formation of phosphoric acid from lecithin, nuclein, etc.[1] Röhmann[2] attributes the acidity of worked muscles to monopotassium phosphate, and the alkaline reaction of the resting muscle to dipotassium phosphate and sodium bicarbonate.

Inorganic Constituents of Muscle.—Among the bases, potassium has the greatest prominence, and sodium next; magnesium, calcium, and small amounts of iron are also found. Of the acids, phosphoric is present in the largest quantities.

The quantity of a given substance present in a tissue is not an evidence of its value, and the salts in the muscles, although present in comparatively small quantities, are absolutely essential, not only to their functional activity, but to their life. According to Loeb,[3] salts are not only present, as such, in the muscle, but the ions Na, Ca, K, and Mg, are in combination with the proteids, and these ion-proteid compounds are essential to its irritability (see p. 58).

Gases of Muscle.—No free oxygen can be extracted, but carbon dioxide may be obtained, in part free and in part in combination. A little nitrogen can also be extracted, but apparently it has no physiological significance. The amount of carbonic acid developed varies greatly with the condition of the muscle; for instance, it is much increased by muscle work. Muscles take up oxygen from the blood freely, especially when active, and when removed from the body may absorb small amounts from the air. Moreover, a certain amount of oxygen comes to the muscle from the food. More oxygen is taken up by the muscle during rest than is liberated as carbon dioxide, but during action the reverse is the case.[4] Oxygen is not retained as free

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[1] Weyl und Seither: *Zeitschrift für physiologische Chemie*, vi. S. 557.

[2] Röhmann: *Pflüger's Archiv*, 1892, l. S. 84, and 1893, lv. 589.

[3] *American Journal of Physiology*, 1900, vol. iii. p. 327.

[4] Ludwig und Sczelkow: *Sitzungsberichte der k. Akad. Wien*, 1862, Bd. xlv. Abthl. 1; and Ludwig und Schmidt: *Sitzungsberichte der math.-phys. Classe d. k. Sächs. Gesellschaft der Wissenschaft*, 1868, Bd. xx.; Regnault and Reiset: *Annales de Chimie et de Physique*, 1849, 3me sér., xxvi.; Pflüger: *Pflüger's Archiv*, 1872, vi.; and others.

oxygen, but is stored in some combination more stable than oxyhæmoglobin. It is by virtue of the combined oxygen that the muscle is enabled to do its work, but the process is not one of simple oxidation. That muscles hold oxygen in available combinations was shown by Hermann, who ascertained that a muscle can contract hundreds of times in an atmosphere free from oxygen, and produce water and carbon dioxide. If a muscle be thus fatigued, it will recover somewhat in case it be supplied with oxygen, but not otherwise (Joteyko et Richet).

Zuntz[1] found that the amount of oxygen absorbed by the body during muscular work gives a proportional measure of the energy expended. He gives the following figures for bicycle-riding:

Rate per hour.	Oxygen absorption per meter.
9 kilometers	4.5 cu. cm.
15 "	4.8 "
21.5 "	5.76 "

A comparison of bicycling and walking showed that by moderate speeds (riding 15 kilometers and walking 6 kilometers per hour) about double the amount of oxygen was used for like distances in walking, but about 22 per cent. more was required during like periods of time in riding.

II. Chemistry of Nerves.

Most of our ideas concerning the chemistry of nerves are based on analysis of the white and gray matter of the central nervous system. The white matter is largely made up of nerve-fibres and supporting tissue, and the gray matter of the bodies of nerve-cells. The peripheral nerve-fibres are a continuation of the structures in the central nervous system, or are composed of similar elements; the active part of the fibre, the axis-cylinder, is an outgrowth of the cytoplasm of the body of a nerve-cell, and the surrounding medullary sheath is a continuation of the material which sheathes the axis-cylinder while in the brain and cord. It is probable, therefore, that the chemistry of the axis-cylinder approaches to that of the cytoplasm of the body of the nerve-cell of which it is a branch, and that the chemistry of the medullary substance is the same outside as inside the central nervous system.

The white matter of the brain of the ox, which is largely made up of nerve-fibres, is composed of about 70 parts water and 30 parts solids, about one-half the latter being cholesterin, about a quarter proteids and connective-tissue substance, and about a quarter complex fatty bodies, neuro-keratin, salts, chiefly potassium salts and phosphates, and traces of xanthin, hypoxanthin, etc.

Analysis of human sciatic nerve gives the following percentage for the principal organic constituents: Proteids, 36.8; lecithin, 32.57; cholesterin and fat, 12.22; cerebrins, 11.30; neurokeratin, 3.07; other substances, 4.0.[2] The nerve-fibre has a delicate sheath, the neurilemma, the exact constitution

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[1] Zuntz: *Pflüger's Archiv*, 1897, Bd. lxx. S. 346.

[2] J. Chevalier: *Zeitschrift für physiologische Chemie*, x. S. 97.

of which is unknown, but which is supposed to resemble the sarcolemma and to be composed of a substance similar to elastin. The fibres are bound together by *connective tissue* which on boiling gives gelatin. Within the neurilemma is the *medullary sheath*, which is composed of two elements—viz. (1) neuro-keratin, a material similar to the horny substance of epithelial structures, which forms a sort of loose trellis, or network, and probably acts as a supporting framework to the fibre; (2) a white, highly refracting, semi-fluid material, which fills the meshes of the neuro-keratin network, and which is composed largely of protagon and cholesterin combined with fatty bodies. Protagon is a complex phosphorized nitrogenous compound, which many observers believe to contain lecithin and cerebrin. According to Noll, it makes up 7.47 per cent. of the dried nerve. Both lecithin and cerebrin are fatty bodies possessing nitrogen, and the former phosphorus. These and some other complex fatty bodies probably exist in addition to protagon in the medullary substance. The formation of the "myelin forms" seen in the medulla of dead nerves is attributed to lecithin. The *axis-cylinder* probably contains most of the proteids of the fibre, chiefly globulins, mixed with complex fatty bodies.

The reaction of the normal living fibre is neutral or slightly alkaline. It is said to become acid after death, but this change is not known to accompany functional activity. Indeed, nothing is known of the physiological import of the chemical constituents of the nerve-fibre or of the chemical changes which occur in the axis-cylinder when it develops or transmits the nerve impulse. The peculiar chemical composition of the medullary substance would suggest that it has a more important function than simply to protect the axis-cylinder. Some have attributed to it nutritive powers, and others have supposed it helped to insulate: it is certain that the axis-cylinder can develop and transmit the nerve impulse without the aid of the medullary sheath, for there is a large class of important nerves—the non-medullated nerves—in which it is lacking.

II. CENTRAL NERVOUS SYSTEM.

INTRODUCTION.

The Unity of the Central Nervous System.—The human nervous system is formed by a mass of separate but contiguous nerve-cells. Indeed, a group of nerve-cells disconnected from the other nerve-tissues of the body, as the muscles or glands are disconnected from each other, would be without physiological significance. To understand, therefore, the physiology of the nervous system, it is important to keep in mind the fact that by dissection it is found to be continuous throughout its entire extent.

When the nervous system is described as formed of a central and a peripheral portion, and the peripheral portion is further divided into its spinal and sympathetic components, the parts distinguished are found to have no sharply marked boundaries separating them, but really to merge one into the other.

For topographical descriptions the convenience of such subdivisions is undoubted; but the physiological processes which it is our purpose to study overstep in so large a measure these limits that the picture of events in the central nervous system would be very incomplete, should they be separately traced only within such prescribed anatomical boundaries.

By virtue of its continuity the nervous system puts into connection all the other systems of the body. Conforming as it does in shape to the framework of the body, its branches extend to all parts. These branches form pathways over which nerve-impulses travel toward the central system—the brain and spinal cord—and, in consequence of the impulses that come in, there pass out from the central system other impulses to the muscles and glands.

All incoming impulses must reach the central system. It is a fact of the greatest significance that until they have entered the central system the incoming impulses do not give rise to those outgoing, for thus all incoming impulses are first brought to the spinal cord and brain, where the outgoing impulses are co-ordinated.

By means of the central system reactions are established in parts of the body not directly affected by the variation of the external conditions. Owing also to the wide connections of the nervous system and the conduction of all incoming impulses to its central parts, a measure of harmony is maintained between the activities of the several systems composing the body. Thus, not only the systems forming the body are in this manner controlled, but the body as a whole, in relation to all things outside of it and forming its environment, is even more plainly under the guidance of these administrative cells.

Phenomena Involving Consciousness.—It is with the brain and especially the cerebral hemispheres that the phenomena of consciousness are most closely linked. Strictly, physiology concerns itself, at present, with the reactions of the nervous system which can be studied without an appeal to consciousness. A moment's consideration shows, however, that in the physiology of the brain the assistance to be obtained by passing beyond the limit thus laid down is of more value than any boundary, and hence, although the field of consciousness is sacred to psychology, physiology should not be deprived of any of the advantages which come from the privilege of occasional trespass.

Growth and Organization.—The physiological connections existing between the nerve-elements in infancy are very incomplete and poorly established, more so than in any other system of the body; in the history of the growth of the nervous system, the increase in weight and change in shape run parallel with an increase in its complexity. This increase in complexity is accompanied by more perfect organization, which results in better and more numerous physiological pathways, thus permitting the system, as a whole, not only to do more perfectly at maturity those things which it could do in some degree at an earlier age, but also, by virtue of its increased complexity, to do at maturity those things which previously it could not do at all.

Growth in the case of this system implies, therefore, an increase in complexity such as nowhere else occurs, and, since this growth can be modified by the experience of the individual during the growing period, the importance of understanding it and its relation to organization is evident.

Plan of Presentation.—Our subject may be discussed under three heads dealing respectively with the physiology of the (1) single cells, (2) groups of cells, and (3) the entire central system.

Part I. The physiology of the nerve-cells, considered as a peculiar kind of tissue-element, endowed with special physiological characters.

Part II. The activities of groups of these elements. The physiological grouping is, of course, mainly dependent on the anatomical arrangement. At the same time, the activities of one group modify those of others. Stated in general terms, the problem in this part is that of *the pathway of any impulse through the central system.*

Part III. The reactions of the system taken as a whole. Here its capabilities as a unit are contrasted with those of the other systems, and its growth, organization, and rhythms of rest and activity are most readily described.

PART I.—PHYSIOLOGY OF THE NERVE-CELL.

A. ANATOMICAL CHARACTERISTICS OF THE NERVE-CELL.

Form of Nerve-cells.—Morphologically the mature nerve-cell is regarded as composed of a cell-body, containing a nucleus, together with other modified inclusions, and possessed of one or more outgrowths or branches. Some of these branches may be very long, such, for instance, as those which form nerve-fibres; other branches are short and differ from the nerve-fibres in their structure.

The terms employed in describing the nerve-elements are as follows: To the entire mass under the control of a given nucleus and forming both cell-body and branches, the term *neurone* is applied. The inclusions within the cell-body have the usual designations. Nerve-cells differ greatly in the number of the branches arising from them. In some cells there appear to be two nerve-fibres arising from the cell-body, in others, only one. For convenience the descriptions about to be given will apply to the latter group only. From most cells there arises one principal branch, which when considered alone is described as a nerve-fibre, but when considered as the outgrowth of the cell-body from which it originates is called the *axone*. The axone, in many cases, has branches, both near its origin from the cell-body and also along its course. These branches are designated as *collaterals*. At their distal ends the main stem of the axone and also the collaterals subdivide

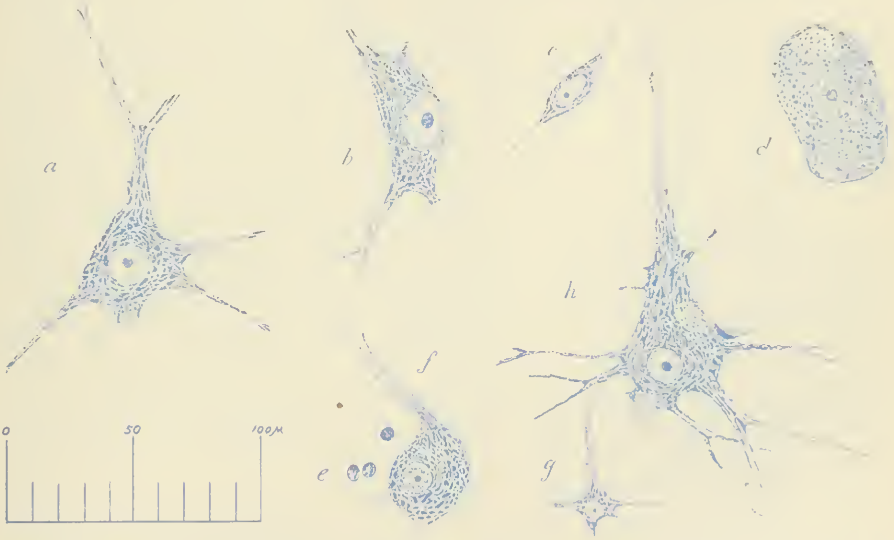

FIG. 67.—A group of human nerve-cells, all drawn to the same scale, from preparations according to Nissl's method, made by Dr. Adolph Meyer, and kindly furnished for this purpose; × 300: *a*, small motor cell from ventral horn of cervical spinal cord; *b*, cell from "Clarke's column," thoracic cord; *c*, small nerve-cell from tip of dorsal horn, thoracic cord; *d*, spinal ganglion-cell, cervical root; *e*, three granules from the granular layer of the cerebellum; *f*, Purkinje's cell from the same preparation as *c*; *g*, small pyramidal cell from the second layer of the cerebral cortex of the central gyri; *h*, giant pyramidal cell from the same region.

into finer twigs, forming the *terminal arborizations.* Contrasted with this principal outgrowth are the other branches of the cell, which are individually much less extensive and which divide dichotomously at frequent intervals. From the tree-like form which they thus acquire they have been designated *dendrites.*

The accompanying illustration (Fig. 67) shows the cell-bodies of several neurones, together with the beginning branches, and also gives some idea of the variations in the size of the cell-bodies as found in man. The nerve-cell body is at first ovoid in shape, although this type is much modified in many cases. As will be seen from Fig. 67, the diameters of nerve-cells range from 4 μ to 65 μ,[1] though in some instances in the spinal cord cell-bodies of even larger diameter are found.

Peculiarities of Nerve-cells.—As compared with the other cells of the body, the best developed nerve-cells are of large size, but the nucleus, proportionately to the remainder of the neurone, is not large. Moreover, its proportional value decreases with the increase in the size of the entire cell. The most striking feature of the nerve-cell, however, is the great length to which its chief branch, the axone, may attain, for in no other tissue does anything like so great a proportion of the cell-substance occur as a branch. Since the axone is the direct outgrowth of the cell-body and can have attained its length only gradually, it is not surprising to find that all varieties of length occur.

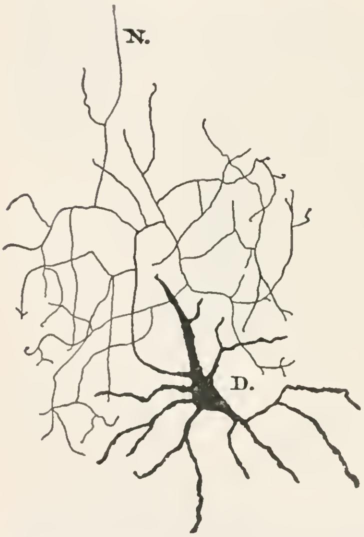

FIG. 68.—A cell, with a short axone, giving off many branches. In such a cell the axone is less in volume than the cell-body. This is the extreme form of the "central cell" of Golgi (Ramón y Cajal). *D.*, dendrites; N., axone.

The form of cell represented in Fig. 68 is one in which the axone shows a very short stem between the cell-body and its terminal twigs. In such an instance the entire extension of the axone may be less than a millimeter. With this are to be contrasted those forms in which the axone is very long and its mass great. What its greatest length may be is easily determined. Within the central system there are cells whose axones extend from the cerebral cortex to the lumbar enlargement (60 centimeters), and again in the peripheral system there are cell-bodies in the lumbar enlargement of the spinal cord, the axones of which extend to the skin and muscles of the foot, a distance of 100 centimeters or more. Among the neurones found in the spinal ganglia of the lumbar region, some cells send one axonic branch to the level of the nuclei of the dorsal funiculi in the bulb and the other branch to the skin of the

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[1] μ = 0.001 of a millimeter.

toes, thus spanning nearly the entire length of the human body. These are the extreme cases, but as the axones are distributed to all intermediate points both in the central and peripheral system every intermediate length is to be found.

Volume Relations.—Calculation shows that the volume of the axone of a large motor cell of the spinal cord when it extends from the lumbar enlargement to the foot, may be 1500 times that of the cell-body. This would include in the term axone both the axis-cylinder and the medullary sheath. If either of these is taken alone, the volume is reduced by one-half.

It is extremely difficult to estimate the volume of the dendrites. In some instances, as in the cells of the spinal ganglia (Fig. 71), they are rarely present, while in the large cells of the cerebellum (Purkinje's cells) they form a mass which must be several times greater than that of the cell-body proper. In most neurones, however, the dendrites have, at best, a volume as great as that of the cell-body.

Size of Nerve-cells in Different Animals.—In considering the size and form of cells in man it becomes of interest to determine how far the observations apply to the lower mammals. The facts are briefly these: It can be said that the smaller mammals usually have the smaller nerve-cells, but the decrease in the volume of the nerve-cells is not proportional to the decrease in the volume of the entire body. For example, Kaiser[1] has shown that the cell-bodies occupying the ventral horn in the cervical enlargement of the spinal cord of the bat, the rabbit, and the monkey are in many cases as large or larger than those found in man.

Though the volume of the cell-body and the *diameter* of the associated axone are approximately similar in any two animals of different size, as, for instance, in a bat and in man, it is evident that the axones could not have the length in the bat that they do in man, and that in this last dimension at least there is a diminution corresponding to the size of the animal.

The bearing of this fact on the comparative physiology of the nervous system is evident, for, under these conditions, as the volume of the entire nervous system is diminished, the number of cell-elements constituting it must also be diminished, and thus the structure of this system in the smaller mammals becomes numerically simplified.

Size and Function.—A nerve-cell contains a mass of living substances capable of being broken down and built up chemically, and there is nothing against the inference that the larger the cell the greater is the quantity of these living substances, and hence the larger the amount of stored energy represented by it. The larger cells are therefore those capable of setting free the greater amount of energy. The energy-producing changes are to be associated with the cell-body rather than with any of the branches. Moreover, the nerve-cells with large cell-bodies, sending out, as they do, branches which are more voluminous than those the cell-bodies of which are small, furnish a greater amount of material to form the terminal twigs into which

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[1] *Die Funktionen der Ganglienzellen des Halsmarkes*, Haag, 1891.

these branches finally split. From this it follows that, in general, the large nerve-cells have more points of connection with the structures about them, as well as the capacity for the liberation of a greater amount of energy.

Growth of Nerve-cells.—The nerve-elements are derived from germinal cells found in the epiblast of the embryo (Fig. 69).

These divide rapidly and in such a way that one daughter cell continues as the germinal cell, while the other moves away from the primitive surface of the body and becomes, without further division, a young neurone, or *neuroblast*. The formation of neuroblasts in man ceases, or becomes very slow and unimportant, by the end of the third month of fetal life.

FIG. 69.—Portion of developing medullary tube (human) seen in frontal section. × 1100 diameters (His): *G*, germinal cell; *N*, neuroblasts.

Two characters of the neuroblast are worthy of careful consideration. First, there is good indirect evidence that, in early life at least, and before their branches have been formed, they are migratory, moving in an amœboid manner. This being so, the perfection with which they arrange themselves in the adult system depends on the accuracy with which they respond to those conditions that determine their migration as well as upon the normal character of these directing influences (mechanical strain;[1] chemotaxis; nutritive attraction or electrical influences).[2] But with so much liberty of movement and with directing influences that are so complicated, the chances for deviation from a fixed arrangement are much enhanced.

Second, very early in the history of the neuroblast the point on the cell-body from which the axone will grow appears in many cases to be determined, and the cell is thus physiologically polarized.[3] This polarity being established, the direction in which the axone first grows is determined, and where the cells are misplaced this polarization can lead to a confusion of arrangement.

The volume of either the germinal cell or of the first form of the neuroblast was found by His[4] to be 697 cubic μ in a human fetus (embryo R-length 5.5 millimeters), aged 3–3.5 weeks; and it can be shown that the mature neurone must often attain a volume more than 50,000 times that of the original neuroblast.

[1] His: *Unsere Körperform*, 1874.

[2] Davenport: *Bulletin of the Museum of Comparative Zoölogy*, Harvard College, Nov., 1895; Herbst: *Biologisches Centralblatt*, 1894, Bd., xiv.; H. Strasser: *Ergebnisse der Anatomie u. Entwickelungsgeschichte*, Merkel and Bonnet, 1891, Bd. i. S. 731.

[3] Mall: *Journal of Morphology*, 1893, vol. viii.

[4] *Archiv für Anatomie und Physiologie*, 1889.

Maturing of the Nerve-cell.—The maturing of the nerve-cell involves several changes. First, the outgrowth of the axone or axones; next, the formation of the dendrites; and, finally, in some cases, the medullation of the axone, while simultaneously and with greater or less rapidity the absolute amount of substance in both cell-body and axone is being increased, together with a chemical differentiation of the cytoplasm and the nucleus. The time in the life-history of the individual at which these several events occur is variable, and may be delayed beyond puberty at least, while the rate at which they occur is different in different cases. Furthermore, many nerve-cells never develop beyond the first stage of immaturity (Fig. 70).

FIG. 70.—*A–D*, showing the phylogenetic development of mature nerve-cells in a series of vertebrates; *a–e*, the ontogenetic development of growing cells in a typical mammal; in both cases only pyramidal cells from the cerebrum are shown; *A*, frog; *B*, lizard; *C*, rat; *D*, man; *a*, neuroblast without dendrites; *b*, commencing dendrites; *c*, dendrites further developed; *d*, first appearance of collateral branches; *e*, further development of collaterals and dendrites (from S. Ramón y Cajal).

Form of the Axone as a Means of Classification.—Of the various devices used to classify nerve-cells, the form of the axone is the most useful.

Physiologically, the nerve-cell is significant as the source and pathway for the nerve-impulses. The current conception of the change called the nerve-impulse is that it begins at one point of the cell and travels from there to the other parts; one of the other parts is the axone, and along this the impulse can be shown to pass. Indeed, the nerve-cell body stimulated at any point may be responsive just an an amœba is responsive at any portion of its surface. When, however, the branches are formed they become the channels through which the impulses pass, and hence assume a special significance without indicating any fundamental change in the structure of the cell. Where the cell has well-developed branches we explain the arrangement by assuming that the impulse enters the cell-body by one branch and leaves it by another.

On examining the mature nerve-cells of man with this idea in mind, two types are found. The first type may be exemplified by the pyramidal cortical cells shown in Fig. 70. Here, from a pyramidal body (*D*) there arise a number of dendrites, while from the lower portion of the cell the axone grows out and branches. In the other type the axone alone grows out. Its branches are but two in number and both are medullated. They pass in opposite directions, and in this type there are, as a rule, no dendrites. Such are the typical spinal ganglion-cells of the mammal. To understand the arrangement in these cases, recourse must be had to the facts of development. The second type begins its development as a diaxonic cell, an axone growing from each pole (Fig. 71). In the adult spinal ganglion of the higher mammals, however, such diaxonic cells are rarely found, the great majority having a single axone which soon divides into two branches.[1]

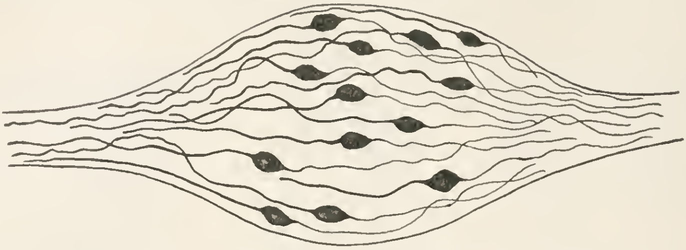

FIG. 71.—Spinal ganglion of an embryo duck; composed of diaxonic nerve-cells (van Gehuchten).

FIG. 72.—Diaxonic changing into monaxonic cells: from the Gasserian ganglion of a developing guinea-pig (van Gehuchten).

Fig. 72 beautifully illustrates the phases of this change as seen in a single section. At first one axone arises from each pole of the ovoid cell-body. Later the cell-body occupies a position at the side of the two axones, which appear to run into one other. Finally the cell-body is separated from the two axones by an intervening stem. The stem has the characters of a medullated nerve-fibre, and from the end of it the two original axones pass off as branches.

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[1] Dogiel: *Anat. Anz. Jena*, 1896, Bd. xii. S. 140-152, describes the several kinds of neurones which take part in the formation of the spinal ganglion.

From this mode of development it is plain that the single stem must be looked upon as containing a double pathway, although it appears to be in all ways a single fibre, for on the one hand it contains the path for the incoming and on the other for the outgoing impulses. Recent investigations have shown in a striking way that cells modified in this manner are by no means limited to the spinal ganglia, but occur in the cortex of the cerebellum and elsewhere. Classifying the nerve-cells, therefore, in the light of these facts, we find: (1) The pyramidal type, in which the dendrites and axone are both well developed, and in which the greater number of the impulses most probably enter the cell by way of the dendrites and leave by way of the axone; (2) The spinal ganglion type, in which originally the impulse passes in at one pole of the cell and out at the other, but in the course of development the *two* axones become attached to the cell-body by a single stem, and by inference there must be in this stem a double pathway. In this latter case there are usually no dendrites.

Growth of Branches.—After the cells have taken on their type-form the branches still continue to grow, not only in length, but also in diameter. In man, for example, the diameter of the nerve-fibres (axones) taken from the peripheral nerves at birth is 1.2–2 μ for the smallest, up to 7–8 μ for the largest, with an average of 3–4 μ, while at maturity it is 10–15 μ for the larger fibres.[1]

Internal Structure of the Neurones.—The status of this problem has been admirably summarized by Barker,[2] to whose book the reader is referred. For our purpose it is sufficient to state that the cytoplasm of nerve-cells is composed of fibrils (the character of which is much discussed), and an intermediate, non-fibrillar material. These constituents are distributed in different proportions in the several parts of the neurone. The axone contains the fibrils most closely packed. The intermediate substance is most evident in the body of the cell, and in general the dendrites more closely resemble in their structure the cell body. Part, at least, of the intermediate material forms the "stainable substance" of Nissl, also called "tigroid," which, in its susceptibility to change under disturbed nutritive conditions, acts like a stored food material. But which portion of the cell acts to conduct the nerve impulse is not known, and the contention that one or the other of the component structures is the conductor of the nerve impulses rests on histological evidence alone. For the present it is sufficient to know that the neurone appears to be conductive in all its gross parts.

While the axone is growing as a naked axis-cylinder, it is usually slightly enlarged at the tip (Cajal), suggesting that it is specially modified at that point. The nutritive exchange on which the increase of the entire axone depends appears to take place along its whole extent, and not to be entirely dependent on material passed from the cell-body into the axone.

Medullation.—After the production of its several branches, the next step

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[1] Westphal: *Neurologisches Centralblatt*, 1894, No. 2.

[2] Barker: *The Nervous System*, 1899, pp. 101-114.

in the growth of the cell is the formation of the medullary sheath about the axone. Not all axones have a medullary sheath, nor is any axone completely medullated. In the sympathetic system there is a very large proportion of unmedullated axones. In the central system the number is also very large, although their mass is small. Of the significance of the medullary sheath we know nothing. The suggestion that it acts to insulate the nerve impulse within a given axis-cylinder has little or no evidence in its favor. The suggestion that it is nutritive is plausible, but important differences in the physiological reactions of the two classes of nerve-fibres have not yet been found, if we except the observation that the non-medullated nerves rapidly lose their irritability at the point of stimulation with the faradic current, thus exhibiting a "stimulation fatigue" not found in nerves unquestionably medullated.

Growth of Medullary Sheath in Peripheral Nerves.—Whatever may be the significance of the medullary sheath, it is usually formed before the neurone has attained its full size. In the peripheral system it depends on the presence of mesodermal cells which envelop the axis-cylinder, forming a tube about it. Each ensheathing cell is physiologically controlled by a nucleus which becomes situated about midway between its extremities. According to Ranvier and his school, the cell-substance is largely transformed into myelin, and the line of junction between two of these sheathing cells forms a node of the nerve-fibre. In the sheath of a growing axone at least two changes can be readily followed: As the axis-cylinder increases in diameter the medullary sheath becomes thicker. The change is such that in the mammalian peripheral system the areas of the axis-cylinder and of the medullary sheath, as shown in cross-sections of osmic acid preparations, remain nearly equal (Fig. 73). On the other hand, the length of the internodal segments tends to increase with an increase in the diameter of the nerve-fibre, and for nerves of the same diameter it is less in man than in the lower animals. In a given fibre the segments are shorter at the extreme peripheral end (Key and Retzius). In the young fibres, also, they are shorter and increase in length with age.

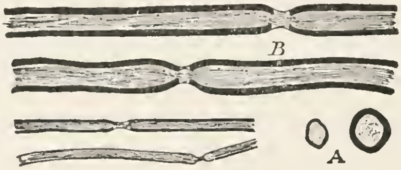

FIG. 73.—Longitudinal (*B*) and transverse (*A*) sections of nerve-fibres. The heavy border represents the medullary sheath, which is thicker in the larger fibres. Human sciatic nerve. × 200 diameters (modified from van Gehuchten).

A physiological significance attaches to these segments, because, as Ranvier long since pointed out, it is at the nodes that various staining reagents easily reach the axis-cylinder. This suggests that normal nutritive exchanges may follow the same path, and thus short internodal segments giving rise to many nodes would represent the condition most favorable to exchange between the axis-cylinder and the surrounding plasma. Thus far, histological observation shows the more numerous nodes where the physiological processes are presumptively most active, and hence supports the hypothesis suggested.

In the peripheral nervous system the nerve-fibres conduct impulses before they acquire their medullary sheaths: witness the activities of new-born rats, in which the whole nervous system is entirely unmedullated. Moreover, Langley[1] has reported, in the regenerating cervical sympathetic nerve, a return of function, while the majority of the fibres are still without their medullary sheaths.

Medullation in Central System.—Concerning the relation of the medullary sheath to the axis-cylinder in the central system, our information is less complete. The elements which give rise to the medullary substance are not known and the myelin is not enclosed in a primitive sheath. There are no internodal nuclei regularly placed, yet Porter[2] has demonstrated in both the frog and the rabbit the existence of nodes in some fibres taken from the spinal cord. The conditions which there exist must be further studied before any general statements concerning the development of the medullary substance in the nerve-centres can be ventured. Yet, it is an important observation that whereas medullation in the peripheral system is mainly completed during the first five years of life, the process continues in the central system, and especially in the cerebral cortex, to beyond the fiftieth year.[3]

Whatever views may be held concerning the capacities of a medullated fibre, it is to be remembered that the medullary sheath does not cover the first part of the axone on its emergence from the cell-body, nor are ultimate branches of the axone medullated in the region of their final distribution.

What has just been said applies to the main stem of the axone. As shown in Fig. 70, the axone often has branches near its origin, the collaterals, and according to the observations of Flechsig[4] these also become medullated. Concerning the time of the medullation of these branches there are no direct observations; but if it is controlled by the same conditions which appear to control the process in the main stem, then, as the branches form their physiological connections later than the main stem, it would follow that their medullation should also occur later, and the studies on the progressive medullation of the cerebral cortex favor such a view.

The acquisition of this sheath occurs in response to a physiological change that appears at the same time along the entire length of the fibre. The process, therefore, is not a progressive one, but is practically simultaneous.

From the observations of Ambronn and Held[5] on rabbits a day or two old, it appears that the efferent (motor) spinal and cranial nerves acquire their

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[1] Langley: *Journal of Physiology*, 1897, xxii. p. 223.

[2] *Quarterly Journal of Microscopical Science*, 1890.

[3] Vulpius: *Archiv für Psychiatrie und Nervenkrank.*, 1892, Bd. xxiii.

[4] *Archiv für Anatomie und Physiologie*, 1889.

[5] Ambronn and Held: *Archiv für Anatomie und Physiologie*, Anatom. Abthl., 1896, S. 208.

sheaths before the corresponding afferent (sensory) nerves are medullated (except in the case of the vestibular branch of the auditory nerve, which is medullated at the same time as the motor nerves). In the central system the continuations of the afferent pathways become medullated before the pyramidal tracts, while in the cerebral hemispheres medullation of the commissural and association fibres follows immediately that of the afferent tracts.

Ambronn and Held[1] have also shown that when the eyelids are prematurely opened in animals born blind, such as the rabbit, dog or cat, and the animal is then exposed to the light, the medullary sheaths are more rapidly formed in the optic nerves exposed to stimulation than in those developing normally.

Changes in the Cytoplasm.—While the nerve-cell is passing from the immature to the mature form, increasing in mass and in the number of its branches, as well as acquiring its medullary sheath, it also undergoes various chemical changes. The stainable substance in the cytoplasm becomes more abundant at maturity and the pigment-granules increase in quantity.[2]

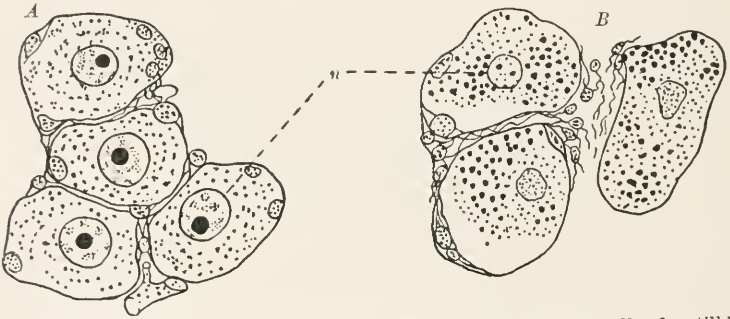

FIG. 74.—To show the changes in nerve-cells due to age: *A*, spinal ganglion-cells of a still-born male child; *B*, spinal ganglion-cells of a man dying at ninety-two years; *n*, nuclei. In the old man the cells are not large, the cytoplasm is pigmented, the nucleus is small, and the nucleolus much shrunken or absent. Both sections taken from the first cervical ganglion, × 250 diameters (Hodge).

Old Age of the Nerve-cells.—But the nerve-cell, though possessing in most cases a life-history coextensive with that of the entire body, eventually exhibits retrogressive changes. These changes of old age consist, in some measure, in a reversal of those processes most evident during active growth. The cell-body, together with the nucleus and its subdivisions, becomes smaller, the stainable substance diminishes and becomes diffused instead of appearing in compact masses,[3] the pigment increases, the cytoplasm exhibits vacuoles, the dendrites atrophy, and the axones also probably diminish in mass. In some instances the entire cell is absorbed. Some of these facts are illustrated by the observations of Hodge[4] on the spinal ganglion-cells of an old man of ninety-two years as compared with those of a new-born child (see Fig. 74).

Since the chemical and morphological variations which occur during the entire growth-cycle are accompanied by variations in the physiological powers,

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[1] *Loc. cit.*, S. 222.

[2] Vas: *Archiv für mikroskopische Anatomie*, 1892.

[3] Marinesco: *Revue neurologique*, October, 1899, No. 20.

[4] *Journal of Physiology*, 1894, vol. xvii.

we are led to anticipate in old age a correlation, on the one hand, between the decrease in the quantity of functional substance in the cytoplasm, and a decrease in the energy-producing power of the cells, and, on the other, between the absorption of the cell-branches and a limitation in the extent to which the neurones may influence one another. Both of these conditions are characteristic of the nervous system during old age.

B. THE NERVE-IMPULSE WITHIN A SINGLE NEURONE.

The Nerve-impulse.—Neurones form the pathways along which nerve-impulses travel. As introductory, therefore, to the study of the composite pathways in the central system, comprising, as they do, several elements arranged in series, it becomes important to study the behavior of the nerve-impulse within the limits of a single cell-element.

Experimentally, the passage of the nerve-impulse is revealed by a wave of change in the form of an electrical variation which passes along the nerve-fibre in *both* directions from the point of stimulation. Under normal conditions, the intensity of the electrical change does not vary in transit, though for moderate electrical stimuli the strength of the electrical change ("action current") is proportional to the strength of the stimulus.[1] It moves in the peripheral nerves of the frog in the form of a wave some 18 millimeters in length, at the mean rate of 30 meters per second, and this rate can be somewhat retarded by cooling the nerves and accelerated by warming them. In mammals the rate in the peripheral nerves has been found by Helmholtz and Baxt to be 34 meters per second, The nerve-impulse can be aroused at any point on a nerve-fibre provided a sufficient length of fibre be subjected to stimulation. Mechanical, thermal, chemical, and electrical stimuli may be used to arouse it, but just how the impulse thus started differs from that normally passing along the fibres, as a consequence of changes in the cell-bodies of which these fibres are outgrowths, is not known. It appears, however, that the impulses aroused by artificial stimuli are usually accompanied by a much stronger electrical variation than accompanies the normal impulses.

In the peripheral system the nerve-impulse, when once started within a fibre or axone, is confined to that track and does not diffuse to other fibres running parallel with it, although it does, of course, extend to all the branches of the axone, whatever their distribution.

The above-mentioned relations have been deduced from the study of the peripheral nerves, and these morphologically are but parts of the axones, the cell-bodies of which are located either in the central system proper or in the spinal or sympathetic ganglia.

The observations apply therefore to but one portion of the nerve-cell, and our present purpose is to determine how far it is possible to apply them to the entire nerve-cell, noting at the same time the modifications thus introduced.

Owing to the small size of nerve-cell bodies there are, of course, very few

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[1] Greene: *American Journal of Physiology*, 1898, vol. i. p. 115.

instances in which a single nerve-cell, or part of such a cell, has been the object of direct physiological experiment. We shall therefore approach the question indirectly by showing what the histological relations have to suggest.

Direction of the Nerve-impulse.—In the case of a given nerve-cell the impulses which we usually consider, pass in one direction only. For instance, along the ventral nerve-roots of the spinal cord, the impulses pass from the cord to the periphery, while in the dorsal roots, so far as the fibres take origin from the cells of the spinal ganglia, these impulses travel in the opposite direction. At the same time experiment has shown that if a nerve-trunk be stimulated at a given point, then the nerve-impulse can be demonstrated as passing away from the point of stimulation in *both* directions.

We are therefore led to inquire what limits are set to the passage of impulses in a direction opposite to the usual one. The narrowest limits, it appears, are those of the single cell in which the impulse has originated. The experimental observations are as follows: When the fibres forming the ventral root of a spinal nerve are stimulated electrically, and the cross-section of the spinal cord, somewhat cephalad to the level at which the root joins it, is explored with an electrometer, there is not found any evidence of nerve-impulses passing cephalad in the substance of the cord. The arrangement of the cells in the cord is such, however, that the cell-bodies which give origin to the fibres forming the ventral root are physiologically controlled by fibres running toward them from every portion of the cord, and under normal conditions these fibres convey impulses to the cell-bodies in question. The experiment shows that when an impulse enters the cell-body by way of the ventral root-fibre, to which it gives origin, the impulse does not stimulate the other elements of the cord.[1]

With the elements forming the dorsal spinal root the case is at first glance apparently different, though in reality it is the same. These elements have the cell-body located in the spinal ganglion. The cells are essentially diaxonic (Fig. 72); one axone extends from the point of division toward the periphery and the other enters the spinal cord, where it forms two branches, both of which course longitudinally for some distance within it (see Fig. 75). In this case, therefore, the normal direction of the effective impulses is from the periphery toward the cord, and within the cord they are delivered to other elements, which carry them in all directions. It is therefore to be expected that the stimulation of the dorsal root-fibres would give rise to impulses passing in both directions in the dorsal columns of the cord. When, however, the dorsal columns of the cord are electrically stimulated in a cross-section made just above the level of the entrance of a dorsal root, then it is found that the electrical variation is to be detected in the nerve-fibers on the distal side of the spinal ganglion. These impulses have therefore passed in a direction the reverse of that usually taken. The fibres which in this instance are stimulated in the cross-section of the cord are, however, outgrowths of the spinal ganglion-cells, and thus, although the

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[1] Gotch and Horsley: *Proceedings of the Royal Society*, 1888.

stimulation of the cord does give rise to an impulse in the afferent spinal nerve, nevertheless the impulse is continually within the limits of one cell-element. This shows that the *reversed* impulse can pass the spinal ganglion, and in doing this it probably traverses the cell-bodies there located. There is, however, no evidence that the stimulation of the dorsal columns of the cord produces outgoing impulses in the dorsal nerve-roots except when the stimulus is applied to the axones, which are outgrowths of the cells of the spinal ganglia.

In the case of the interpolation of the cell-body in the course of the axones there is every reason to think that the nerve-impulse traverses the body of the cell itself. This is suggested by the changes caused in the cell-body of the spinal ganglion-cells as the result of stimulating the peripheral axone. Moreover, some observers report an appreciable delay (0.036 second) in the passage of the nerve-impulse through the cell-body in the case of those cells which form the spinal ganglion.[1] This delay has recently been denied.[2]

The observations of Steinach,[3] on the capacity of the afferent nerves of the frog to conduct the centripetal impulses through the region of the spinal ganglion, indicate that impulses may pass this region when the cell-bodies are very probably excluded from forming a part of the possible pathways, thus showing that the two branches of the T-process are physiologically continuous. These results do not show, however, that the centripetal impulses fail, *under normal conditions*, to pass to the cell-bodies also. It may be pointed out that this is another piece of evidence in favor of the view that within the limits of *a single neurone or fraction of a neurone* there is no limitation to the passage of a nerve-impulse in all directions, wherever it is started.

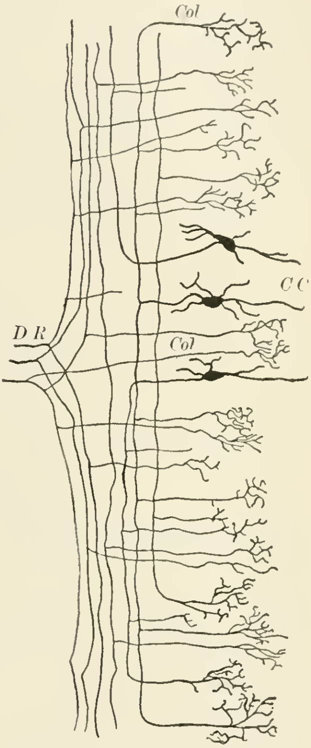

FIG. 75.—A longitudinal section of the cord to show the branching of incoming root-fibres in dorsal columns. At the left are three (*D R*) root-fibres, each of which forms two principal branches. These give off at right angles other branches, collaterals, *Col*, which terminate in brushes. *C C*, central cells, whose axones give off similar collaterals (Ramón y Cajal).

Double Pathways.—If the view is correct, that in passing through the spinal ganglion the normal impulse traverses the cell-body, then the nerve-

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[1] Gad and Joseph: *Archiv f. Anatomie u. Physiologie*, 1889.

[2] Moore and Reynolds: Proceedings of the Fourth International Physiological Congress, held at Cambridge, 1898. Supplement, vol. xxiii, *Journal of Physiology*. These authors deny the delay.

[3] Steinach: "Ueber die centripetale Erregungsleitung im Bereiche des Spinalganglions," *Pflüger's Archiv*, 1899, Bd. 78.

impulse passes to and fro along the common stem which joins the cell-body with the two branches (*vide* Fig. 72), the stem itself having all the characters of a medullated fibre.

The study of this modification brings with it the following suggestion: If the single stem in the modified spinal ganglion-cells must by virtue of its development contain a double pathway, it is fair to inquire whether the same may not be true of the other forms of the nerve-cell in which the axone also appears to be single. Among the cortical cells the arrangement of the branches is such that, for aught that is known, the stem of the axone may functionate in the manner suggested, and contain more than one pathway.

The same arrangement must exist in the case of cells like those represented in Fig. 76, in which the axone arises from the base of a dendrite at some distance from the cell-body, and in which nerve-impulses arriving over the dendrites and leaving by the axone must normally follow the portion of the cell-branch which is common to both, passing along it first in one direction and then in the other. This last result has been extended by Sherrington,[1] who found that he could produce movements of the hind limb in both monkeys and cats when the cord had been sectioned just below the bulb, and the stimulus was applied to the fibres in the fasciculi graciles at that level. The reaction is explained by the passage of impulses down the dorsal columns (in a direction reverse to the normal), and their distribution by way of the collaterals to the efferent elements located in the ventral horns.

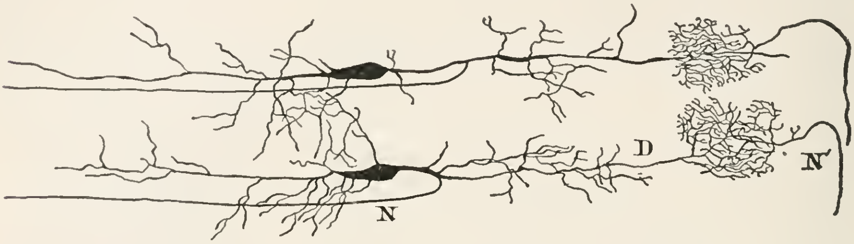

FIG. 76.—Showing the relations between the terminal branches of the dendrites (*D*) and of the axones (*N'*) of the optic fibres where they come together in the superficial layer of the optic lobe of the chick; also showing the origin of the axone (*N*) from a dendrite (van Gehuchten).

Significance of Cell-Branches.—Since the outgoing nerve-impulses are isolated in the axone until they reach the terminal twigs, it follows that the impulses destined to produce an effect beyond the cell limits will do so at the extremities of the branches. This leads to the question how far the possession of branches is necessary to the functional activity of a nerve-cell either for the reception or transmission of an impulse. Since it has been pointed out that the spinal cord of the newt and fish is capable of conducting impulses even before the dendrites are developed, it follows that the transmission of impulses is in some way dependent on the condition of the cell-wall, independent of cell-branches. This modification may exist at points where there are no branches, or during this early period be a general property of the

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[1] *Proceedings of the Royal Society*, 1897, lxi. 243–246.

wall, and only later become the peculiar property of those portions which are drawn out to form the tips of the branches. But not only the capacity to receive, but also the capacity to deliver impulses is a function of the ends of the branches, and the cell-wall at these points must therefore be peculiarly modified with a still further differentiation, determining the direction in which the impulses may pass. Each dendrite may represent at least one pathway by which impulses reach the cell-body. If, then, there are many dendrites, the cell-body is subject to a more complicated series of stimuli than if the branches are few. It will be remembered that the young nerve-cell has no dendrites, that the first branch to be formed is the axone, and that the completion of the full number of dendrites is a slow process. The pathways formed by the dendrites are therefore continually increasing up to maturity (Fig. 77). The relation between the "climbing fibre" and the dendrites of the Purkinje cell illustrates this arrangement.

FIG. 77.—Climbing fibre from human brain: *a*, nerve-fibre; *b*, Purkinje's cell (Cajal).

Generation of Nerve-impulses.—The impulses which arrive at the cell-body produce there chemical changes. These changes, when they reach a given volume, cause a nerve-impulse which leaves the cell-body by way of the axone. If the nerve-impulse is, as we assume, dependent on the chemical changes occurring in the cytoplasm, then it must vary according to these changes, which in turn can hardly be similar when the incoming impulses that arouse them arrive along different dendrites. We know that a stimulus applied directly to the axone will give rise to a nerve-impulse; but, as we shall see later, the chemical changes accompanying the passage of this impulse are too slight to be detected. Whether in the cell-body equally slight changes would give rise to an impulse cannot be determined.

Birge[1] found upon stabbing the spinal cord of a frog with a needle in

[1] Birge: *Arch. f. Anat. u. Physiol.*, Physiol. Abthl., 1882, S. 471.

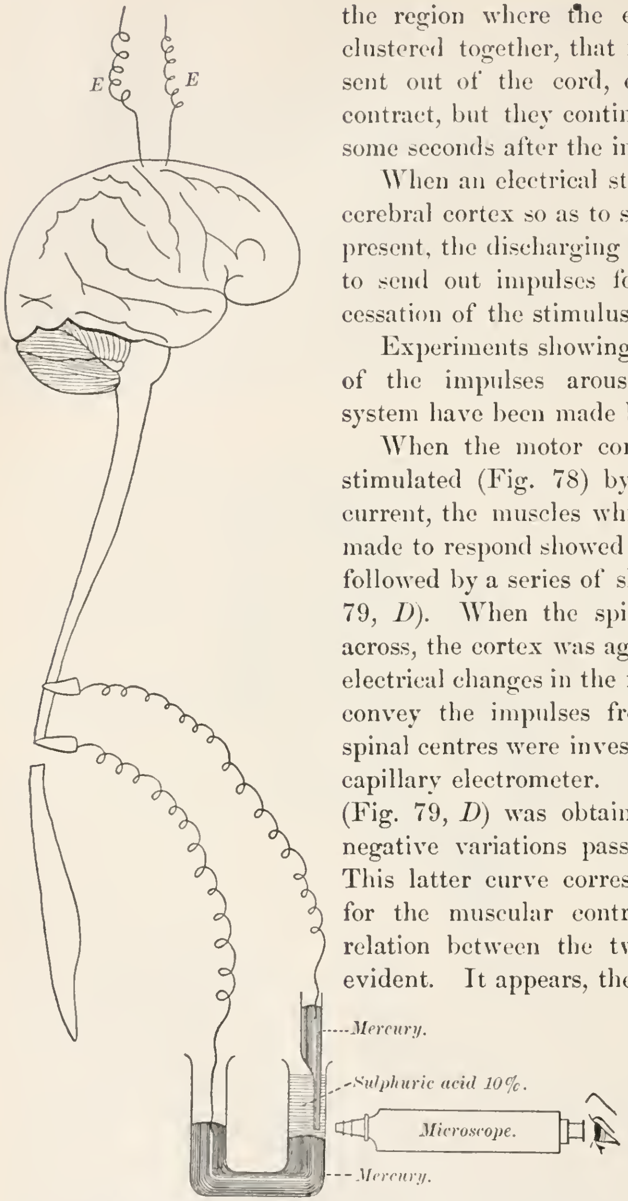

FIG. 78.—Schema illustrating the experiment for determining the number of separate nerve-impulses passing down the spinal cord upon stimulation of the cortex (from experiments on the monkey; Horsley): *E*, *E*, electrodes, intended to be on the "leg area." Where the cord is interrupted, one non-polarizable electrode is placed over the cut end of the pyramidal fibres going to the lumbar enlargement; the other, on the side of the cord. These lead to the capillary electrometer, in which the column of mercury moves each time an impulse passes.

the region where the efferent cell-bodies are clustered together, that not only were impulses sent out of the cord, causing the muscles to contract, but they continued to be sent out for some seconds after the injury.

When an electrical stimulus is applied to the cerebral cortex so as to stimulate the cells there present, the discharging cells may also continue to send out impulses for some time after the cessation of the stimulus.

Experiments showing the multiple character of the impulses aroused within the central system have been made by Gotch and Horsley.[1]

When the motor cortex of a monkey was stimulated (Fig. 78) by means of the faradic current, the muscles which by this means were made to respond showed a long tonic contraction followed by a series of shorter clonic ones (Fig. 79, *D*). When the spinal cord had been cut across, the cortex was again stimulated, and the electrical changes in the fibres of the cord which convey the impulses from the cortex to the spinal centres were investigated by means of the capillary electrometer. By this means a curve (Fig. 79, *D*) was obtained as a record of the negative variations passing along these fibres. This latter curve corresponds with the record for the muscular contraction, and hence the relation between the two series of events is evident. It appears, therefore, that the cortical cells after the cessation of the stimulus still continue to discharge in a rhythmical manner. When the cortex had been removed, and the electrodes were applied directly to the underlying fibres, the discharge of the impulses was found to cease with the stoppage of the stimulus. The presence of the cortex was therefore necessary for the continued discharge (Fig. 79, *C*). The attempt

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[1] *Proceedings of the Royal Society*, London, 1888.

was also made to determine the rhythmic character of the negative variations in the motor nerve-trunk between the cord and the contracting muscle, but the changes there present, though sufficient to cause contractions of the muscle, were not strong enough to be recorded by a delicate capillary electrometer. This result suggests that the impulses sent out from the spinal cord by the normal discharge of the motor nerve-cells may differ from the impulses artificially aroused in the lesser intensity of the electrical changes that accompany them.

Rate of Discharge.—The rate at which the nerve-cells discharge, as shown by the number of impulses which produce tetanus of a muscle indirectly excited, either by artificial stimulation of the nerve-elements in animals or by voluntary impulses in man, is about ten impulses per second. It appears that at least the cortical cells and those of the spinal cord have the same rate of discharge, and that this rate is the same in some mammals (dogs, cats, rabbits, and monkeys) as in man. Hence a tendency to discharge about ten times a second may be assumed as characteristic of the mammalian nerve-cell.[1]

Points at which the Nerve-impulse can be Aroused.—It is probable that the excitation of any part of a nerve-cell is capable of producing a nerve-impulse, whether the stimulus be applied at the tips of the dendrites or to the axone in its course.

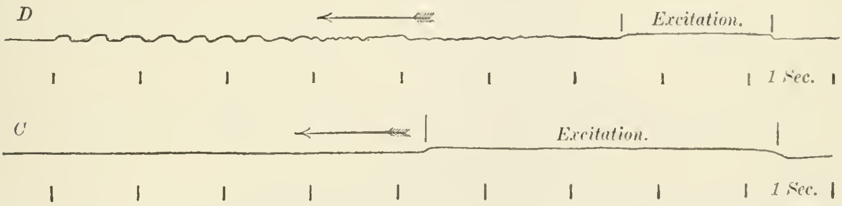

FIG. 79.—From a photographic record of the movements of the column of mercury in a capillary electrometer (Gotch and Horsley). The arrow shows the direction in which the record is to be read. The upper curve (*D*) shows the period of excitation by the interrupted current; this is followed by a series of waves in the record showing a number of separate impulses sent down from the cortex after electrical stimulation has ceased. In the lower curve (*C*), the exciting electrodes were applied to the white matter directly, the cortex having been removed. The record shows that in this case no impulses pass after the stimulation has ceased.

Irritability and Conductivity.—In general, parts of the system which are irritable are also conductive, but there are special cases in which the irritability of the nerve-fibre can be distinctly separated from its conductivity, the latter being present while the former is absent.

It is an old observation that on stripping down the phrenic nerve by compressing it between the thumb and forefinger and sliding these along the nerve, a contraction of the diaphragm is caused. The part of the nerve thus stimulated is soon exhausted. If, now, the same operation is repeated on a portion of the nerve lying nearer the spinal cord, contraction of the diaphragm again follows. This result was originally used to support the theory of a

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[1] Schäfer and Horsley: *Journal of Physiology*, 1885, vol. vii.; Schäfer, *Ibid.*

nerve-fluid, and was held to demonstrate that after the nerve-tubes in the portion of the trunk compressed had been emptied so that no reaction followed further pressure, then if the pressure were applied still nearer the cord, the fluid from that part of the nerve could be driven forward and a contraction of the diaphragm would result. The notion of a nerve-fluid in the sense in which that term was used by the earlier physiologists has long since been abandoned; but for our purpose, the experiment is important as showing that under such treatment irritability and conductivity do not disappear at the same time, but that the fibres remain conductive after they cease to be irritable.

It has been shown also that[1] in young regenerating motor-fibres it often happens that while no response is to be obtained by the direct stimulation of the regenerated peripheral portion, yet the stimulation of the central and fully grown portion does cause a contraction of the muscles controlled by these fibres. In this case the newly formed fibres can conduct an impulse which gives rise to a contraction, although such an impulse cannot be aroused by directly stimulating them.

Summation of Stimuli in Nerve-cells.—In an axone a single stimulus if followed by a single nerve-impulse; on the other hand, the studies which have been made to determine the number of weak stimuli necessary to discharge afferent cell-elements, when stimulated by way of the afferent nerves, indicate that there may be a summation of stimuli—*i. e.*, the discharge does not follow until a series of stimuli has been given.[2]

Whether, however, the delay in the response is due to the failure of the cytoplasm of the receiving cell to discharge until repeated impulses have reached it, or whether the modification of the cell which causes the delay is a process taking place at the point where the impulse passes over from the branches of one cell to those of another, is not directly determined by the experiments. The indirect evidence is, however, entirely in favor of the view that the delay which is notable in the arousal of a reflex response occurs at the point where the impulse passes from one cell to another.

C. THE NUTRITION OF THE NERVE-CELL.

The metabolic processes within the nerve-cell are continuous, and the chemical changes there taking place involve not only those prerequisite to the enlargement of the cell during growth, but also those leading to the formation of such substances as by their katabolism cause the nerve-impulse. The passage of the nerve-impulses probably alters the osmotic powers of the cell-wall toward the surrounding plasma, and this of course is fundamental to the nutritive exchange. It follows, therefore, that the passage of nerve-impulses is one factor determining the nutrition of these cells.

Histologically we look upon the cell-bodies as the part in which the most

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[1] Howell and Huber: *Journal of Physiology*, 1892, vol. xiii.

[2] Ward: *Archiv f. Anatomie u. Physiologie*, 1880; Stirling: *Arbeiten aus den physiologischen Anstalt in Leipzig*, 1874.

active changes occur, since the network of blood-vessels is most dense about them, indicating that the metabolic processes are here most active[1] (Fig. 80).

Chemical Changes.—For the direct microchemical determination of special substances within the nerve-cells there are but few methods, though some phosphorus-bearing substances (nucleins) can be demonstrated,[2] and the occurrence of chemical changes due to activity and to age are very evident. Macallum[3] has demonstrated the presence of iron in the stainable substance of Nissl. There is general consensus that the alkalinity of the nerve-tissues is decreased during activity, and this decrease in alkalinity may amount at times to a positively acid reaction. This change, too, is better supported by the observations made where the cell-bodies are numerous than by those made where the fibres are alone present.

Fatigue.—Not only is the food-supply to the nerve-cells, as represented by the quality and quantity of the plasma, variable, but the cells themselves are subject to wide variations in their power to utilize these food materials, and deviations from the normal in either of these respects means a diminution in the physiological powers of the cell, which we may call fatigue. In the nervous system the signs of fatigue are both physiological and histological, but it is to the latter changes only that attention will be here directed.

FIG. 80.—Frontal section through the human mid-brain at the level of the anterior quadrigeminum (Shimamura). On the left side the blood-vessels have been injected; on the right the gray matter is indicated by the heavy lines. It appears by this that the blood-vessels are most abundant in the gray matter.

If a faradic current is applied intermittently to the mixed nerve-trunk going to a limb, changes are to be observed in the cell-bodies belonging to the spinal ganglia of the several roots forming the nerve (Hodge).

When this experiment is made on a cat, and, after death, the sections from the stimulated are compared with those of the corresponding, but unstimulated, spinal ganglion, a picture like that represented by Fig. 81, is obtained.[4]

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[1] Shimamura: *Neurologisches Centralblatt*, 1894, Bd. xiii.

[2] Lilienfeld and Monti: *Zeitschrift für physiologische Chemie*, 1892, Bd. xvii.

[3] Macallum: *British Medical Journal*, London, 1898, vol. ii. p. 778.

[4] Hodge: *Journal of Morphology*, 1892.

The sections indicate that the cytoplasm, together with the enclosed nucleus and nucleolus, as well as the nuclei of the enclosing capsule of the cell, have all suffered change by this treatment. The stimulus was applied for only fifteen seconds of each minute, the remaining forty-five seconds being given to rest. In this way the cells here figured had been stimulated over a period of five hours. The nuclei of the sheath are flattened, the cytoplasm of the nerve-cells somewhat shrunken and vacuolated. With osmic acid the nuclei of the stimulated cells stain more darkly and the cytoplasm less darkly than in a resting cell. In the nerve-cells the nucleus is shrunken and crenated, and the nucleolus is also diminished in size.

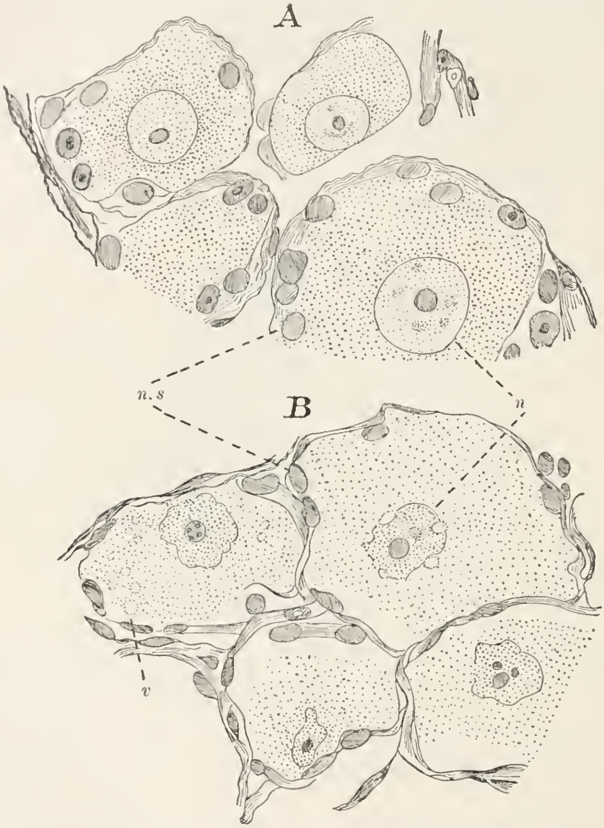

FIG. 81.—Two sections, *A* and *B*, from the first thoracic spinal ganglion of a cat. *B* is from the ganglion which had been electrically stimulated through its nerve for five hours. *A*, from the corresponding resting ganglion, The shrinkage of the structures connected with the stimulated cells is the most marked general change. *n*, nucleus; *n, s*, nuclei of the capsule; *v*, vacuole; × 500 diameters (Hodge).

In the first experiments the attempt was made to demonstrate a measurable change within the nerve cell-bodies as the result of stimulation. Assuming the nuclei of these cells to be approximately spherical, and calculating their volume as spheres, the shrinkage amounted to that shown in the following table:

Table showing the Decrease in the Volume of the Nucleus of Stimulated Spinal Ganglion-cells of Cats. Stimulation for fifteen seconds alternating with rest for forty-five seconds (Hodge).

Stimulation continued for	Shrinkage in the volume of the nuclei of the stimulated cells.
1 hour.	22 per cent.
2.5 hours.	21 "
5 "	24 "
10 "	44 "

This table further shows that the shrinkage is greater, the greater the time during which the stimulus was applied. There is thus established not only the fact of a change in the cell, but also a relation between the amount of this change and the length of time during which the stimulus was allowed to act. The results when expressed by a curve yield the following:

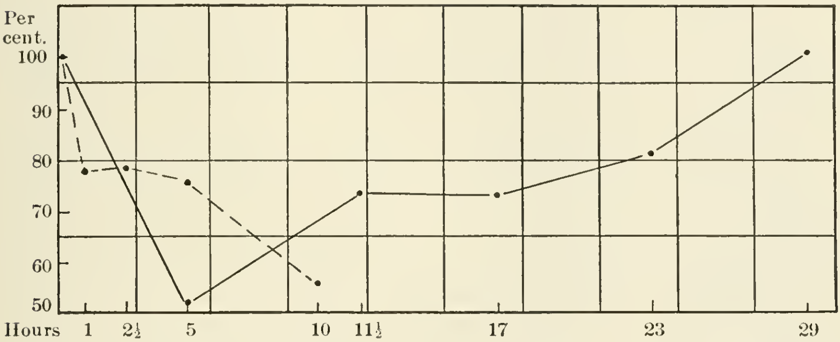

FIG. 82.—The broken line indicates the volume of the nuclei of the spinal ganglion-cells of a cat after stimulation for the times indicated. The solid line indicates the volume of the nuclei, first after severe stimulation for five hours, and then in other cats, also stimulated for five hours, but subsequently allowed to rest for different periods of time. The period of rest is found by subtracting five hours from the time at which the record is made. After twenty-four hours of rest the nucleus is seen to have regained its normal volume (Hodge).

Whether these changes could be considered similar to the normal physiological variations depended on whether it was possible to demonstrate recovery from them. This was accomplished in the following manner:

Under fixed conditions a cat was stimulated in the usual way and the amount of shrinkage in the nuclei of the spinal ganglion-cells was determined. This was found to be almost 50 per cent. Four other cats were similarly treated and then allowed various periods (six and a half, twelve, seventeen, and twenty-four hours) in which to recover. The results appear in Fig. 82.

Having thus shown that the change was physiological in the sense that it was one from which the cells could recover, it remained to be shown that the features of the change were discernible in the living cell, and were not caused secondarily by the actions of the reagents employed in preparing the sections.

For the study of the living cell, frogs were chosen, and the cells of the sympathetic ganglia examined. In these experiments, cells from different frogs were prepared under two different microscopes and kept alive in the same way by irrigation with a nutrient fluid. In one case, however, the cell was stimulated by electricity, while in the other no stimulation was applied. During the time of the experiment the cell which was not stimulated remained unchanged, while the stimulated cell went through the series of changes exhibited in Fig. 83.[1]

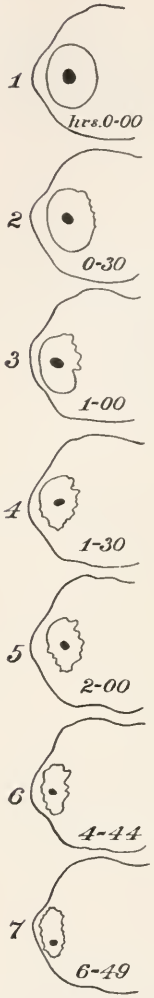

Fig. 83.—Showing the changes in the form of the nucleus resulting from the direct electrical stimulation of the living sympathetic nerve-cell of a frog. The hour of observation is given within each outline. The experiment lasted six hours and forty-nine minutes. A control cell treated during this time in the same manner, except that it was not stimulated, showed no changes (Hodge).

It followed that if these changes were really significant of normal processes they should be found in the nerve-cells of those animals which show well-marked periods of activity, alternating with periods of rest. To determine this, birds and bees were examined, one set of preparations being made from animals which were killed at the beginning of the day, after a night of rest, and the other from those killed at the end of the day, after a period of activity. The cells from the latter animals were found altered in a way similar to that following direct stimulation of the axone. The changes were demonstrated in the cells of the spinal ganglia of English sparrows, of the cerebrum of pigeons and cerebellum of swallows, and of the antennary lobes of bees. These observations therefore support the conclusions drawn from the appearances following direct stimulation.

Other observers[2] have obtained similar results.

The motor cells of the spinal cord and cells of the retina (dogs, Mann) have been added to the list of those showing fatigue changes. In the sympathetic cells of the rabbit, both Vas and Mann found, after a short period of stimulation, a preliminary swelling of the cell-body, and the same has been noted by Mann in the case of retinal cells in the dog.

The application of these observations to changes in the human nervous system has thus far been made only in a casual way, but enough has been already observed to make certain that the results are applicable.

It will be noted that the changes above described follow variations in the amount of stimulation, the nutrient conditions represented by the surrounding plasma remaining nearly constant. This latter, however, may undergo

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[1] Hodge: *Journal of Morphology*, 1892, vol. vii.

[2] Vas: *Archiv für mikroskopische Anatomie*, 1892; Mann: *Journal of Anatomy and Physiology*, 1894.

alteration, and recent observations show that in various forms of poisoning by inorganic substances or in zymotic diseases the nervous system and especially the cell-bodies are affected early and in a profound manner.[1]

Fatigue in Nerve-fibres.—There is no evidence for fatigue changes in nerve-fibres. For the full discussion of this question the reader is referred to page 96.

Atrophic Influences.—When a nerve-cell is not kept active by the impulses passing within it, it usually atrophies and may degenerate. The reason for this appears to be that the loss of those changes which accompany the nerve-impulses decrease the vigor of the nutritive processes.

For the detailed study of metabolic changes within the cell-body the method of Nissl[2] has been of prime importance. This method consists in fixing and hardening the nerve-tissue in 96 per cent. alcohol and staining with hot methylene blue. As a result, the cell-bodies especially, retain the stain, and in the cells there is a "stainable substance" characteristically arranged in small masses.

For a given animal the arrangement of the "stainable substance" is characteristic of the cells from different divisions of the nervous system. In a general way, too, cells occupying homologous positions in the central system of mammals tend to have the substance arranged in a similar manner. But the characteristic picture is modified in any given case by the age of the animal and by the pathological conditions which may have surrounded the cell chosen for study. The changes in the picture may be described as variations in (1) the stainable substance; (2) in the non-stainable fibrillar framework which appears to enclose the former.

In both of these, variations may be accompanied by gross physical changes, *i. e.*, alterations in the size of the cell-body, the nucleus and its parts, and alterations in the position of the nucleus, which may appear pushed to the periphery of a swollen cell, or even extruded from it. These physical changes are, of course, the effects of the action of the alcohol and other reagents employed on the cells altered from the normal, and while these physical changes serve most admirably to distinguish the normal from the abnormal cells, they do not necessarily represent the condition of the abnormal cells during life, a cell with an extruded nucleus, for example, being a case in point. These changes may ultimately cause the death of the element.

The stainable substance is found to be extremely sensitive to variations in the physiological conditions surrounding the cell, and therefore to be most important for the revealing of the effect of all sorts of changed conditions, such as starvation, activity, fatigue, injury to the axone, or injury to the afferent neurones bringing impulses to this particular cell, and, finally, the effects of toxins circulating in the blood.

[1] Schaffer: *Ungarisches Archiv für Medicin*, 1893; Pandi: *Ibid.*, 1894; Popoff: *Virchow's Archiv*, 1894; Tschistowitsch: *Petersburger medicinische Wochenschrift*, 1895.

[2] The publications of Nissl have not yet been printed in a compact form. The voluminous bibliography of the author is given by Barker: *The Nervous System*, 1899, pp. 105, 106.

Amputation in Man.—When the nerves to a limb have been severed, the consequent changes in the spinal cord depend on the age of the patient at the date of operation, the length of time elapsing between the operation and death, and the level on the limb at which the amputation was made. When the amputation occurs early in life, and the time before death is long, and the level of the amputation high, the alterations are maximum, and consist in an atrophy in the peripheral efferent nerve-fibres, slight atrophy (or sometimes complete disappearance) of the spinal ganglion-cell bodies, atrophy of dorsal root-fibres and their continuations within the cord, and, on the ventral side, disappearance or atrophy of the motor (efferent) cell-bodies in the ventral horn of the cord, together with their axonic outgrowths, the ventral root-fibres, the effect extending outward through the peripheral nerve to the point of section (see Fig. 84). The final appearances are brought about by slow changes, often requiring years for their completion, and hence most of the cases examined tend to show less change than is here described.[1]

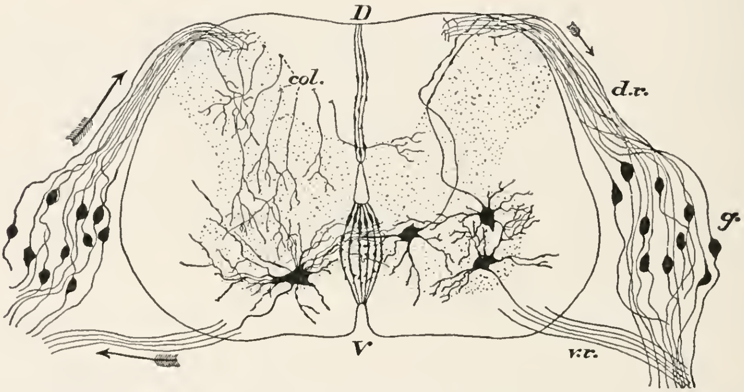

FIG. 84.—Cross-section of the spinal cord of the chick, × 100 diameters (van Gehuchten); *D*, dorsal surface; *V*, ventral surface; *d. r*, dorsal root; *v. r*, ventral root; *g*, spinal ganglion. On the left the arrows indicate the direction of the larger number of impulses in the dorsal and ventral roots respectively. The small arrow on the right dorsal root calls attention to the fact that some axones arising in the ventral lamina emerge through the dorsal root and convey impulses in the direction indicated.

The disturbance caused in the two sets of cells is, however, not the same. In the case of the cells of the spinal ganglion, the chief pathway by which they are stimulated under normal conditions is so far mutilated that probably only a small number of impulses passes over them. That some do pass is indicated by the sensations apparently coming from the lost limbs—sensations which are often very vivid and minutely localized.[2]

Thus the cell-bodies located in the spinal cord are to a great degree deprived by such an operation of one principal group of incoming impulses, namely—those which arrive through the dorsal root-fibres that are most closely associated with them; but at the same time there remain many other ways in which these same cells are normally stimulated. The efferent path-

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[1] Marinesco: *Neurol. Centralbl.*, 1892 (reviews the literature); Gregoriew: *Zeitschrift f. Heilkunde*, 1894, Bd. xv.

[2] Weir Mitchell: *Injuries of Nerves*, Philadelphia, 1872.

way from these cells is incomplete, and the impulses which must pass along the stumps are inefficient. That impulses do pass along the stumps of the efferent roots is beyond question, since, when the distal portion of an efferent nerve is cut off, the cell can be shown to still discharge through the portion of the fibres connected with the cell-bodies, and, finally, there is always a tendency for the cut fibre to regenerate, which indicates activity through its entire length.

Wherever in the central system a group of fibres forms the chief pathway for the impulses arriving at a given group of cells then the destruction of these afferent fibres brings about the more or less complete atrophy of the cells about which they terminate, and this effect is the more marked the younger the animal at the time of injury. Examples of this relation are found in the behavior of the nuclei of the sensory cranial nerves.

Thus the activity of a given cell contributes to the strength of its own nutritive processes, and different cell-elements, so far as they are physiologically associated, stand in a nutritive or trophic relation to one another such that the receiving cell is in some measure dependent for its nutrition on the cell which stimulates it.

Degeneration of Nerve-elements.—All parts of a nerve-cell are under the control of that portion of the cell-body which contains the nucleus; in this respect the nerve-elements are similar to other cells which have been studied, and in which the nucleated portion of the cell is found to be alone capable of further growth. It was shown by Waller[1] that when separated from the cell-body of which it was an outgrowth, a nerve-fibre belonging to the peripheral nerve soon degenerate from the point of section to its final distribution. The process is designated as secondary or "Wallerian degeneration." According to recent studies on this subject,[2] this degenerative change occurs practically simultaneously along the entire length of the portion cut off. The changes following the section of medullated nerve-fibres consist in a fragmentation of the axis-cylinder followed by its disappearance; enlargement and multiplication of the nuclei of the medullary sheath, and absorption of the medullary substance, so that in the course of the fibres there remains at the completion of the process the primitive sheaths together with the sheath-nuclei. In the early stages of this process the medullary sheath, moreover, undergoes some changes, the result of which is that it stains more deeply with osmic acid, and hence appears very black in comparison with the normal fibres about it (Marchi). These changes, as shown by the method of Marchi, may follow even slight injuries to the nerve-fibres—such as compression for a short time.

Concerning the progress of degenerative changes in the non-medullated fibres information is scanty. Bowditch and Warren[3] observed that when the sciatic nerve of the cat was sectioned, degeneration of the motor and

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[1] *Nouvelle méthode anatomique pour l'investigation du Système nerveux*, Bonn, 1851.

[2] Howell and Huber: *Journal of Physiology*, 1892, vol. xii.

[3] *Journal of Physiology*, 1885, vol. vii.

vaso-constrictor fibres in the peripheral portion went on at about the same rate. Stimulation of the peripheral part of the nerve gave a vaso-dilator reaction after the vaso-constrictor reaction had entirely disappeared, suggesting that the constrictor fibres degenerate more rapidly than do the dilators, although it is not improbable that the dilator fibres in this location really belong to the medullated class (Howell). After five days no vaso-motor reaction at all could be obtained. In a recent study by Tuckett[1] of the degeneration of the non-medullated fibres contained in the branches springing from the superior cervical ganglion, it is stated that the degeneration, as traced by histological and physiological methods is complete within thirty to forty hours after section of the fibres, and that the degenerative changes involve only the core of the fibres, the outside sheath and nuclei being unaffected.

In the central system, the distal portion of the fibres separated from the cell-body degenerate, as at the periphery, and this reaction has therefore formed a means by which to study the architecture of the central system. The details of the process are, however, not clear.

Nutritive Control.—So far, then, as the principal outgrowth of the nerve-cell is concerned, it is found to be always under the nutritive control of the cell-body from which it springs. The changes which take place when the spinal roots are cut will serve to illustrate this control (see Fig. 85). Section of the dorsal root at the distal side of the spinal ganglion at 3, causes a degeneration of all the fibres which form the dorsal nerve-root distal to the ganglion. Section of the dorsal root at 1, causes degeneration, central to the section, of those nerves which are outgrowths from the cell-bodies of the spinal ganglion. Section of the ventral root at 2, causes a degeneration distal to the point of section in those fibres which form the ventral root and which arise from the cells within the spinal cord. In each case, therefore, the necessary degeneration occurs on the side of the section away from the cell-body. The fraction of the neurone on the other side of the section may also degenerate under certain conditions, but the degeneration is not inevitable.[2]

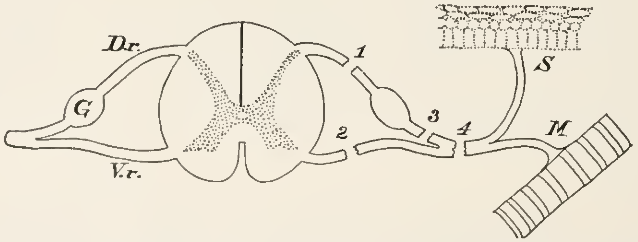

Fig. 85.—Schema of a cross-section of the spinal cord, showing the dorsal and ventral roots and the points at which they may be interrupted: *D. r.*, dorsal root; *V. r.*, ventral root; *G*, ganglion; *M*, muscle; *S*, skin; 1, lesion between ganglion and cord; 2, lesion between muscles and cord; 3, lesion between skin and ganglion; 4, combination of 2 and 3.

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[1] Tuckett: *Journal of Physiology*, 1896, vol. xix.

[2] Bregmann: *Arbeiten aus dem Institut für Anatomie und Physiologie des Centralnervensystems an der Wiener Universität*, 1892–93.

It is sometimes stated that degeneration takes place in the *direction* of the nerve-impulse. In a general way this is true, since the impulses usually travel from the cell-body along the axone. In the case of the fibres arising from the cells of the spinal ganglion it is not true, since the section at the distal side of the ganglion causes degeneration away from the spinal cord, while that on the proximal side of the ganglion causes degeneration toward the spinal cord; yet in both axones the impulse is in the same direction—namely, toward the cord (see Fig. 85).

Degeneration of the Cell-body.—It was discovered by von Gudden[1] that when the nerves of young animals are pulled away from their attachment with the central system, they most frequently break just at the point where they emerge from the cord or brain axis. When an efferent nerve is thus broken, in animals just born or very young, the remaining portion—*i. e.*, the cell-bodies with so much of their axones as lie within the central system—may atrophy to complete disappearance.

The bearing of such a fact is very direct. If in man there is reason to think that an injury was suffered during fetal life, there is a possibility that the injury may not only have prevented the further development of the cells involved, but may also have caused the complete destruction of some of them, in which case, of course, the architecture of the damaged region is necessarily abnormal.

Such complete disappearance as the result of early injury has not been shown for cells which lie entirely within the central system. Those forming the spinal ganglia may die, however, after interruption of the axones, even when the animal is mature (van Gehuchten). In the case of those central cells which form the sensory nuclei, like the sensory nucleus of the fifth nerve, or of the vagus, pulling out the nerve-trunk formed by the axones of the afferent ganglion cells, causes only an atrophy of the central cells, and not their complete disappearance.[2]

Regeneration.—When the two ends of the sectioned nerve are brought together under favorable conditions, the peripheral portion may be regenerated. This regeneration occurs only in axones possessing a nucleated (medullated or unmedullated) sheath, or in the anatomical prolongations of these, such as the dorsal root-fibres which penetrate the spinal cord.[3] In the typical medullated peripheral nerve this process occurs in the following steps as described by Howell and Huber:[4]

While the fragmentation and absorption of the myelin in the distal portion of the cut nerves is going on, the protoplasm in the neighborhood of the sheath-nuclei tends to increase. These enlarged masses of protoplasm then appear as a thread of substance within the old nerve-sheath. A new sheath is, however, soon formed on the protoplasmic thread, and the whole consti-

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[1] *Archiv für Psychiatrie*, 1870, Bd. ii.

[2] Forel: *Festschrift zur von Nägeli und von Kölliker*, Zürich, 1891.

[3] Baer, Dawson, and Marshall: *Journal of Experimental Medicine*, 1899, vol. iv. No. 1.

[4] *Journal of Physiology*, 1892, vol. xiii.

tutes an "embryonic fibre." The embryonic fibres lying on one side of the cut, unite with those on the other, union taking place in the intervening cicatricial tissue. Next the myelin appears in isolated drops, usually near the nuclei, and these subsequently unite to form a continuous tube, the formation of the myelin proceeding centrifugally from the wound. Then follows the outgrowth of the new axis-cylinder slightly behind the organization of the myelin into the tubular form.

It must not be forgotten that the last act, the formation of the axis-cylinder, is the important event; and while the whole process of repair may require many months, the rate at which the axis-cylinder, when started, grows out from the central end may be comparatively rapid. As a rule, regeneration does not occur in the central system,[1] and thus the method of experimentally causing degeneration has been one used for the study of the architecture of both the brain and cord.

That the regeneration is due to an outgrowth from the central stump has been clearly shown by Huber,[2] who inserted a bone tube between the cut ends of the sciatic nerve of the dog, and obtained regeneration of the nerve with a return of function, although the initial interval between the two parts of the nerve was more than three centimeters. The rate of growth from the central end has been specially studied by Vanlair.[3] In the facial nerve of the rabbit, function was restored in eight months after section, and in the pneumogastric and ischiadic nerves of the dog in about eleven months. In the latter case, this gives an average rate of growth of about 1 millimeter a day. In the scar-tissue between the two parts of the nerve the rate is not more than 0.25 millimeter a day, and hence the return of function tends to be delayed by any increase in the distance between the cut ends of the nerve. It appears also that the return of the cutaneous sensibility is more rapid than the return of motion (Howell and Huber), from which we infer that the afferent fibres (from the skin) regenerate more rapidly than the efferent fibres to the muscles.

Vanlair found that when the regenerated sciatic nerve of a dog was cut a second time, it not only again regenerated, but did so more rapidly than in the first case.

Much interest has always attached to the exact course taken by the regenerating fibres. They appear in a general way to be guided by the old sheaths of the peripheral portion. But the peripheral nerves contain both afferent and efferent fibres, and it would appear most probable that in the process of reformation the new fibres should undergo much rearrangement. Since the peripheral portion of the nerve acts as a guide to the growing fibres, the experiment has been tried of cross-suturing two mixed nerves. This has been done with the median and ulnar nerves in dogs. Reunion of the crossed

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[1] Worcester: *Journal of Experimental Medicine*, 1898, vol. iii. p. 597, describes a case of apparent regeneration of a fibre-bundle in the mid-brain, and cites the literature.

[2] *Journal of Morphology*, 1895, vol. xi.

[3] *Archives de Physiologie normale et pathologique*, 1894.

nerves occurred and sensation and motion returned to the affected parts of the limbs.[1] It is plain that by this arrangement the skin and muscles at the periphery must have acquired central connections with the spinal cord very different from those normal to them.

From the experiments of Cunningham,[2] it appears that the results of the cross-suturing of nerve-trunks are about what other facts would lead us to expect. If the trunks concerned control muscles acting in a similar manner, then cross-suturing produces but slight incoördination as a result; where, however, the central trunks normally innervate antagonistic muscles, then incoördination follows and persists. The stimulation of the cerebral cortex at the centre for a given muscle group always causes impulses to pass along the efferent fibres which normally innervate that group, no matter to what muscles these fibres may have been secondarily attached by cross-suturing. Moreover, striped muscles which normally exhibit rhythmic contractions lose this function when their innervation is changed by cross-suturing to a nerve-trunk which normally innervates an arhythmic muscle. Thus the central nervous system, in dogs, at least, does not adapt itself to the changed conditions introduced by cross-suturing.

In a series of investigations, Langley[3] has been able to show that when the preganglionic fibres of the thoracic nerves, which send branches to different groups of cells in the superior cervical ganglion, are allowed to regenerate after section, the several bundles of fibres appear to find and become attached to the cell-group which they normally controlled, since stimulation of the several roots after regeneration gave the reactions which were characteristic for them. However, there is reason to think that the arrangement after regeneration is not exactly the same as that before, and that some fibres have strayed from their original connections. Further, Langley[4] has been able by cross-suturing to establish a connection of the lingual and the vagus nerves respectively with the cervical sympathetic nerve, and so with the superior cervical sympathetic ganglion. Thus we have evidence that fibres other than those normally associated with the ganglion cells can at times form functional connections with them and carry impulses which excite them to their normal functions. This result has an important bearing on the theory of the stimulation of one element by another. The reaction following the indirect excitation of these cells depends, therefore, on the connections made by their axones, and not on the source of the fibres which excite them. The regeneration thus far described has been that of the axone by the cell-body or perikaryon. Concerning the regeneration of the dendrites, we have no information.

The possibility of the formation in mammals of new nerve-cells by the division of nerve-elements which are already mature and have been functional, has been claimed.

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[1] *Journal of Physiology*, 1895, vol. xviii.

[2] Cunningham: *American Journal of Physiology*, 1898, vol. i.

[3] Langley: *Journal of Physiology*, 1897, vol. xxii. p. 215.

[4] Langley: *Ibid.*, 1898–9, vol. xxiii. p. 240.

Karyokinetic figures in mature nerve-cells after injury have been demonstrated, but we have yet to learn exactly what cells can exhibit this reaction, and what becomes of them at the end of the nuclear changes. As there is no reason to think that in mammals such a neoformation of neurones in the nervous system has any significance for the general physiology of the animal, we shall pass the point with a mere reference to the literature.[1]

PART II.—THE PHYSIOLOGY OF GROUPS OF NERVE-CELLS.

A. ARCHITECTURE AND ORGANIZATION OF THE CENTRAL NERVOUS SYSTEM.

Since the nerves form the pathways by which the sensory surfaces of the body are put into connection with the central system, and also the pathways by which this system in turn is rendered capable of controlling the tissues of expression, it becomes at once important to determine over what nerves the impulses arrive, how they travel through that system, and by what other nerves they are again delivered at the periphery. The arrangement of these paths as found in the adult human nervous system is our principal object; at the same time it should not be forgotten that the reactions of simpler mammalian systems have furnished the greater number of facts, and to them we must constantly refer.

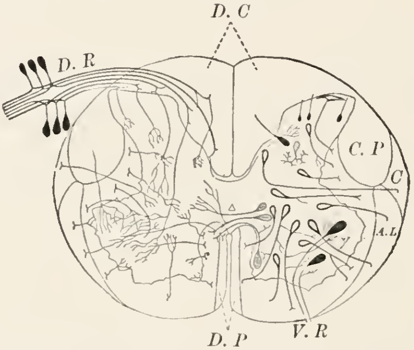

FIG. 86.—Schema of the arrangement of the human spinal cord as seen in cross-section; for clearness the afferent fibres are shown on the left side only, efferent and central cells on the right side only (von Lenhossek); *D. R.*, dorsal root; *V. R.*, ventral root; *D. P.*, direct pyramidal fibres; *C. P.*, crossed pyramidal fibres; *C.*, direct cerebellar tract; *A. L.*, antero-lateral tract; *D. C.*, dorsal columns. The various classes of cell-bodies are indicated by the manner of drawing.

General Arrangement of the Central Nervous System.—As the typical arrangement of the neurones is found in the spinal cord, the schematic representation (Figs. 86, 87) of a cross-section through this part will most readily illustrate it.

In accordance with this arrangement of the nervous system, as shown in

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[1] Tedeschi, A.: *Anatomisch-experimentellen Beitrag zum Studien der Regeneration des Gewebe des Centralnervensystems. Beiträge zur pathologischen Anatomie und zur allegemeinen Pathologie,* Jena, 1897, xxi. 43–72, 3 pl.

Figs. 86, 87, the elements which compose it fall into three groups: (1) *The afferent neurones;* those whose function it is to convey impulses due to external stimuli from the periphery, including the muscles and joints, to the central system. The expression "external stimuli" is in this case intended to include beside those outside of the body, also such stimuli as act within the tissues of the body but outside of the central nervous system; for example, those acting on tendons and muscles, and affecting the afferent nerves which terminate in them. The dorsal roots of the spinal cord arise from the cell bodies in the spinal ganglion. Sir Charles Bell (1811) showed that these roots are sensory, since in animals stimulation of the central end of the severed root causes reflex movements and expressions of pain, while in man stimulation of these fibres in the stump of an amputated limb may give rise to all the sensations which would be derived from their stimulation in the normal limb.

In some vertebrates a few efferent axones leave the spinal cord by the dorsal roots. These fibres can be seen in the chick (Fig. 87). In the frog stimulation of the peripheral end of the severed dorsal root may cause contraction of the skeletal muscles.[1] There is no good evidence, however, that these fibres are present in mammals.

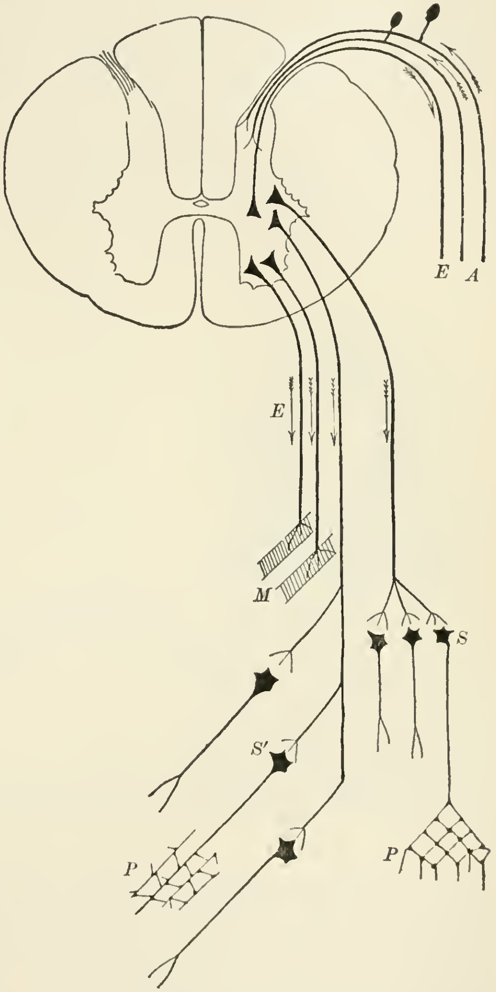

Fig. 87.—Schema of the distribution of the efferent fibres of the spinal roots: *A*, afferent fibres in the dorsal root only; *E, E*, efferent fibres in both dorsal and ventral roots. In the ventral root one group of efferent fibres goes to *M*, the striped muscles; another group to ganglion-cells, *S*, forming a single sympathetic ganglion, or to *S′*, cells located in more than one sympathetic ganglion, but all connected with one efferent fibre by means of its collaterals; *P*, peripheral plexuses into which the axones of some sympathetic cells run.

(2) *The central neurones;* those the axones of which never leave the central system, and the function of which is to distribute within this system the impulses which have there been received.

(3) *The efferent neurones;* or those the axones of which pass outside of

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[1] R. J. Horton-Smith: *Journ. Physiol.*, vol. xxi. p. 101.

the central system, and which carry impulses to the periphery. In this last group, again, two minor divisions may be made, namely: (*a*) the efferent elements, the cell-bodies of which lie within the central system, as is the case with those giving rise to the ventral roots; (*b*) those forming the peripheral ganglia entirely outside of the central system—the sympathetic ganglia and the more or less solitary cells which take part in the formation of the peripheral plexuses.

It was Sir Charles Bell who also showed the motor character of the ventral roots. Nevertheless the observation was soon made, that while stimulation of the central end of the severed ventral root was always without apparent effect, the stimulation of the peripheral end in addition to the typical motor responses might sometimes cause expressions of pain. This latter result was obtained even when the mixed nerve trunk, beyond the union of the two roots, had been severed, so that the only possible pathway for the impulses was through the junction of the two roots to the spinal ganglion, and so by the dorsal root to the cord. It appears probable from studies on the degeneration of the root fibres that the peripheral axones of some afferent neurones on their way to the meninges do run back toward the cord within the ventral root, and that it is the stimulation of these fibres which gives rise to the phenomenon of "recurrent sensibility" as it is called.

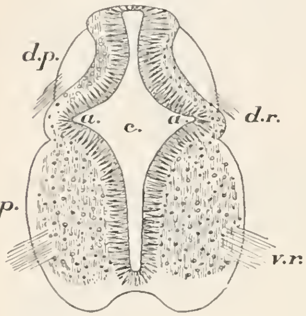

Fig. 88.—Cross-section in the cervical region of a fetal human spinal cord at the sixth week; × 50 diameters (v. Kölliker): *c.* central canal; *a. a.*, groove separating the two laminæ; *d. p.*, dorsal lamina; *v. p.*, ventral lamina, in which alone are located nerve-cells the axones of which leave the central system; *d. r.*, dorsal root; *v. r.*, ventral root.

The "afferent neurones" (1) have their cell-bodies collected to form the spinal ganglia.[1] The distal branches of these cells form the peripheral sensory nerves, and the proximal branches combine to form the dorsal nerve roots. On entering the walls of the spinal cord these latter fibres divide into two principal longitudinal branches which lie about the dorsal horns and form the major part of the dorsal columns. From time to time the ends of these branches, or their collaterals, enter the gray matter of the cord.

Thus, in a cross-section of the cord, the dorsal column and the gray matter represent the localities where the axones of the afferent elements are found. The afferent *cranial* nerves which can be homologized with the afferent spinal nerves have a corresponding distribution in the bulb.

The "efferent neurones" (3) have their cell-bodies only in the ventral horns of the spinal cord, or the homologous localities in the bulb and brain stem. See Figs. 88, 89, which show the part of the medullary tube divided

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[1] Recent work on the spinal ganglia shows that in addition to the elements usually described, they probably contain cells, the axones of which are distributed entirely within the spinal ganglion, and also cells which send their branches to the distal side only of the ganglion. See Dogiel: *Anat. Anz. Jena*, 1896, Bd. xii.

by His into the ventral and dorsal laminæ during development. The ventral horns of the gray substance form part of the ventral laminæ.

The cells of the sympathetic system which are interpolated in one portion of the pathway formed by the efferent elements lie, of course, entirely outside of the central system. (See Fig. 87.) The central neurones (2) occupy all parts of the central system, and hence where the bodies or branches of the first two groups are absent, the system is composed of central neurones only.

Arrangement of the Cells Forming the Several Groups.—All three groups of elements are grossly arranged so as to be bilaterally symmetrical with reference to the dorso-ventral median plane of the body. There are some minor exceptions to this general statement, but these are not known to have any physiological significance.

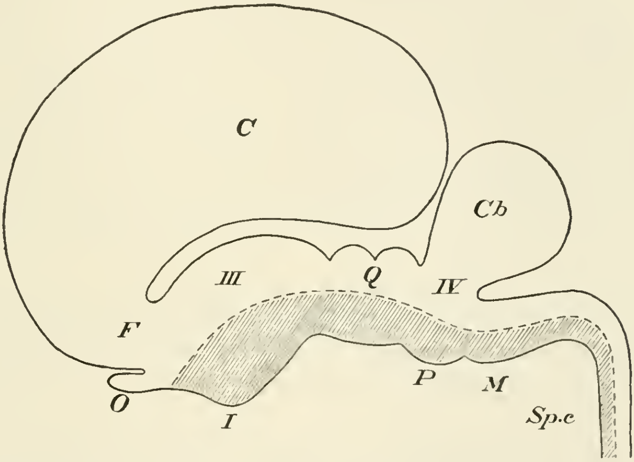

FIG. 89.—Schema showing the encephalon and cord; the unshaded portion is that derived from the dorsal lamina; the shaded that from the ventral (from Minot): *C*, cerebrum; *Cb*, cerebellum; *F*, foramen of Monro; *I*, infundibulum; *M*, bulb; *O*, olfactory lobe; *P*, pons; *Q*, quadrigemina; *Sp.c*, spinal cord; *III*, third ventricle; *IV*, fourth ventricle.

The main axones of the afferent elements are distributed almost entirely to the dorsal columns, and to the gray matter of that side of the cord on which they enter, though some crossing occurs in the dorsal commissure. In the cord, the efferent elements have their cell-bodies mainly on the side of the cord from which the efferent fibres emerge. In the case of some cranial efferent nerves the arrangement is different. There is found, for instance, a partial decussation of the fibres of the oculo-motorius; complete decussation in the case of the patheticus, and no decussation in the case of the abducens. It is the central cells which furnish almost all the axones forming the commissures, the decussating bundles and the projection systems, while the association tracts arise entirely from them.

Segmentation.—The grouping of the cell-bodies of the afferent fibres is originally segmental, one spinal ganglion corresponding to each segment of the trunk. In the brain, the original segmental arrangement has been greatly modified. In the trunk, too, the distribution of the distal portion of the afferent nerves is segmental, the area of skin involved forming a band about the body. On the other hand, the distribution of the proximal branches forming the dorsal roots is such that while part of the axones and their collaterals establish connection with the cord and bulb near the level at which the axone joins it, the principal divisions of the axone often pass along the cord a greater or less distance in both directions, and thus a long stretch of the cord may receive impulses by way of a single afferent element.

In some of the lower vertebrates the arrangement of the "efferent" cells is plainly segmental, but in man and the higher mammals this is hardly to be demonstrated. In the least modified parts of the cord, the efferent fibres do arise from cell-bodies mainly within the segment from which the ventral root emerges. But this massing of the efferent cell-bodies is largely obscured by the presence of central cells through the entire length of the ventral horns, while in the portions of the cord controlling the limbs the columns of cells furnishing fibres to a given ventral root may extend through as many as three segments of the cord. The distribution of the efferent fibres is evidently segmental in plan, though highly modified everywhere except in the thoracic cord supplying the portion of the trunk between the limbs. The principal peculiarity in the group of central cells is the great increase in the mass of them as we pass from the cord cephalad, the cerebrum, for example, being composed entirely of central cells.

Relative Development of Different Parts.—The bulk of the three subdivisions which have been named is very unequal. The central system is far more massive than the afferent and efferent taken together, but the relation cannot be stated with any exactness, since the mass of the peripheral system is not definitely known.

Connections between Cells.—In determining the connection between cells which permits a nerve impulse in one cell to stimulate another, the fact that the axone is the outgrowth of a cell-body, and that each cell is an independent morphological unit, forms the point of departure. Under these circumstances the question of the connection between cells takes the more explicit form of the question whether cell-branches may become continuous by secondary union. In several vertebrates there is good histological evidence that such secondary union occurs in a few cases in the central system.

In one type the axone of one element spreads out and encloses the cell-body of a second after the manner of a cup holding a ball. In other cases it appears that the terminals of a given axone may even penetrate the cell substance of the receiving neurone.

These are examples of concrescence. In the majority of cases, however, a close approximation of the parts of two nerve-cells is alone to be seen (Fig. 90). The termination of the discharging axone may be by fibrils or expanded disks, and occur either close to or upon the body, dendrites, or even collaterals[1] of the receiving neurone. If, as seems probable, the dendrites form an important pathway by which the receiving neurone is

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[1] Held: *Archiv f. Anat. u. Physiol.*, Anat. Abthl., Leipzig, 1897.

excited, then a cell with many dendrites should offer more receiving points than one with few. It is perfectly evident, however, that in many cases the dendrites are not the only pathway by which impulses may travel toward the cell-body.

Theories of the Passage of the Nerve-Impulses.—Accepting the view that, with the exceptions just noted, the nervous system is composed of discontinuous but closely approximated cell-elements, it remains to explain how impulses arising within the limits of one element are able to influence others. The relation between two neurones is quite comparable to that between a muscle and the nerve-fibres controlling it, but the recognition of that fact does not afford us much assistance.

As an hypothesis the passage of the stimulus may be assumed to depend on chemical changes set up at the tips of the terminals and affecting the surrounding substance, which, thus affected, acts to stimulate some point on the wall of the neighboring cell, either along a dendrite or on the cell-body itself.

The suggestion has been made that in some cases the space between two neurones may be varied by amœboid changes in the dendrites and terminals of the elements concerned. Although much may be said *a priori* in favor of this hypothesis, good histological evidence is still wanting.

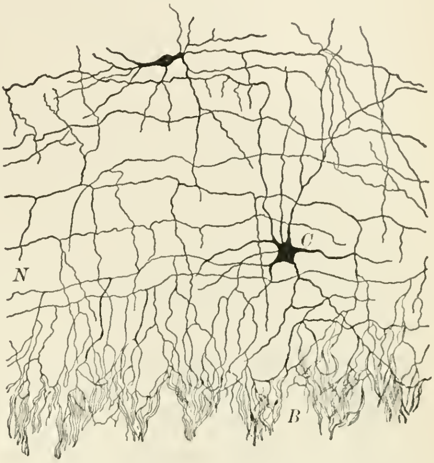

Fig. 90.—Showing at the lower edge of the figure a series of basket-like terminations of axones which surround the bodies of the great cells of Purkinje in the cortex of the cerebellum (Ramon y Cajal): *C*, cell-body; *N*, axones; *B*, basket-like terminations arising from cell *C*, and enclosing the cells of Purkinje.

The structural changes which permit the stimulation of one element to affect another are completed slowly, and, as we shall later see, these changes continue in some parts of the human nervous system up to middle life.

From what has just been stated, it follows that the nervous system of the immature person is quite a different thing from that of one mature, since in the former it is more schematic, more simple, the details of the pathways not having been as yet filled out. Moreover, considering the slow and minute manner in which the central system is organized by the growth of the cell-branches, it is the last place where there should be expected structural uniformity in the details of arrangement.

B. Reflex Action.

Conditions of Stimulation.—The conditions necessary for the generation of a nerve impulse are an external stimulus acting on an irritable neurone. While life exists, stimulation of varying intensity is always going on, and hence there is no moment at which the nervous system is not stimulated, and no moment at which the effectiveness of this stimulus is not varied. The response to this continuous and ever-varying stimulation is not necessarily always evident, but occasionally intensification of the stimuli renders them so strong that an evident reaction follows.

Though the foregoing statements suggest that the chief variable is that represented by the stimulus, the strength of which changes, yet as a matter of fact the variations in the physiological (chemical) condition of the nerve-cells are equally important; but neither factor can be studied independently.

The term "central stimulation" has been sometimes employed. For example, the spasmodic movements of the young child, when there is no change noticeable in the external stimuli acting upon it, are sometimes attributed to this cause; but these, although doubtless due to central changes, altering the irritability of the cells, are most properly classed with the reactions which follow the external stimulus. The misconceptions here to be avoided are those of supposing that the nervous system is at any time unstimulated, and that the evident responses follow a change of the external stimulus only.

When the impulse in one cell-element is used to arouse an impulse in another, as in all experiments where the nerve-cells are examined in a physiological series, the strength of the impulse from the second is not easily predicted. This is explained as due to variations in the ease with which the impulse in one element stimulates the next, and also to the variations in the second cell of those conditions which determine the intensity with which it shall discharge.

When an impulse has once entered the central system by way of a dorsal nerve root, it is found to follow the course of the afferent axones within the central system, and thus must be distributed almost simultaneously to a length of cord coextensive with that of the branches of the afferent axones. The arrangement makes possible the stimulation of a large number of central cells, and thus greatly increases the distribution of the initial disturbance. In the case of some of the cells about which the branches of the axone end, the impulse will not be adequate to cause in them a discharge, although it may still produce a certain amount of chemical change in them. The impulse thus tends to disappear within the system by producing, in part, chemical changes strong enough to cause a discharge of the next element in the series and, in an increasing number, similar changes of a less intensity.

Diffusion of Central Impulses.—If the previous description has been correct, two very important events occur: in the first place, the impulse reaches a far greater number of cells than evidently discharge, and in the second, the pathway followed by the impulses which do produce the discharge is by no means the only pathway over which the impulses can or do travel.

Simple Reflex Actions.—We turn next to an examination of these groups of neurones in action.

The simplest and most constant of the co-ordinated reactions of the nervous system are termed reflex. The term involves the idea that the response is not accompanied by consciousness, and is dependent on anatomical conditions in the central system which are only in a slight degree subject to physiological modifications. This view of reflex activities is in a large measure justified by the facts, but at the same time it must be held subject to many modifications, and it is not possible to make a hard and fast line between reflex and voluntary reactions.

The principal features of a reflex act may be illustrated by following a typical experiment:

If the central nervous system of a frog be severed at the bulb, so as to separate from the spinal cord all the portions of the central system above it, and the brain be destroyed, the animal is for a time in a condition of collapse. If, after recovering from the immediate shock, such a frog be suspended by the lip, it will remain motionless, the fore legs extended and the hind legs pendent, though very slightly flexed. If such a frog were dissected down to the nervous system, there would be found the following arrangement: Afferent fibres running from the skin, muscles, and tendons, and entering the cord by way of the dorsal nerve-roots. The central mass of the spinal cord itself in which these roots end, each root marking the middle of a segment. Within the cord and stretching its entire length are to be found the *central cells*, interpolated more or less numerously between the terminals of the afferent neurones and the cell-bodies of the efferent neurones. From each segment of the cord go the ventral root-fibres passing in part to the muscles and in part to the ganglia of the sympathetic system. The mechanism demanded for a reflex response is an afferent path leading to the cord; cells in the cord by which the incoming impulses shall be there distributed; and a third set of efferent elements to carry the outgoing impulses to the terminal organ which gives the response. It is important to consider in detail what occurs in each portion of this reflex arc.

In a frog thus prepared, stimulation of the skin in any part supplied by the sensory nerves originating from the spinal cord causes a contraction of some muscles.

Influence of Location of Stimulus.—The muscles which thus contract tend to be those innervated from the same segments of the cord which receive the sensory nerves that have been stimulated. Thus stimulation of the skin of the breast causes movements of the fore limbs, and stimulation of the rump or legs corresponding movements of the hind limbs. It is noticeable, however, that wherever the stimulus is applied the hind limbs have a tendency to move at the same time that the muscles most directly concerned contract.

If the attempt is made to correlate these variations in reaction with variations in the structure of the cord, we have to picture the simplest reactions (from the same level) as dependent on the formation of terminals on the afferent fibre just after its entrance into the cord and in the immediate neighborhood of an efferent neurone. In the second case either the afferent axone is extended some distance through the cord forming several terminations by its collaterals, or a central cell is excited and serves to carry the impulse to a distance.

Segmental Reactions.—In attempting to explain this associated contraction of the leg muscles, it must be remembered that the hind legs are, *par excellence*, the motile extremities of the frog, and therefore all general movements involve their use. We infer from this, moreover, that the arrangement in the spinal cord of the frog is not such that the sensory impulses coming into any segment tend to rouse exclusively the muscles innervated by that segment, but that these incoming impulses are diffused in the cord unevenly and in such a way as to easily involve the segments controlling the legs. As reflex co-ordinating centres, therefore, the several segments of the cord have not an equal value.

When the stimulus is applied on one side of the median plane, the responses first appear in the muscles of the same side; and if the stimulus is slight they may appear on that side only. The incoming impulses are therefore first and most effectively distributed to the efferent cells located on the same side of the cord as that on which these impulses enter. Such a statement is most true, however, when the stimulus enters the cord at the level where the nerves to the limbs are given off. At other levels the diffusion to the limb centres may take place more readily than to the cells in the opposite half of the same segment. When the muscles on the side opposite to the point of stimulation contract it is found that they correspond to the group of muscles giving the initial response on the side of the stimulus. The diffusion then tends to cross the cord and to involve the cells located at the same level as that at which the incoming impulses enter it.

There is some reason to think that when the impulses enter the cord toward the lumbar end the path by which the diffusion takes place with least resistance is not the shortest one between the two groups of cells, but a path toward the cephalic end of the cord, so that the impulses tend to pass up the cord on one side and down on the other.[1]

Strength of Stimulus.—In a reflex response the strength of the stimulus influences the extent to which the muscles are contracted, the number of muscles taking part in the contraction, and the length of time during which the contraction continues. That the strength of the stimulus influences the extent to which the contraction of a given group of muscles takes place is easily shown when, for example, the toe of a reflex frog which has been suspended is stimulated by pinching it or dipping it in dilute acid. In this case, if the stimulus be slight, the leg is but slightly raised, whereas, if the stimulus be strong, it is drawn up high. In the same way by altering the stimulus the muscles which enter into the contraction may be only those controlling the joints of the foot, whereas, with stronger stimuli, those for the knee and hip are successively affected, thereby involving a much larger number of muscles. Here, too, we infer a spread of the incoming impulses which is orderly, since the several joints of the limb are moved in regular sequence.

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[1] Rosenthal und Mendelssohn: *Neurologisches Centralblatt*, 1897, Bd. xvi. S. 978.

The responses which are thus obtained are not spasmodic, but are contractions of muscles in regular series, giving the appearance of a carefully coördinated movement—a movement that is modified in accordance both with the strength of the stimulus and its point of application. Moreover, such a movement may occur not only once, but a number of times, the leg being alternately flexed and extended during an interval of several seconds, although the stimulus is simple and of much shorter duration.

Continuance of Response.—The continuance of the response after the stimulus has been withdrawn must be, of course, the result of a long-continued chemical change at some point in the pathway of the impulse, and it appears probable by analogy with the results obtained from the direct stimulation of the central cortex, or the spinal cord, that in these cases the stimulating changes are taking place (p. 188) in the central cells or efferent cells[1] as well as in the skin supplied by the afferent nerves.

Latent Period.—It has been observed that in the case of a reflex frog—that is, a frog prepared as described above, with the spinal cord separated from the brain—an interval of varying length elapses between the application of a stimulus and the appearance of a reaction. The modifications of the interval according to variations in the stimulus have been carefully studied. When dilute acid applied to the skin is used as a stimulus, this latent interval decreases as the strength of the acid is increased. When separate electrical or mechanical stimuli are employed, the reaction tends to occur after a *given number* of stimuli have been applied, although the time intervals between the individual stimuli may be varied within wide limits. The experimental evidence for electrical stimuli shows that the time intervals may range between 0.05 second and 0.4 second,[2] while the number of stimuli required to produce a response remains practically constant.

Summation of Stimuli.—A single stimulus very rarely if ever calls forth a reaction if the time during which it acts is very short, and hence there has developed the idea of the summation of stimuli, implying at some part of the pathway a piling up of the effects of the separately inefficient stimuli to a point at which they ultimately become effective.[3]

The details of the changes involved in this summation and the place at which the changes occur, are both obscure, but it would seem most probable that summation is an expression of changes in the relations between the final twigs of the afferent elements and the cell-bodies of the central or efferent elements, which permit the better passage of the impulse from one element to the other, for the evidence strongly indicates that the course of the impulse can be interrupted at these junctions.

The foregoing paragraphs have been concerned mainly with changes occurring in the afferent portions of the pathway. Next to be considered is

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[1] Birge: *Archiv für Anatomie und Physiologie* (Physiol. Abthl.), 1882, S. 484.

[2] Ward: *Ibid.*, 1880.

[3] Gad und Goldscheider: "Ueber die Summation von Hautreizen," *Zeitschrift für klinische Medicin*, 1893, Bd. xx. Hefte 4–6.

the amount of central nervous matter which must be present in the frog's spinal cord in order that the reactions can take place.

Reactions from Fractions of the Cord.—If the construction of the cord was strictly segmental (a condition nearly approached in some worms and arthropods), in the sense that each segment contained the associated nerves for a given band of skin and muscle, there should be no disturbance on dividing the cord into its anatomical segments; and practically among the invertebrates, where the ganglionic chain is thus arranged, the single segments can perform alone all the reactions of which they are capable under normal conditions.[1] In such invertebrates the only change effected by the combination of the segments is that of co-ordinating in time and in intensity the reactions of the series. If, on the other hand, the segments of the cord were more or less dependent upon one another, and not physiologically equivalent, modifications of various degrees would arise according to the segments isolated. It has been found that the spinal cord of the frog may, under special conditions, be reduced to three segments and reactions still be obtained.

During the breeding season the male frog, by means of his fore legs, clasps the female vigorously and often for days. If, at this season, there is cut out from the male the region of the shoulder girdle bearing the fore limbs together with the connected skin and muscles, and the three upper segments of the spinal cord, then an irritation of the skin will cause a reflex clasping movement similar to that characteristic for the normal male at this season.

Reactions in Other Vertebrates.—It must not be thought, however, because it is the custom to emphasize the reflex activities of the lower vertebrates, and to show that these reflexes can be carried out even by fractions of the spinal cord alone, that, therefore, the spinal cord is particularly well developed in them. Comparative anatomy shows in the lower vertebrates a simplicity in the structure of the cord quite comparable with that found in the brain, and, as we ascend the vertebrate series, both parts of the central system increase in complexity. In this increase, however, the cephalic division takes the lead; and further, by means of the fibre-tracts from it to the cord, the cell-groups in the cord are more and more brought under the influence of the special sense-organs which connect with the encephalon. The physiological reactions of the higher vertebrates are especially modified by this latter arrangement. It is, therefore, true that the cord, as well as the brain, is in man more complicated anatomically than in any of the lower forms, and this is true in spite of the fact that the independent reactions of the human cord are so imperfect.

When an amphioxus is cut into two pieces and then put back in the water, a slight dermal stimulus causes in both of them locomotor movements, such as are made by the entire animal.

When a shark (Scyllium canicula) is beheaded, the torso swims in a co-ordinated manner when returned to the water. Separation of the cord from the

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[1] Loeb: *Einleitung in die vergleichende Gehirnphysiologie und vergleichende Psychologie*, Leipzig, 1899.

FIG. 91.—To show the nuclei of origin and of termination of the third to the twelfth cranial nerves, inclusive, in man. In the nuclei of origin (motor nuclei) the axones are drawn as arising from the bodies of nerve-cells. In the nuclei of termination the relation which exists is typified by the splitting of the axone into a terminal brush. Aside from the nuclei of the cranial nerves, there are represented only the nuclei of origin and termination for the first cervical nerves: Radix anterior cervicalis I., and Radix posterior cervicalis I., and the Funiculus posterior together with the nuclei of termination for its fibres; Nucleus Goll Burdach. The Latin names of the nerves and other structures are placed over the localities to which they apply. The cranial nerves also bear their numbers in Roman numerals. (From *Icones Neurologicæ*: Strümpell and Jakob.)

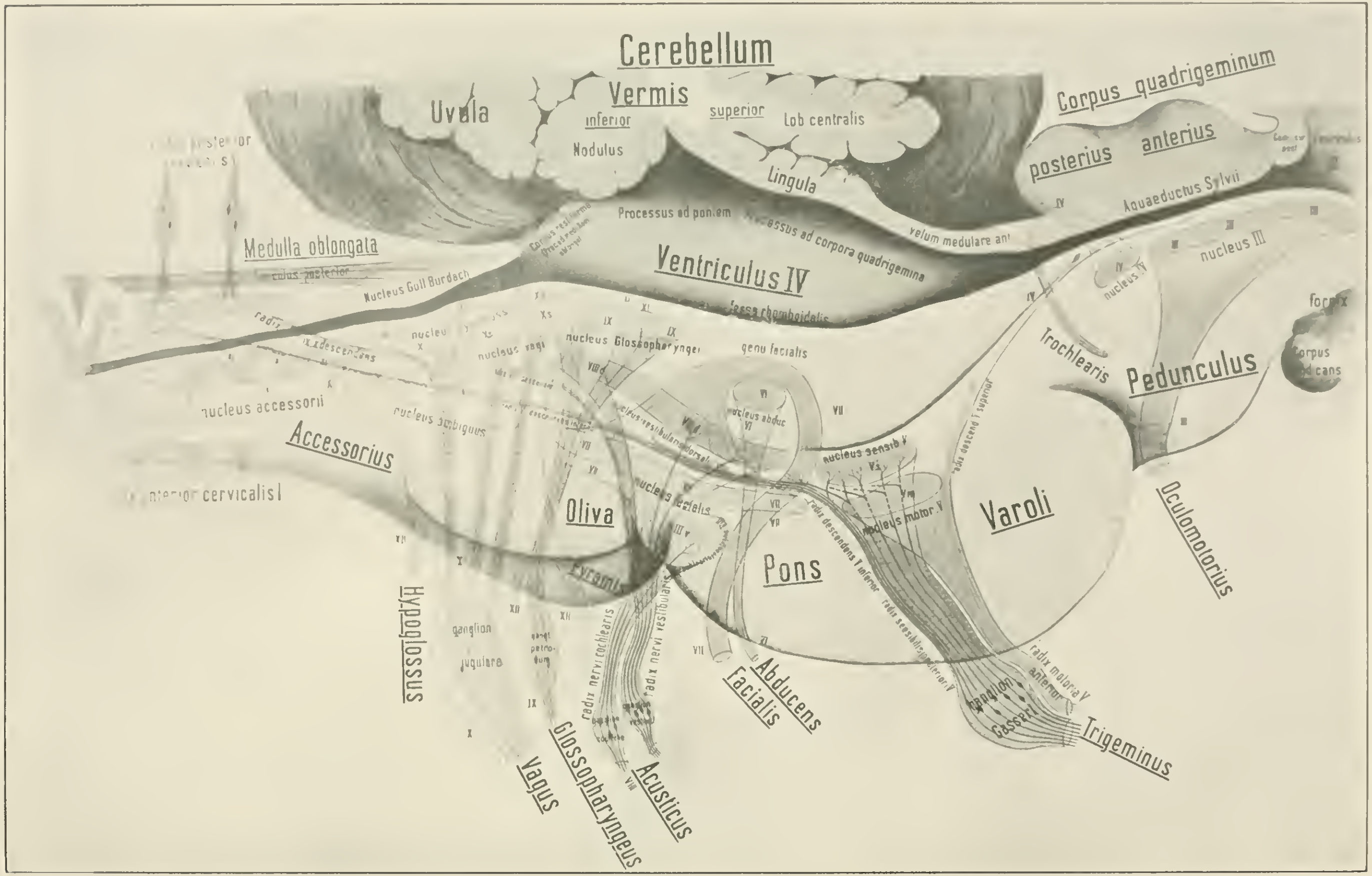
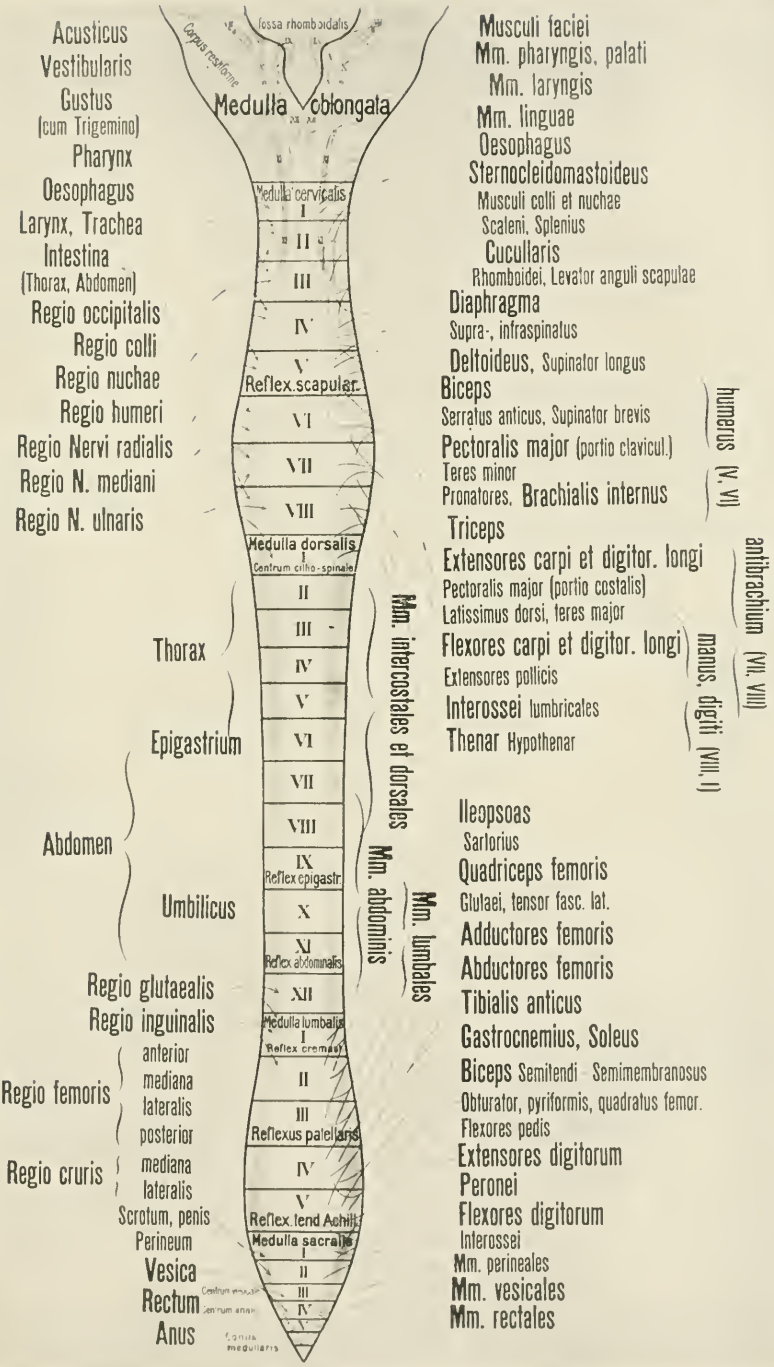

Cerebellum
Uvula
Vermis
inferior
Nodulus
superior
Lob centralis
Lingula
Corpus quadrigeminum
posterius
anterius
Aquaeductus Sylvii
velum medulare ant
Processus ad pontem
Processus ad corpora quadrigemina
Corpus restiforme
Medulla oblongata
Nucleus Goll Burdach
Ventriculus IV
fossa rhomboidalis
radix descendens
nucleus X
Xs
nucleus vagi
nucleus Glossopharyngei
IX
XI
genu facialis
VIII
nucleus accessorii
nucleus ambiguus
Accessorius
nucleus vestibularis dorsal
nucleus abduc VI
VII
nucleus sensib V
Vs
Vm
nucleus motor V
Oliva
nucleus facialis
Pyramis
Pons
Varoli
radix descendens V inferior
radix descend V superior
IV
nucleus IV
nucleus III
Trochlearis
Pedunculus
fornix
Corpus candicans
Oculomotorius
XII
X
Hypoglossus
ganglion
jugulare
ganglion petrosum
IX
Vagus
Glossopharyngeus
radix nervi cochlearis
radix nervi vestibularis
VIII
Acusticus
VII
Facialis
VI
Abducens
ganglion
Gasseri
radix motoria V
anterior
Trigeminus

FIG. 92.—Diagrammatic representation of the lower portion of the human bulb and spinal cord.

The cord is divided into its four regions: 1, medulla cervicalis; 2, medulla dorsalis; 3, medulla lumbalis; 4, medulla sacralis. Within each region the spinal segments bear Roman numbers. On the left side of the diagram the locality supplied by the sensory (afferent) neurones is indicated by one or more words, and these latter are connected with the bulb or the segments of the cord at the levels at which the nerves enter. The afferent character is indicated by the arrow-tip on the lines of reference.

On the right-hand side the names of muscles or groups of muscles are given, and to them are drawn reference lines which start from the segments of the cord in which the cell-bodies of origin have been located.

Within the cord itself, the designations for several reflex centres are inscribed in the segment where the mechanism is localized. For example, Reflexus scapularis, Centrum cilio-spinale, Reflexus epigastricus, Reflexus abdominalis, Reflexus cremastericus, Reflexus patellaris, Reflexus tendo Achillis, Centrum vesicale, Centrum anale (the last two on the left side of the diagram). (From *Icones Neurologicæ*, Strümpell and Jakob.)


Acusticus
Vestibularis
Gustus
(cum Trigemino)
Pharynx
Oesophagus
Larynx, Trachea
Intestina
(Thorax, Abdomen)
Regio occipitalis
Regio colli
Regio nuchae
Regio humeri
Regio Nervi radialis
Regio N. mediani
Regio N. ulnaris
Thorax
Epigastrium
Abdomen
Umbilicus
Regio glutaealis
Regio inguinalis
Regio femoris
anterior
mediana
lateralis
posterior
Regio cruris
mediana
lateralis
Scrotum, penis
Perineum
Vesica
Rectum
Anus
Corpus restiforme
fossa rhomboidalis
Medulla oblongata
Medulla cervicalis
I
II
III
IV
V
Reflex. scapular.
VI
VII
VIII
Medulla dorsalis
I
Centrum cilio-spinale
II
III
IV
V
VI
VII
VIII
IX
Reflex epigastr.
X
XI
Reflex abdominalis
XII
Medulla lumbalis
I
Reflex cremast.
II
III
Reflexus patellaris
IV
V
Reflex. tend. Achill.
Medulla sacralis
I
II
III
IV
V
Centrum vesicale
Centrum anale
Conus medullaris
Mm. intercostales et dorsales
Mm. abdominis
Mm. lumbales
Musculi faciei
Mm. pharyngis, palati
Mm. laryngis
Mm. linguae
Oesophagus
Sternocleidomastoideus
Musculi colli et nuchae
Scaleni, Splenius
Cucullaris
Rhomboidei, Levator anguli scapulae
Diaphragma
Supra-, infraspinatus
Deltoideus, Supinator longus
Biceps
Serratus anticus, Supinator brevis
Pectoralis major (portio clavicul.)
Teres minor
Pronatores, Brachialis internus
humerus (V, VI)
Triceps
Extensores carpi et digitor. longi
Pectoralis major (portio costalis)
Latissimus dorsi, teres major
Flexores carpi et digitor. longi
Extensores pollicis
Interossei lumbricales
Thenar Hypothenar
antibrachium (VII, VIII)
manus, digiti (VIII, I)
Ileopsoas
Sartorius
Quadriceps femoris
Glutaei, tensor fasc. lat.
Adductores femoris
Abductores femoris
Tibialis anticus
Gastrocnemius, Soleus
Biceps Semitendi Semimembranosus
Obturator, pyriformis, quadratus femor.
Flexores pedis
Extensores digitorum
Peronei
Flexores digitorum
Interossei
Mm. perineales
Mm. vesicales
Mm. rectales

brain does not deprive a ray (Torpedo oculata) of the power of perfect locomotion. The same is true of the ganoid fish. In the case of the cyclostome fish (Petromyzon) the beheaded trunk is, in the water, inactive, yet, on gentle mechanical stimulation, it makes inco-ordinated responses; but, put in a bath formed by a 3 per cent. solution of picro-sulphuric acid, locomotion under the influence of this strong and extensive dermal stimulus is completely performed. In the case of the eel the responsiveness even to the picro-sulphuric acid bath is evident in the caudal part of the body alone. In the bony fish this capability of the spinal cord to control locomotion has not been observed.[1]

In these experiments the central system is represented by the entire spinal cord with the associated nerves, or by some fraction of it; but so simple, constant, and independent are the reactions of the cord under normal conditions that a strong stimulus is able to elicit the characteristic responses from even a fragment of the system. The higher we ascend in the vertebrate series the less evident do the independent powers of the cord become.

Tarchanow[2] has shown that beheaded ducks can still swim and fly in a co-ordinated manner, and among mammals (dog and rabbit) Goltz and Ewald[3] and others have demonstrated that if the lumbar region be separated from the rest of the cord by a cut and the animal allowed to recover from the operation it will with proper care live for many months, and not only are the legs responsive to stimulation of the skin, but the reflexes of defecation and urination are easily induced by slight extra stimulation. An instructive reaction occurs when such an animal is held up so that the hind legs hang free. When thus held, the legs slowly extend by their own weight and then are flexed together. The reaction becomes rhythmic and may continue for a long time. It is assumed in this case that the stretching of the skin and tendons due to the weight of the pendent legs acts as a stimulus, and in consequence the legs are flexed. This act in turn removes the stimulus, and as a result they extend again, to be once more stimulated and drawn up.

In man, as a rule, death rapidly follows the complete separation of any considerable portion of the cord from the rest of the central system, especially if the separation be sudden, as in the case of a wound. But Gerhardt[4] has recorded the retention of the reflexes in a case of compression of the cord by a tumor, the case having been under observation for four and a half years; and Hitzig,[5] a case in which a total separation between the last cervical and first thoracic segments had been survived for as long as seven years. The principal reaction to be observed in such cases is a contraction of the limb muscles in response to stimulation of the skin, such as a drawing up of the legs when the soles of the feet are tickled. No elaborate reflexes are, however, retained such as would be necessary in acts of locomotion.

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[1] Steiner: *Die Functionen des Centralnervensystems und ihre Phylogenese*, 2te Abth., "Die Fische," 1888.

[2] Tarchanow: *Pflüger's Archiv*, 1885, Bd. xxxiii.

[3] Goltz und Ewald: *Ibid.*, 1896, Bd. lxiii.

[4] *Neurologisches Centralblatt*, 1894, S. 502.

[5] *Loc. cit.*

It thus appears that the reflex responses, namely, simple reactions unaccompanied by consciousness, are in man mainly given by the unstriped muscle-tissue and by glands, and only in a minor degree by the striped muscles. Moreover, while the typical reflex is a reaction over which we cannot exercise direct control, the normal individual has some power over many of these reactions; for example, the impulse to micturition or defecation can be thus delayed, respiration arrested, and, in some instances, so remote a reaction as the beat of the heart either accelerated or slowed at will.

It is of interest to note that many reflexes which in the young are not controlled, as micturition, for instance, become so gradually, a change most probably dependent on the growth of axones from the cephalic centres into the cord, thus subjecting the cord-cells to a new set of impulses which modify their reactions. That such is the case is indicated by the fact that extreme fright or anæsthetics, which diminish the activities of the higher centres, often cause these reactions to take place involuntarily. Other reflexes are present in early life, but disappear later; such are the sucking reflex of the infant, and the remarkable clinging power of the hands, by which a young child is enabled to hang from a bar, thus supporting the weight of its entire body, often for several minutes. This last capacity soon begins to wane, and usually disappears by the second month of life.[1]

Co-ordination of the Efferent Impulses.—Incessantly the efferent impulses pass out from the cord to the muscles and glands. With each fresh afferent impulse those which go out are modified in strength and in their order, but just how they shall be co-ordinated is dependent on so many and such delicate conditions that even in the simplest case the results are to be predicted only in a general way.

The attempt to determine the spread of the impulse in the cord by observing the order in which the various muscles of the thigh and leg contract in response to thermal stimuli was made by Lombard.[2] In a reflex frog the tendons of the leg and thigh muscles were exposed at the knee, and each attached to a writing-rod in so ingenious a manner that simultaneous records of fifteen muscles could sometimes be obtained. The stimulus was a metal tube, filled with water at 47°–61° C., which was applied to the skin. Under these conditions, it was remarkable that a continuous stimulus was often followed, not by a single contraction of the muscles, but by a series of contractions, suggesting that in the central system the cells were roused to a discharge and then for a time concerned with the preparation for sending out new impulses, and that during this latter period the muscles were relaxed.

Apparently a high degree of uniformity in the conditions was obtained in these experiments, but at the same time the reactions were far from uniform, in either the latent time of contraction or the order in which the contraction of the several muscles followed, although certain muscles tended to contract first, and certain series of contractions to reappear. The co-ordination of the

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[1] Robinson: *Nineteenth Century*, 1891.

[2] *Archiv für Anatomie und Physiologie*, 1885.

contractions is therefore variable in time, even under these conditions. These variations are probably due either to the fact that the impulses are not distributed in the centre in the same manner on each occasion; or if they are thus distributed, the central and efferent cells vary from moment to moment in their responsiveness. That these cells should so vary is easy to comprehend, for all the cell-elements in such a reflex frog are slowly dying. In this process they are undergoing a destructive chemical change, and with these destructive changes are generated weak impulses sufficient to cause their physiological status continually to vary, thus modifying the effects of any special set of incoming impulses acting upon them.

It is not to be overlooked also that the dissection of the muscles tested, and the removal of the skin about them, deprived the spinal cord of the incoming impulses due to the stretching of the skin by the swelling of the contracting muscles and disturbed the order and intensity of such sensory impulses as come in from the tendons and the muscles themselves. The observations of both Bickel[1] and Hering[2] show that these impulses are not necessary for accurate reflex movements of the frog's leg, and thus weaken the force of the suggestion just made. However much these impulses may add to the regularity of the muscular responses, Lombard concludes that the discharge of one efferent cell is not necessary in order that another efferent cell may discharge, but that each discharging cell stands at the end of a physiological pathway and may react independently.

Purposeful Character of Responses.—When the muscular responses of a reflex frog to a dermal stimulus are studied, they are seen to have a purposeful character, in that they are often directed to the removal of irritation. This is demonstrated by placing upon the skin on one side of the rump a small square of paper moistened with dilute acid. As a result, the foot of the same side is raised and the attempt made to brush the paper away; if the first attempt fails, it may be several times repeated. When the irritation has been removed the frog usually becomes quiet. If the leg of the same side be held fast after the application of the stimulus, or if the first movements fail to brush away the acid paper, then the leg of the opposite side may be contracted and appropriate movements be made by it. Emphasis has been laid by various physiologists upon reactions of this sort as showing a capability of choice on the part of the spinal cord, thus granting to the cord psychical powers. Against such a view it must be urged that the movements of the leg on the side opposite to the stimulus do not occur until after the muscles of the leg on the same side have responded. When these responses are inefficient because the leg is prevented from moving or because they fail to remove the stimulus, the prime fact remains that *the stimulus continues to act* and the diffusion of the impulses in the cord goes on, involving in either case the nerve-cells controlling the muscles of the opposite leg. The adjustment of the reaction of the leg, on whichever side it occurs, is, however, far

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[1] Bickel: *Pflüger's Archiv*, Bd. lxvii.

[2] Hering: *Archiv für experimentelle Pathologie und Pharmakologie*, Bd. xxxviii.

from precise; and although the movements of the leg, when the stimulus is applied far up on the rump, differ from those which follow the application of the stimulus to the lower part of the thigh, yet in either case they are very wide, and in both cases the foot is brushed across a large part of both the rump and leg. Considering, therefore, the rather general character of these movements, and the fact that the movements of the opposite leg only follow after a continued stimulus to the leg of the same side has produced an ineffective response, it is best to explain the result by the diffusion of the impulses within the cord, leaving quite to one side the psychical element. Such reflex actions are in a high degree predictable, but in reality this has little significance, since there is but one general movement that a frog in such a condition can make, whether the stimulus be applied to the toes or the rump—namely, the flexion of the leg—so that under these circumstances the prediction of the kind of movement is a simple matter. The extent of the contraction is related to the intensity of the stimulus, and is in turn dependent on the excitability of the central system, which can be increased or diminished in various ways. The modification of the reaction as dependent on the location of the stimulus can be in a measure predicted, but the modification is wanting in precision just in so far as the movements themselves are wanting in this quality.

Reflexes in Man.—In the normal individual reflexes involving striped muscles are found in the tendon reflexes, of which the knee-kick is an example, in winking, and the whole series of reflex modifications of respiration, such as coughing, sneezing, and the like.

The activities of the alimentary tract are examples of reflex actions involving the contraction of muscles in deglutition, defecation, and similar peristaltic movements in other hollow viscera. These muscle-fibres are for the most part unstriped. So, too, micturition, the cremaster reflex, emission and vaginal peristalsis, and the reactions of parturition are to be classed here. Moreover, the entire vascular system is controlled in this manner, the contraction and distention of the small arteries being in a large measure in response to stimuli originating at a distance; while as a third group, we have the glands, the activity of which is almost entirely reflex. For the discussion of the various reflexes mediated by the cranial nerves, the reader is referred to the special sections dealing with the cardiac, vasomotor, and respiratory centres in the bulb and the pupillary centres in the mid-brain.

Periodic Reflexes.—Not all reflexes are to be obtained from the same animal with equal intensity at all times. In general, frogs in the spring-time and in early summer, after reviving from their winter sleep, are highly irregular in their reflex responses—so irregular that students are advised not to attempt the study of these reactions at this season. On the other hand, it is during the spring that mating occurs, and during this period the male clasps the female and exhibits the peculiar reflex which has already been described. Comparable with this variation in the frog must be the changes which occur in the spinal cords of migratory birds, which, both in the spring and in the fall, are capable of such extended flights, or in the system of hibernating animals and all animals exhibiting well-marked periodic variations in their habits of life.

Variations in Diffusibility.—The degree in which any set of incoming impulses is diffused and modifies the responsiveness of the central system depends, in the first instance, on the physiological connections of the fibres by which they travel, and, in the second, on the particular condition in which the central cells happen to be found. It is observed that by means of drugs it is possible to alter the diffusibility of incoming stimuli to an enormous extent. Strychnin and drugs with a similar physiological action have this as one of their effects.

Influence of Strychnin.—The experimental study of strychnin-poisoning shows the following relations: A frog poisoned by the injection of this drug is easily thrown into tetanus whether the brain is intact or has been removed previous to the injection. The drug is found to have accumulated in the substance of the spinal cord.[1] The peculiar change wrought in the nervous system is such that a slight stimulus will cause an extended and prolonged tetanic contraction of the skeletal muscles—*i. e.*, the diffusion of impulses within the cord is very wide and efficient to an unusual degree. The direct application of strychnin to the spinal cord has been carefully studied by Houghton and Muirhead.[2] When the strychnin solution was applied locally to the brachial enlargement of the spinal cord of a brainless frog, a subsequent stimulation of the skin of the arms produced tetanic contractions of the arms, and later, after the poison had acted for a time, of the entire trunk and legs. On the other hand, stimulation of the legs in such a case produced a slight reflex or none at all. Since, in order to cause contraction of the leg muscles, the efferent cells controlling the muscles of the leg must be discharged —and in the one case when the stimulus was applied to the arm region these cells discharged so as to cause a tetanic spasm, while in the other, when the stimulus was applied to the legs, they discharged only slightly—the alteration in the cord produced by the drug must affect some other group than these efferent cells. Since, moreover, a tetanus of the legs could be caused by the stimulation of the skin of the arm, the application of the drug being to the brachial enlargement only, it appears that the central cells, or those conducting the impulses entering by the dorsal root-fibres in the brachial region to the nuclei of the lumbar enlargement, are probably affected; and, further, that it is on the bodies of these cells that the drug must act, since they alone were in the locality at which the drug was applied. The application of the drug to the dorsal root-ganglia and to the nerve-roots between the ganglia and the cord proved to be without effect, so that the two parts which can possibly be influenced are the terminations of the sensory afferent nerves within the cord and some portion (the dendrites?) of the central cells with which these terminations are associated. But whether the change is in both these structures or only in one cannot now be determined.

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[1] Lovett: *Journal of Physiology*, 1888, vol. ix.

[2] *Medical News*, June 1, 1895.

The diffusion of impulses in the central system depends anatomically not only on the amount of branching among the axones of the individual central cells, but also on the association of many cells together, so as to accomplish a wide distribution of the impulses. In the case of the afferent elements, as we have seen, the diffusion depends on the branching of the axones alone.

Peripheral Diffusion.—Turning next to the efferent system, we find the conditions for diffusion dependent on the arrangement of several cells in series. When a group of efferent cells discharges, we know from the arrangement of the ventral roots that the impulses leave the cord mainly along the fibres which comprise these roots; but where the lateral root is present they may also pass out over it, as well as over the few efferent fibres found in the dorsal roots. These axones carrying the outgoing impulses have two destinations: (1) The voluntary or striped muscle-fibres; (2) the sympathetic nerve-cells, grouped in masses to form the vagrant ganglia (see Fig. 93).

When the impulses are thus sent out there is in the case of motor nerves no diffusion, the effect being limited to the peripheral distribution of the efferent axones, by way of which the impulses leave the central system. The fibres going to the voluntary muscles form, however, but one portion, which has just been indicated as group (1). The connections of the remaining group (2), passing to the sympathetic ganglia, are still to be examined.

Sympathetic System.—Associated with the cerebro-spinal system by the efferent axones, and by these alone, is the series of vagrant ganglia and also of peripheral plexuses containing ganglion-cells, which taken together form the sympathetic system.[1] This system is composed of neurones always monaxonic, but sometimes with, and sometimes without well-marked dendrites. The cells are more or less grouped in ganglia, and these ganglia interpolated between the efferent axones of the spinal nerve-roots on the one hand and the peripheral plexuses or terminal tissues on the other. The number of cells in the ganglia is greater than the number of spinal root axones going to them, and hence their interpolation in the course of the ventral root-fibres increases the number of pathways toward the periphery, as is shown in Fig. 93. In speaking of the fibres concerned, it is desirable to distinguish between the pre-ganglionic, or those originating in the medullary centres and passing to the ganglia; and the post-ganglionic fibres, or those originating in the cells of the ganglia and passing to the periphery.

Following the histological observations of Gaskell,[2] previously quoted, and the physiological studies of Langley,[3] an outline of the relations of the sympathetic cells, based on the arrangement found in the cat, is briefly as follows:

Pre-ganglionic fibres—*i. e.*, those growing out of cell-bodies located in the

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[1] Gaskell: *Journal of Physiology*, 1885, vol. vii.; von Kölliker, "Ueber die feinere Anatomie und die physiologische Bedeutung des sympathischen Nervensystems," *Verhandlungen Gesellschaft deutscher Naturforscher und Aertze*, 194, Allgemeiner Theil, 1894. [2] *Loc. cit.*

[3] Langley: "A Short Account of the Sympathetic System," Physiological Congress, Berne, 1895.

FIG. 93.—Schema of the neurones forming the sympathetic nervous system (Huber: *Journal of Comparative Neurology*, 1897, vol. vii.).

A *solid black line* designates the axone from an efferent neurone, with its cell-body in the ventral horn of the cord, and the terminal brush ending in a striated muscle (*m.n.*).

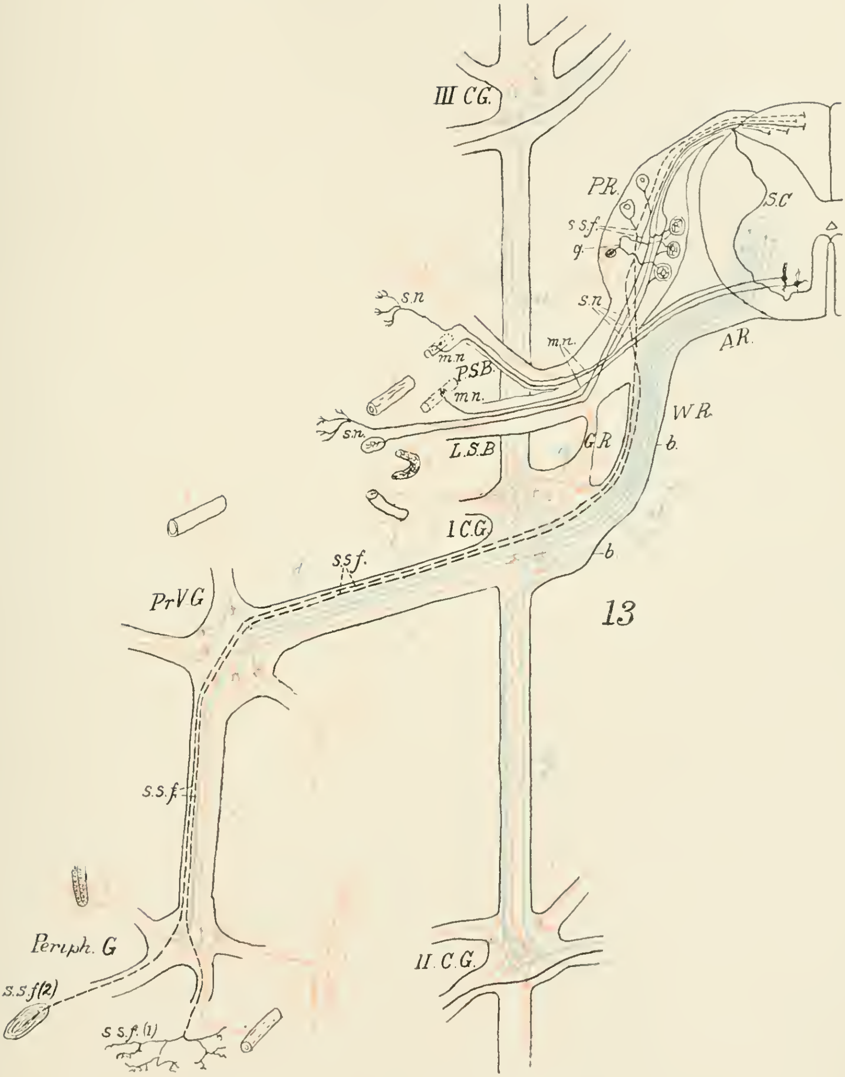
A *black line crossed by short dashes* designates the axone from an afferent neurone, the cell-body of which is in the spinal ganglion, and the peripheral axone of which terminates in the epidermis or some special sense-organ (*s.n.*).

An *interrupted black line* indicates an axone of similar origin to the one just described, but distributed with the fibres of the sympathetic system (*s.s.f.*). At the periphery it terminates in a free ending (*s.s.f.*(1)) or in a Pacinian corpuscle (*s.s.f.*(2)).

A *blue line* shows a pre-ganglionic fibre (of Langley), the cell-body of the neurone being located in the lateral horn of the cord. The axone leaves the cord by the ventral root (as a fibre of very small calibre), passes in the white ramus (*W.R.*), and terminates by a pericellular basket about the body of a sympathetic neurone (drawn in *red*).

The various places where such an axone may terminate are indicated as follows: *a*, axone passing through the chain-ganglion (*I.C.G.*) to terminate within the next higher chain-ganglion; *b*, axone passing as does (*a*), but terminating in the next lower chain-ganglion (*II.C.G.*); *c*, two axones ending in a ganglion of this same segment (*I.C.G.*); *d*, axone passing through the chain-ganglion of the segment and ending in a prevertebral ganglion (*Pr.v.G.*); *e*, axone passing through both a chain-ganglion and a prevertebral ganglion to end in a peripheral ganglion (*Periph.G.*); *f*, axone which gives off a collateral branch to one ganglion (*I.C.G.*) and passes on to terminate in a more distal ganglion (*Pr.v.G.*). Fibres arranged like (*f*) probably account for some of the reflexes obtained from sympathetic ganglia; *g* and *h*, axones representing fibres which regularly pass to any given ganglion from the ganglia above and below it. The sympathetic neurones are drawn in *red*, and about their cell-bodies terminal baskets of other axones (always in blue) are shown. They enter the mixed nerve by the gray ramus (*G.R.*). *m*, the axones of the sympathetic neurones, terminate: *i*, in the muscular coats of the blood-vessels (vaso-motor endings); *j*, in the muscular coats of the viscera (viscero-motor endings), and in heart-muscle (not specially shown in the figure); *k*, in glands (secretory fibres); *l*, in other sympathetic ganglia (a doubtful form of termination).

The figure further shows two "afferent" sympathetic neurones (Dogiel), in *dotted red*; *o*, arising in a peripheral ganglion (*Periph.G.*) and terminating in the prevertebral ganglion (*Pr.v.G.*); *p*, arising in the chain-ganglion (*I.C.G.*) and passing to the spinal ganglion, to terminate about Dogiel's spinal ganglion-cell of "type two," *q* (represented in *solid black*); *q*, spinal ganglion-cell (Dogiel's "type-two"), the terminals of which form baskets about the bodies of the ordinary spinal ganglion-cells.


III CG.
P.R.
S.C
s.s.f.
g.
s.n
s.n
m.n.
m.n
P.S.B.
m.n.
A.R.
W.R.
s.n.
L.S.B
G.R
b.
I C.G.
b.
s.s.f.
Pr V G
s.s.f.
Periph. G
s.s.f(2)
s.s.f.(1)
II. C.G.

13

cord—arise from the first thoracic to the fourth or fifth lumbar, and from these segments only (Gaskell). The fibres are medullated. Langley's experiments indicate that no sympathetic cell sends a branch to any other sympathetic cell, but other observers do not admit his results as conclusive. It has been shown that the pre-ganglionic fibres are interrupted in the ganglia. The post-ganglionic fibres are in part medullated, though sometimes medullation occurs only at intervals, but in the main they are gray or unmedullated.

The cerebro-spinal axones end in the ganglia in such a manner that the branches of the pre-ganglionic axone are distributed to a number of the ganglion cell-bodies, and these cells in turn send their axones either directly to the peripheral structures controlled by the sympathetic elements or to the plexuses such as are to be found in the intestine and about the blood-vessels.

The same pre-ganglionic fibre may have connections with several cells in one ganglion, or, by means of collaterals, connect with one or more cells in a series of ganglia (Langley).

Manner of Diffusion.—It has been found that while the cells in a sympathetic ganglion are so arranged that one pre-ganglionic fibre may be in connection with a group of cells, and thus the impulses which pass out of the ganglion be more numerous than those which entered it, yet the several groups of cells within the ganglion are not connected. In the peripheral plexuses there appears to be a different arrangement.[1]

It has been observed upon stimulation of the branches of the cœliac plexus in the dog that the several branches, though unlike in size, bring about nearly the same quantitative reaction in the constriction of the veins, from which we infer that though entering the peripheral plexus by different channels, the impulses find their way to the same elements at the end, owing to a multiplicity of pathways within the plexus.[2]

Experiments with strychnin on the more proximal sympathetic ganglia do not show any increased diffusibility following the application of the drug; but, on the other hand, Langley and Dickinson[3] have shown that nicotin applied to the superior cervical sympathetic ganglion of the cat produces a condition whereby electrical stimulation below the ganglion, which in the normal animal is followed by dilatation of the pupil, is without effect. Since the application of the drug to the nerve-fibres on either side of the ganglion is ineffective, when, at the same time, the application to the ganglion itself is effective, it is inferred that the drug acts by altering some peculiar relation existing within the ganglion, and the relation which is assumed to be thus modified is that between the fibres terminating in the ganglion and the cells which they there control. The passage of the efferent impulses through other sympathetic ganglia is likewise blocked by nicotin.

Evidence for Continuous Outgoing Impulses.—Under normal conditions striped and unstriped muscular tissues are always in a state of slight

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[1] Berkeley: *Anatomischer Anzeiger*, 1892.

[2] Mall: *Archiv f. Anatomie u. Physiologie*, 1892.

[3] *Proceedings of the Royal Society*, 1889, vol. xlvi.

contraction or tonus. When the nerves controlling any such set of muscles are cut, or their central connections injured, the muscles at first relax.

If a frog be hung up vertically after removing the brain, the cord remaining intact, it is found that the legs are slightly flexed at the hip and knee. If now the sciatic nerve be cut upon one side, the leg on the side of the section hangs straighter, indicating that the muscles have relaxed a little as the result of the section of the nerve; if, in the same animal, the smaller arteries in the web of the foot be examined both before and after the section, it is found that after the section they have increased in diameter. Conversely, artificial stimulation of the peripheral stump causes a contraction of the vessels, but it is not possible in so rough a way to imitate the tonic contraction of the skeletal muscles.

It is inferred from these experiments that normally there pass from the central system along some of the nerve-fibres impulses which tend to keep the muscles in a state of slight contraction. Destruction of the entire cord abolishes all outgoing impulses, and produces a complete relaxation of these muscles.

Though the intensity of these outgoing impulses is normally always small, yet it is subject to significant variations. The difference between the tone of the muscles of an athlete in prime condition and those of a patient recovering from a prolonged and exhausting illness is easily recognized, and this difference is in a large measure due to the difference in the intensity of the impulses passing out of the cord. Among the insane, too, the variations in this tonic condition follow in a marked way the nutritive changes in the central system, and both facial and bodily expression have a value as an index of the strength and variability of those impulses on which the tone of the skeletal muscles depends. Indeed, so wide in the insane is the variation thus brought about that when the expressions of an individual at one time in a phase of mental exaltation, and at another in that of mental depression, are compared, it appears hardly possible that they can be those of the same person.

This continuous outflow of impulses from the central system is indicated also by the continuous changes within the glands, and the variations in these metabolic processes according to the activities of the central system.

Rigor Mortis.—Even in the very act of dying the influence of these impulses can be again traced. The death of the central nerve-tissues being expressed as a chemical change, causes impulses to pass down the efferent nerves, and these impulses modify those chemical changes which, in the muscles of a frog's leg, for example, lead to rigor mortis. It thus happens that a frog suddenly killed and then left until the onset of rigor, will under ordinary circumstances show rigor at about the same time in both legs. If, however, the sciatic nerve on one side be cut immediately after the death of the animal, the beginning of rigor in that leg is much delayed, thus showing that the nervous connection is an important factor in modifying the time of this occurrence (Hermann).

The Nervous Background.—We return now to the conditions which modify the spread of the impulses within the central system, when this system is represented by the spinal cord of a reflex frog. Admittedly, there is in the case chosen but a fraction of the central system. It has been shown that all incoming impulses tend to spread over a large part of the central system. In a reflex frog, therefore, the cord is cut off from the remote effect of impulses which normally enter the system by way of cells located in the portion removed. Moreover, in the complete nervous system the incoming impulses tend to be transmitted to the cephalic end, and in some measure give rise to impulses returning within the central system and affecting the efferent cells. In a fragment of the central system like the cord such impulses taken up by the central cells must pass so far as the axones are intact; but as these for the most part end at the level of the section, such impulses are lost, in the physiological sense, at that point.

The fact, therefore, that the experiments with spinal reflexes are conducted on a portion of the central system has two important physiological consequences. In the first place, there are wanting incoming impulses, direct or indirect, from the portion removed; on the other hand, through the section of the afferent axones, in their course within the central system, there is a direct diminution in the number of the pathways by which the impulses arriving at the cord may be there distributed. It is most probable that in the frog, at least, the reduction of the central mass does not so much diminish the number of pathways by which the impulses may be immediately distributed by way of the afferent and central elements, as it diminishes the number of impulses which by way of the portion removed arrive at the efferent cells and modify their responsiveness.

The modification of the responsive cells under more than one impulse is well illustrated by an experiment of Exner:[1] A rabbit was so prepared that an electric stimulus could be applied to the cerebral cortex at a point the excitation of which caused contraction of certain muscles of the foot. One of these muscles was attached to a lever so that its contraction could be recorded, and a second electrode applied to the skin of the foot overlying the muscle. The discharging efferent cells in the cord were in this case subject to impulses from two directions, one from the cortex and one from the skin of the foot. With a current of given strength stimulation of the cortex alone caused a contraction of the muscle, and stimulation of the skin of the foot alone, a similar contraction. When both were stimulated simultaneously the extent of the contraction was greater than when either was stimulated alone. If now the strength of the stimulus applied to the skin of the paw was so reduced that alone it was inefficient, then a stimulus from the cortex which produced a reaction as indicated by the first cortical stimulus in Fig. 94 (*A*, *a*), put the efferent cells in such a condition that the stimulus from the skin (*A*, *b*, Fig. 94), applied within 0.6 of a second, produced a second contraction of the muscle, although alone the stimulus from the skin had proved inefficient. Here the first efficient stimulus from the cortex had rendered

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[1] Exner: *Archiv für die gesammte Physiologie*, Bd. xxvii.

the discharging cell for a short period of time more excitable. In the same figure the record shows that if a longer interval—here more than three seconds—be allowed to elapse, then the second stimulus from the skin remains inefficient. A similar relation between the two incoming impulses is also found to hold when the stimulus from the skin is made to precede. The curve *B*, Fig. 94, shows the results when both stimuli are inefficient. In this the stimuli (*b* and *a*) produce no effect when given several seconds apart, but when they occur within a short interval (*b′* and *a′*)—in this case 0.13 of a second—a contraction of the muscle follows. These various experiments, taken together, show in a beautiful way that in the cases chosen the two sets of impulses tend to reinforce each other, whether they are efficient or inefficient, and without regard to the order in which they come.

This relation between the discharging cell and those by which it is stimulated can be illustrated in still another way. It was observed by Jendrassik[1] that when a patient was being tested for the height of his knee-kick, a voluntary muscular contraction, or an extra sensory stimulus, occurring about the same time that the tendon was struck, had the effect of increasing the height of the kick. This relation was studied in detail by Bowditch and Warren,[2] and they were able with great exactness to measure the interval between the contraction of the muscle used for reinforcement and the time at which the tendon was struck. The curve shown in Fig. 95 represents the results of these experiments. It indicates that, up to 0.4 of a second, the closer together these two stimuli occur the greater the reinforcement. At an interval of 0.4 of a second no effect is produced by the muscular contraction. Increasing the interval only very slightly has, however, the effect of greatly diminishing the height of the knee-kick—*i. e.*, decreasing the strength of the discharge of the efferent cells—and this effect is not lost until the interval is increased to 1.7 seconds, when the voluntary muscular contraction ceases to modify the response. A given efferent cell is thus modified in its discharge according to the several stimuli that act upon it.

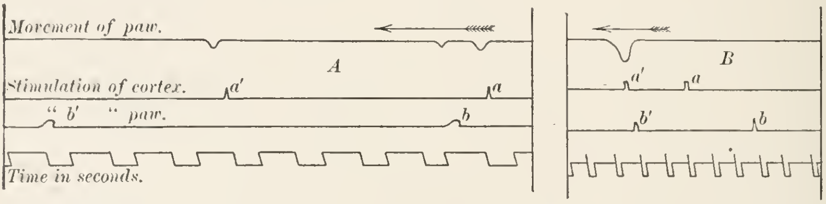

FIG. 94.—To show the reinforcing influence of stimuli applied to the cerebral cortex and to the skin of the paw, on the movements of the paw of a rabbit (Exner). The arrows indicate the direction in which the curves are to be read. In curve *A* the cortical stimulus at *a* causes a movement of the paw. Dermal stimulus, within a second, at *b* causes a movement of the paw. Cortical stimulus at *a′* causes a movement of the paw. Dermal stimulus several seconds later at *b′* is ineffective. In curve *B* dermal stimulus at *b* is ineffective. The cortical stimulus at *a* several seconds later is also ineffective. The dermal stimulus at *b′* is ineffective, but if followed within 0.13 second by a cortical stimulus at *a′* a movement of the paw occurs.

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[1] *Deutsches Archiv für klinische Medizin*, Bd. xxxiii.

[2] *Journal of Physiology*, 1890, vol. xi.

Effects of Afferent Impulses.—Studies on inactivity show that a certain amount of exercise in any given cell is necessary for its proper nutrition, and if the excitation fall below the point which causes this, the responsiveness of the cell is diminished.

For example, a strychnized reflex frog on being dipped into a solution of cocaine loses in so large a measure its irritability that its responsiveness falls far below that of a normal frog.[1]

In this case the central system is deprived by the action of the cocaine of the impulses which even in the absence of any special form of irritation normally arrive from the skin, and the abolition of these impulses causes a diminution in central responsiveness. Effects which can thus be accomplished in a few seconds by cutting off the afferent impulses from the skin may of course follow any slow diminution in these impulses, although all such slow changes are much more likely to be accompanied by some sort of compensation whereby other afferent impulses in a measure take the place of those which have been suppressed. The loss of these impulses which rouse the cells to activity is usually a more important condition than direct nutritive change, and must for this reason always be kept in view.

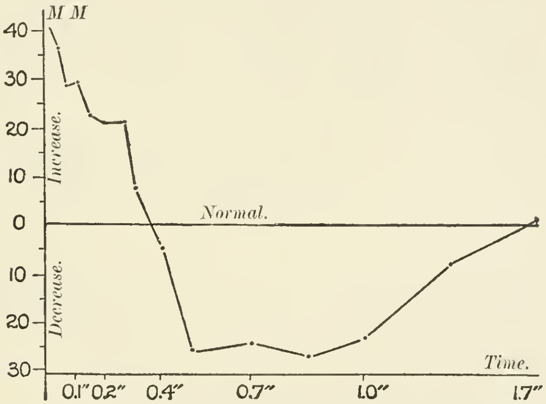

FIG. 95.—Showing in millimeters the amount by which the "reinforced" knee-kick varied from the normal, the level of which is represented by the horizontal line at 0, "normal." The time intervals elapsing between the clinching of the hand (which constituted the reinforcement) and the tap on the tendon are marked below. The reinforcement is greatest when the two events are nearly simultaneous. At an interval of 0.1″ it amounts to nothing; during the next 0.6″ the height of the kick is actually diminished the longer the interval, after which the negative reinforcement tends to disappear; and when 1.7″ is allowed to elapse the height of the kick ceases to be affected by the clinching of the hand (Bowditch and Warren).

Inhibition.—Evidence is accumulating to show that all the active tissues of the body may be influenced through their nerves in two opposite ways. That is, stimulation may increase or diminish their activity.[2] Thus the physiological processes in the glands, nerve-centres, or muscles can be so varied. In most cases, nerves which cause inhibition are, except in the central nervous system, distinct from those causing increased activity. The

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[1] Poulsson: *Archiv für experimentelle Pathologie und Pharmakologie*, 1885, Bd. xxvi.

[2] Meltzer: "Inhibition," *New York Medical Journal*, May, 1899.

chemical changes in the inhibited muscle of the heart are peculiar and different from those occurring during excitation. For instance, Gaskell[1] found that a *positive* variation of the muscle current occurred in the hearts of both the tortoise and crocodile upon stimulating the peripheral end of the vagus; while stimulation of the accelerator nerves caused the usual *negative* variation. Further, Gaskell pointed out that during the inhibition of the heart-muscle the anabolic processes were in excess, so that the cessation of inhibition was followed by an increase in the strength of the heart-beats.

If we now turn to the observations bearing on inhibition in the central nervous system, there are to be found numerous experiments, of which the following is a type: Let one leg of a reflex frog be stimulated by pinching it, or by dipping the toe in weak acid: a withdrawal of the stimulated leg will follow. Now repeat the experiment, at the same time pinching or otherwise stimulating the skin on the opposite leg. It will then be found that either the latent period of the reacting leg is much prolonged or that the reaction fails completely. This is a very simple example of a type of inhibition which is continually occurring.

The inhibitory effects are, however, not limited to the motor responses of the central system. It is an observation of the ancients that the greater obscures the lesser pain, and, in a general way, all strong sensations prevent the appreciation of the weaker ones, whether they be in the terms of the same or of a different sense.

Within the central nervous system very remarkable examples of inhibitory phenomena have been investigated, chiefly by Sherrington.[2] Boubnoff and Heidenhain[3] were the first to record the observation that under certain conditions stimulation of the cerebral cortex might cause a relaxation of some extensor muscles of the limbs when these were in a state of tonic contraction.

Sherrington was able to show that the stimulation of the cortical area for the flexors of the arms also gave rise to impulses leaving the cortex and causing a (inhibition) relaxation of the antagonistic extensors.

On stimulating the cortical area for the extensor muscles a corresponding relaxation of the flexors could be observed. Thus the cortical area for the contraction of a given group of muscles coincides with the area for the inhibition of the group antagonistic to it. Sherrington has also demonstrated the important role of this inhibitory process in mediating muscular co-ordination shown in movements of the eye. When all the muscles of the eye are paralyzed, the eyeball held by the connective tissues about it looks straight ahead. Sherrington cut the nerves to all the muscles of the left eyeball (monkey) except the external rectus. Under these conditions the eye, when at rest, looked toward the left. Stimulation of the cortical centers, which cause a conjugate deviation of both eyes to the right, was followed by a

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[1] Gaskell: *Journal of Physiology*, vol. vii.

[2] Sherrington: *Ibid.*, vol. xvii.

[3] Boubnoff und Heidenhain: *Pflüger's Archiv*, xxvi.

movement of the operated eye toward the median plane (the right), and to the position in which it would be held by the elastic tissues alone. This could be explained only through a relaxation or inhibition of the external rectus muscle, as a consequence of the cortical stimulation. Further experiments support the explanation, and also show that the cells, the activity of which is thus inhibited, must lie below the cerebral cortex, for the inhibition follows when the fibre-bundles below the cortex are directly stimulated, the cortex having been first removed.

The general bearing of these results is of the greatest importance. As has been pointed out by Hughlings-Jackson,[1] damage of any sort to a portion of the nervous system may, in the simplest case, decrease the activity of the group of neurones controlled by the damaged part by cutting off the stimulating impulses from them ; or, on the other hand—and this is often overlooked—it may permit them to become abnormally active by the stoppage of some impulses exerting an inhibitory control. Further, whether impulses from a given set of cells shall prove stimulating or inhibitory depends on the *other* impulses affecting the receiving cell group, and on the time relations between these several sets. This consideration serves to indicate the complex relations which may underlie the manifestations of disease in the central nervous system.

As to the mechanism for these inhibitory reactions, it can be safely said that for the most part the effects are not dependent on the existence of a special class of inhibitory nerves, and the most we can think of structurally is a different but not necessarily constant dendritic pathway for the cellulipetal impulses causing inhibition.

C. REACTIONS INVOLVING THE ENCEPHALON.

On attempting to distinguish between a voluntary and a reflex act from the physiological standpoint we find the chief difference to be that the voluntary act is not predictable, because, according to the capabilities of the animal, it may be more variable in form than is the reflex response, and also because, instead of necessarily occurring within a short interval after the stimulus, as does the reflex, the voluntary response may be delayed even for years.

Reflexes have been illustrated by the reactions from a portion of the spinal cord. It is to be remembered, however, that *any* of the sensory cranial or spinal nerves can serve as a pathway for the afferent impulses, and any of the groups of efferent cells situated in the ventral horns or their homologues in the brain stem, can carry the efferent impulses needed. Further, it must be remembered that it is these same afferent cells which always furnish the first set of impulses, and the efferent cells controlling the muscles and glands which furnish the last set of impulses in *both* reflex and voluntary reactions. The processes then which distinguish the two forms of reactions must take place in the central cells. We turn, therefore, to the nervous connections of the encephalon with the cord, since it is by means of these connections that

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[1] Hughlings-Jackson : *Lancet*, 1898, vol. i.

the impulses travel to the many series of central cells which are concerned in the simplest voluntary responses.

For the most complex voluntary reactions the entire central system is necessary, and especially the cortex of the cerebral hemispheres, while it has already been shown that the impulses which cause reflex actions can make their circuit in a very limited portion of the spinal cord. In the case of voluntary reactions the impulses take a longer pathway and involve a larger series of central nerve-elements, since from the point at which they enter the system they must pass to the cephalic end and back again to the efferent elements. At the same time, in a voluntary reaction, a greater number of impulses combine to modify the discharge from the efferent cells.

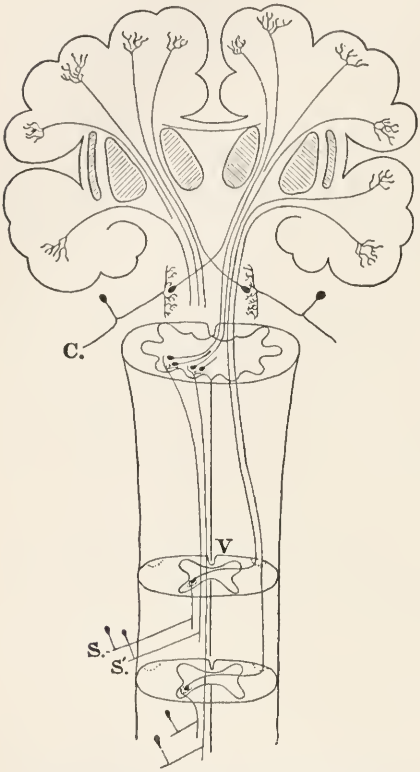

Fig. 96.—Schema showing the smaller pathway of the sensory impulses. On the left side, *S*, *S'*, represent afferent spinal nerve-fibres; *C*, an afferent cranial nerve-fibre. This fibre in each case terminates near a central cell, the axone of which crosses the middle line and ends in the opposite hemisphere. The interruption of the larger pathway in the thalamus is not indicated (van Gehuchten).

In order that the encephalon may be included in the pathway of the impulses entering the cord, it is necessary that pathways formed by axones should, on the one hand, extend up to the encephalon, and, on the other, back from it to the cord.

Fig. 96 indicates how the first part of this path is composed of the afferent elements of the dorsal spinal nerve-roots. The long paths in the dorsal funiculi of the cord are formed by the ascending branches of the afferent axones, and these terminate, for the most part, about the cell-bodies which form the nuclei of the dorsal funiculi at the junction of the cord and bulb. From these nuclei a second series of axones passes out, decussates at once, and then the axones pass forward in the medial lemniscus to find a second ending in the ventral cell masses of the thalamus, or possibly to continue up to the cortex. From this point a third group of neurones, with their cell-bodies in the thalamus, send out their axones to the cerebral cortex.

The cranial afferent nerves, which are not nerves of specific sensations (*i. e.*, the fifth, the vestibular portion of the eighth, the ninth, and tenth), probably have corresponding connections in the central system.

The impulses which are brought in by the afferent fibres also pass, in a large measure, to cells in the dorsal horn of the spinal cord by way of the collaterals and the ascending branches of the afferent axones, which end before they reach the nuclei of the dorsal funiculi. The cells in the dorsal horns send their axones in large numbers across the cord to the lateral columns of the opposite side, to reach the thalamus through the medial lemniscus, and thence to the cortex.

Of the many disputed points in this pathway, the most important relates to the interruption of the axones of the lemniscus in the ventral portion of the thalamus. The recent researches of Tschermak[1] indicate that probably there are two groups of neurones concerned, one of which sends its axones without interruption to terminate in the cortex, while the axones from the other are interrupted at the level of the thalamus. The latter group is the larger and probably the more important for the general reactions of the central system.

The pathways which are here sketched have been worked out mainly by the study of degenerations, in large part resulting from experimental lesions.

When the dorsal roots are crushed or sectioned between the spinal ganglion and the cord, the prolongation of the afferent fibre within the cord degenerates throughout its entire extent. The degeneration extends in the dorsal columns down the cord two or three centimeters from the level of the section, and also up the cord as far as the nuclei of the dorsal columns located at the commencement of the bulb. If the section is made near the caudal end, the degeneration may in consequence run through the entire length of the cord. Moreover, it occurs mainly on the side of the cord to which the sectioned nerves belong. Take, for example, the area of degeneration caused by the section in a dog of the dorsal roots on the left side between the sixth lumbar and second sacral nerves. The degeneration in the lower lumbar region is represented in Fig. 97, *a*, in the upper lumbar region in *b*, and in the thoracic region in *c* and *d*. The section *e* passes through the cervical enlargement. On passing cephalad the area of degeneration becomes smaller. This is interpreted to mean that all along, between the caudal and cephalic limits, fibres are given off from the main bundle to the intermediate levels of the cord. Here is evidence of an arrangement that is always to be kept in view. Though a number of fibres among those degenerating after section of the dorsal roots may run the longer course to the bulb, the larger portion run a short or an intermediate course, and are, therefore, distributed at different points between the termini. Injury to the dorsal roots at different levels shows, moreover, that the fibres from a given level which run the length of the dorsal columns do not mingle indiscriminately with those from other levels, but form a bundle; and as that bundle passes cephalad in the cord, it tends to lie nearer the middle line. Hence in the upper cervical cord, where the bundles from all levels are present, a cross-section shows the bundles which entered lowest down to be located nearest the dorsal surface and the median septum.

From these relations it is evident that comparatively few of the dorsal root-fibres run the entire length of the dorsal funiculi, since the majority

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[1] Tschermak: *Archiv für Anatomie und Physiologie*, Anat. Abthl., 1898, S. 291–400.

terminate somewhere between this extreme limit and their point of entrance.

Since the fibres[1] in the dorsal funiculi of the cord degenerate on destruction of the dorsal roots, it is inferred that they must be morphologically continuous with certain fibres in the roots, and, since the dorsal roots are afferent pathways, they too must form part of the afferent pathway in the cord.

The continuation of the other paths for the afferent impulses must, however, be formed by the axones of the central cells with which the dorsal root-fibres connect as they terminate at the several levels of the cord.

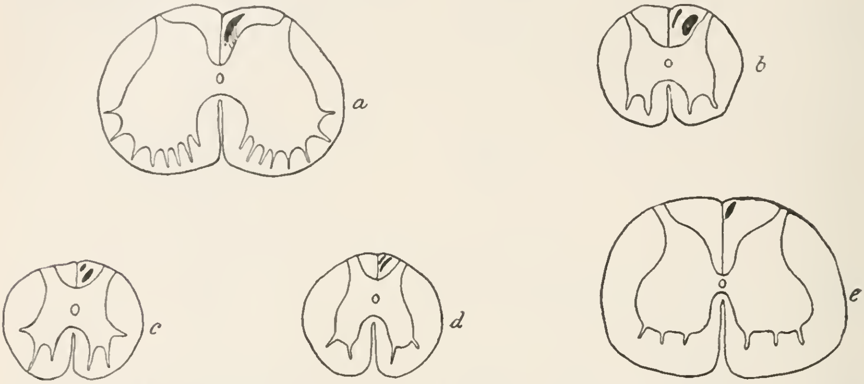

Fig. 97.—The sections are from five levels of the spinal cord of a dog. The dorsal roots on one side had been sectioned in two groups: first, the twenty-eighth, twenty-seventh, and twenty-sixth spinal nerves; and second, the twenty-second and twentieth: *a*, shows a schematic picture, representing a cross-section of the spinal cord taken just below the level of the twenty-second spinal root. The black spot represents the principal bundle of degenerated fibres as it appears in the dorsal column. At this level the bundle is rather near the median septum, but if sections further caudad were examined in series it would be found that the bundle constantly approached the dorsal horn, and finally fused with it at the level where the injured nerves joined the cord. If, on the other hand, a section be taken from the level between the twenty-second and the twentieth nerves—that is, after passing the level at which the second group of sectioned nerves joins the cord—there are to be seen two bundles of degenerated fibres marked by black spots in the sections (*b*, *c*, *d*). The last bundle to enter the cord, and the one lying nearer the dorsal horn, is, of course, formed by the degenerating fibres from the second group of roots. In the sections *c*, *d*, *e*, taken respectively at the level of the eighteenth nerve, the middle of the thoracic cord and the cervical enlargement, it is seen that both degenerated bundles grow smaller; that they shift toward the median septum and approach one another; and, finally, that they completely fuse in the cervical region (*e*).

Degeneration after Hemisection of Cord.—Upon hemisection of the cord involving one lateral half, the ascending fibres which degenerate appear in the dorsal columns, in the dorso-lateral ascending tract, and in the ventro-lateral ascending tract. The number of degenerated fibres is large on the side of the lesion, but on the opposite side there are also degenerated fibres in all these localities, although they are by no means so numerous. It is inferred that all the fibres which thus degenerate form paths for the afferent impulses.

The impulses which come in over a dorsal root on one side can, therefore, find their way cephalad either by the direct continuations of the dorsal root-fibres running in the dorsal column mainly on the side of the lesion or through the interpolation of central cells, the axones of which appear degen-

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[1] The bundles of "endogenous fibres" not arising from spinal ganglion-cells are neglected here.

erated in both lateral columns, but more numerously on the side of the lesion.[1]

The tracts which undergo secondary degeneration after this treatment include, therefore, those formed by the axones arising from central cells. These neurones have their cell-bodies arranged in columns running the length of the cord. In the neighborhood of these columns some of the dorsal root-fibres terminate. In the bulb we are familiar with such groups of cells, well marked as the "nuclei of the dorsal funiculi or columns," and the corresponding cells in the cord, though far less clearly segregated, are the homologues of those in the bulb. If this is granted, then the fibres which are outgrowths from these central cell-groups, whether in the cord or bulb, are also homologous.

Corroborative of what has been said on the subject of afferent pathways in the cord are the results of Pelizzi.[2] He studied dogs, making use of the method of Marchi, whereby the nerve-sheaths of fibres beginning to degenerate or the nutrition of which is disturbed give a characteristic reaction. He found, after hemisection of the cord, the same lesions that have been described above, with the addition that the changes could also be followed in some of the fibres of the ventral roots. More significant, however, is the fact that section of the lumbar and sacral dorsal roots, without direct injury to the cord, gave rise to modifications of the medullary sheaths, detectable by the method of Marchi, in all the localities just named.

A distinction must be made at this point. Secondary degeneration in the central system means eventual destruction of the severed fibre. The method of Marchi shows a characteristic change in fibres entering upon this degeneration, but this method also shows changes in the sheaths of elements which are only physiologically connected with those about to undergo secondary degeneration, but which themselves are, as a rule, not ultimately destroyed. Under the usual conditions of experiment, complete degeneration is confined within the morphological limits of a single cell-element, but the physiological changes in the cells overstep this limit, as shown by Marchi's reaction.

Physiological Observations on Afferent Pathways.—Making use of the fact that strong stimulation of the sensory fibres, such as those in the sciatic nerve, causes a rise in blood-pressure, Woroschiloff[3] sought to block the passage of the impulses causing this reaction by section of the cord in different ways in the upper lumbar region of the rabbit. It appears that in this animal the reaction was most diminished—that is, stimulation of the sciatic produced least rise in the blood-pressure—when the lateral columns of the cord had been cut through; and that the effect of section of the lateral column on the side opposite to that on which the stimulus was applied was greater than the following section of the column on the same side. These experiments form a very definite part of the evidence which directs our attention to the lateral columns of the cord as a principal afferent pathway.

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[1] Kohnstamm: *Neurologisches Centralblatt*, 1900, S. 242.

[2] *Archives italiennes de Biologie*, 1895, t. xxiv.

[3] *Berichte der math.-phys. Classe d. k. Gesellsch. d. Wissen. zu Leipzig*, 1874.

The physiological observations of Gotch and Horsley[1] indicate that when in a monkey a dorsal root is stimulated electrically 80 per cent. of the impulses pass cephalad on the same side of the cord, while the remainder cross. Of the 20 per cent. that cross, some 15 per cent. pass up in the dorsal columns. This leaves only 5 per cent. of the impulses to pass up by the contra-lateral columns. These experiments, therefore, give less importance to the lateral columns than was to be expected from the observations of Woroschiloff. The dorso-ventral median longitudinal section of the cord in the monkey (sixth lumbar segment)[2] shows an ascending degeneration in a small part of the dorsal area of the direct cerebellar tracts and of the ventro-lateral tracts, as well as in the columns of Goll. This would indicate that the section had cut fibres which crossed the middle line and ran cephalad in these localities.

Osawa[3] found that when the cord in a dog was hemisected (in the upper lumbar or lower thoracic region) the animal showed for the most part no *permanent* disturbance of sensation or motion.

If the cord was first hemisected on one side, and later on the other side, the second hemisection being made a short distance above or below the first, sensation and motion persisted behind the section, although they were somewhat damaged. After three hemisections, alternating at different levels, there still remained a trace of co-ordinated movement possible to the hind legs, although the sensibility of the parts could not be clearly demonstrated. The path thus marked out for some afferent impulses is certainly a tortuous one, and at present not readily to be explained. It must be remembered, however, that our information concerning the short pathways in the cord is very slight.

Nerves of Common Sensation.—In order to analyze the afferent pathways still further, we next inquire whether among the dorsal nerve-roots which pass between the cord and periphery there are separate nerve-fibres for each of the modes of sensation represented by pressure, heat, cold, pain, and the muscle-sensations. The data available for determination of this question are not of the best, but are still of some value.

The number of dorsal root nerve-fibres on both sides was estimated (in a woman twenty-six years of age) by Stilling to be approximately 500,000.[4] Stilling's estimate for the ventral root fibres in the same individual was 300,000.

The area of the skin in a man of 62 kilograms (136 pounds), and twenty-six years of age, was found by Meeh to be 1,900,000 square millimeters.[5]

From the study of the nerves going to the muscles of the dog, Sherring-

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[1] Croonian Lectures: *Philosophical Transactions of the Royal Society*, 1891.

[2] Grünbaum: *Journal of Physiology*, 1894, vol. xvi.

[3] *Untersuchungen über die Leitungsbahnen im Rückenmark des Hundes*, Strassburg, 1882.

[4] It seems probable that both these estimates were too low.

[5] A slight correction is called for here, owing to the fact that the area of skin includes that for the head, while the sensory nerves enumerated do not include the fibres going to the head. The general relations given below would not, however, be significantly modified by the alteration of the data.

ton[1] reports that from one-third to one-half the number of these muscular fibres arise from the dorsal root ganglion, and are therefore afferent in function.

If we assume that two-fifths of the number of sensory fibres, or 200,000, go to the muscles and joints, this would leave but 300,000 sensory fibres remaining, or one nerve-fibre to innervate, on the average, about six square millimeters of skin.

The experiments on tactile and temperature discrimination all indicate that the innervation of the skin is very unequal. The average distribution which has just been suggested must therefore be subject to local modifications that are very wide. Woischwillo[2] has determined that in man the skin of the arm is three times better supplied with sensory nerves than that of the leg. In both arm and leg the relative abundance of the sensory nerves increases toward the extremity of the limb. This increase is specially marked in the leg. Assuming, however, one nerve-fibre to six square millimeters of the skin to be the average relation, it becomes a serious matter to postulate separate groups of fibres for each mode of dermal sensation, since each time a new set of fibres is admitted the area of the skin innervated by any other set with a given function is thereby increased.

This being the case, there are good anatomical reasons for limiting the number of categories of nerve-fibres.

In every case the fibres carrying the impulses which come from the skin arise as outgrowths of the spinal ganglion-cells. Trophic nerves as a special category are not recognized, nor reflex nerves, the functions attributed to the latter being now explained by the collaterals of the afferent fibres. At present it is sometimes maintained that there must be special nerves for pain, pressure, heat, and cold. The evidence for those of pressure and heat and cold is the most satisfactory.

Pain.—Upon severe stimulation of the skin or muscles the normal person experiences a distinct sensation of pain. There is, however, great variation in the intensity of this sensation when the same stimulus is applied to different persons.

If we include abnormal persons, it is found that while in a few cases complete absence of painful sensations has been noted—the other sensations remaining normal—there are at the other end of the scale those cases in which pain is produced by many stimuli which would not have this effect on persons in ordinary health. The capability of a given stimulus to produce pain is therefore subject to wide variations according to the general condition of the subject.[3] The same stimulus has different effects in a given individual according to several circumstances. Peripheral irritation, such as an inflammatory process in the skin, greatly increases the intensity of the pain caused by the stimulation of the nerves supplying the locality. Continued stimula-

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[1] Sherrington: *Journal of Physiology*, 1894–5, vol. xvii.

[2] "Ueber das Verhältniss des Kalibers der Nerven zur Haut und den Muskeln des Menschen," Inaug. Diss. (Russian), 1883; *vide Centralblatt für Nervenheilkunde*, 1883, Bd. vi.

[3] Strong: *Psychological Review*, 1895, vol. ii. No. 4.

tion of the sensory nerves of the muscles and viscera has the same effect.[1] Local anaesthetics, such as cocaine, may reduce the sensibility to zero, and the same follows the general anaesthesia produced by chloroform, ether, nitrous oxide, morphine, and similar drugs. Painful sensations are distinct and powerful only when the stimulus is applied to general sensory nerve-trunks—*i. e.*, those mediating cutaneous, muscular, and visceral sensibility—while the nerves which mediate the special sensations of light, sound, taste, and smell do not give pain even on excessive stimulation.

Limiting our observation, therefore, to the nerves of cutaneous sensibility, it is found in exceptional cases that the sensations of pressure, heat, and cold may all be present to a normal degree, and yet increasing the stimulus be without effect in causing any painful sensations whatever. This would represent a condition of complete analgesia. Moreover, the capacity of the skin to cause abnormal painful sensations upon the adequate stimulation of each of these groups of nerves may be associated (in lesions of the central system) with any one group alone, the abnormal pain-sensations thus produced being either excessive or deficient.

We advance the hypothesis, therefore, that each of these three sensations, if pushed to excess, is usually accompanied by pain of gradually increasing intensity. Therefore it is most probable that these nerves when slightly stimulated mediate their proper sensations, but when this stimulus is pushed to excess they can give rise to pain also, and that in the last instance this sensation of pain may prove exclusive of any other. If this view is correct, it appears improbable that special pain-nerves exist.

As various experiments show, increasing either the strength of the peripheral stimulus, the number of fibres to which it is applied, or the irritability of the terminals of the fibres, will assist in arousing painful sensations. In the last analysis the physiological condition for pain is excessive stimulation, which by all analogy must mean excessive discharge within the central system. The changes following this discharge into the central system are not such as lead to co-ordinated muscular responses, but to convulsive reactions of a very irregular character. Where this process takes place in the central system we do not know. As to normal analgesia, it must be looked upon as dependent on a condition in which excessive stimulation cannot be produced; and we find this condition normally present only in the case of the nerves of special sense.

Since in the pathological conditions one sort of sensibility may be lost while the others remain, it has been inferred that there are separate fibres for the conveyance of each sort of sensation. This idea was expressed in the law of the specific energies of nerves as formulated by Joannes Müller, who pointed out that in many cases the same nerve might be stimulated in any way—mechanically, electrically, or chemically, as well as in the normal physiological manner; and that in all cases the mode of the response was the same—a sensation of light or taste or contact, as the case might be. Hence it was

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[1] Gad und Goldscheider: *Zeitschrift für klinische Medicin*, Bd. xx.

argued that the mode of the sensation was independent of the kind of stimulus, but dependent on the nature of the central cells among which the afferent fibres terminated. It will be seen, however, that this argument does not touch the character of the nerve-impulses in any two sets of nerves, and we have no observations by which to decide whether the nerve-impulses passing along the optic nerve-fibres are, for example, similar or dissimilar to those which pass along the auditory fibres.

If the nerve-impulses are always all alike, there seems no escape from the inference that separate nerve-fibres convey the impulses destined to give rise to different sensations. At the same time, it is just possible that the nature of the impulses and of the resultant sensation is, in the nerves of cutaneous sensibility, determined by the form of the peripheral stimulus, and that, as a consequence, different branches of the same nerve-fibres may be conceived of as susceptible to different forms of stimulation, and thus the two different sensations follow from the partial stimulation of the same nerve-fibres.

The second possibility, that the nerve impulse has different characters in different afferent nerves, and further may be modified by the nature of the normal stimulus (pressure or temperature), is not to be too readily rejected, as Hering at least argues in favor of such a view.[1]

Pathway of Impulses in the Spinal Cord.—The question arises how these impulses are distributed among the afferent tracts which are recognized in the cord, and whether these tracts form special paths for the impulses that rouse the several sensations of pressure, temperature (heat and cold), and pain. Since it is necessary to know the sensations of the subject, this problem can be, in some ways, best studied in man. Here, owing to wounds or disease, it may so happen that some of these sensations are lost or greatly diminished, and it is to be determined whether this loss is constantly associated with the interruption of definite tracts. Unfortunately, however, the material for such a study is very meagre.

In man the typical group of symptoms following hemisection of the spinal cord above the lumbar region has long been known as Brown-Séquard's paralysis. The clinical observations on cases suffering from such a lesion have been recently summarized by Oppenheim[2] as follows:

1. A paralysis of the homo-lateral muscles. In the case of the leg, the effects are most intense and persistent in the flexors of the thigh and shank, and the extensors of the foot.

2. When the two sides of the body are contrasted, there appears to be a homo-lateral hyperæsthesia, accompanied by contra-lateral anæsthesia.

3. As to the several forms of sensation, the following may be stated:

(*a*) The muscle sensations (Bathyästhesia, Oppenheim): the defect is never contra-lateral; sometimes, however, it is bilateral, but in most cases is homo-lateral.

(*b*) The contact sensations are very often not affected at all—sometimes

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[1] Hering: "Zur Theorie der Nerventhätigkeit," *Akademischer Vortrag*, Leipzig, 1899.

[2] Oppenheim: *Archiv für Physiologie*, Physiol. Abthl., Suppl. Bd., 1 Heft, July, 1899.

slightly, and in the latter case the hyperæsthesia may appear on either or both sides.

(*c*) The prominent and almost constant sensory symptom is the contralateral loss of the sensation for pain and temperature.

On the basis of a case[1] in which the lateral columns of the cord and the gray matter of both horns on the same side were the seat of damage, and in which there was a total loss of pain on the opposite side of the body without impairment of tactile sensibility, it may be inferred that the pain-impulses cross soon after entering the cord, and pass cephalad by some path lying within the damaged area.

A second case[2] is recorded in which a stab-wound divided all of one-half of the cord plus the dorsal column of the other half. There was here a loss of sensibility to pain on the side opposite the lesion, together with the loss of tactile sensibility on both sides, pointing, therefore, to the dorsal columns as the paths for the tactile impulses. The experiments on the lower animals contradict this conclusion.

The observations of Turner[3] on monkeys, in which hemisection of the cord had been made in the lumbar and thoracic regions indicate that all sensory impulses cross immediately after entering the cord, yet section in the cervical region showed that the impulses roused by touching the skin pass in part on the same side of the cord as the section, the other sensory impulses being, however, completely crossed.

On the other hand, from his work on hemisection of the thoracic cord of the monkey at different levels,[4] Mott found the disturbance of sensibility of all forms mainly on the side of the section.

Hemisection of the Cord.—From experiments on monkeys and a few cats Schäfer reports the following physiological changes after hemisection of the spinal cord in animals: "In the first few days complete motor paralysis of all parts supplied with nerves below the section. The limb or limbs on the paralyzed side swollen and warm (vasomotor paralysis) and lessened outflow of lymph and the skin dry (diminution of sweat). Knee-jerk exaggerated. Sensation not lost on the same side as the lesion, but at first appears dulled. (There is a difficulty in arriving at a clear decision on account of the motor paralysis rendering the animal unable to move the limb.) After a few days, unmistakable signs of feeling and localizing even a slight touch, and this long before the motor paralysis has passed off. The animals generally disregard a clamp-clip on the skin of the paralyzed limb, but not always; this phenomenon usually lasts until the return of movement in the muscles of the limb.[5] I have seen no signs of paralysis either motor or sensory on

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[1] Gowers: *Clinical Society's Transactions*, 1878, vol. xi.

[2] Müller: *Beiträge zur pathologische Anatomie und Physiologie des Rückenmarkes*, Leipzig, 1871.

[3] *Brain*, 1891.

[4] Mott: *Journal of Physiology*, 1891, vol. xvii.

[5] It will be seen that my observations on this point agree generally with those of Mott (*Phil. Trans. B.* 1892), although my conclusions are somewhat different. Mott, in my opinion, lays too much stress on the results of the clip test (Schäfer).

the side opposite to the hemisection in any case in which this has been strictly confined to the one half of the cord.[1] Sometimes the adjacent posterior column of the other half is injured, and in that event there is impairment of sensation for a time on both sides below the lesion. The motor paralysis, at first complete, becomes gradually incomplete, and finally is difficult or impossible to determine. But purely voluntary movements are not recovered or but very imperfectly, although all the ordinary associated movements of the limb are recovered. After about three or four weeks it is difficult to detect any sort of paralysis, but the limb which has been paralyzed is thinner than the other."

If the hemisection is made above the level of the eighth cervical nerve, the pupil on the same side is relatively contracted and remains so. The dilator fibres and the pilomotor fibres in the cervical sympathetic do not degenerate, but remain excitable. The pupil reacts to light and shade in spite of its being persistently smaller than the other. Excitation of the motor cortex of the opposite cerebral hemisphere produces, as a rule, no movements in the limbs which have been paralyzed, even if the associated movements have long returned.

As will be seen from the foregoing paragraphs bearing on the afferent pathways found in the spinal cord of man and the higher mammals, the evidence for the path of the cutaneous impulses is decidedly contradictory.

In addition to the cutaneous impulses there are the sensory impulses from the viscera, muscles, and tendons, which find their path cephalad probably along the direct cerebellar tract as well as by the long pathways in the dorsal columns. After hemisection of the cord the "muscular" sensations are usually lost on the side of the section, and the observations of Tschermak, already mentioned, point to the long fibres in the dorsal funiculi as the pathway for the impulses from the muscles and joints.

Indeed, the lack of good evidence for the conduction of any impulses—save those from the muscles and joints—by long tracts in the cord, has led Starr[2] to suggest that the dermal impulses are transmitted by short pathways through the cord.

Since, then, the dorsal and lateral columns of the cord appear to contain the chief afferent paths for the sensory impulses, the next step in following the pathway is to find the terminations of these tracts, whether long or short. Of the latter nothing can be said. The long tracts in the dorsal columns are connected with the nuclei of those columns (nuclei of Goll and of Burdach) on the same side. The cells of these nuclei send their axones cephalad; in part they decussate in the sensory crossing and contribute to the formation of the lemniscus, by way of which they pass either directly to the cerebral cortex about the central gyri, or reach this only after interruption in the

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[1] Ferrier and Turner (*Brain*, 1891) describe loss of sensibility in the opposite hind limb in the monkey. Brown-Séquard, as is well known, obtained this result in the rabbit. (See also Ferrier, *Functions of the Brain*, and *Croonian Lectures*, 1890.)

[2] Starr: *Transactions of the American Neurological Association*, Twenty-third Meeting, 1897, p. 7.

thalamus. It will be remembered that these fibres of the dorsal columns are physiologically joined with the contra-lateral thalamus and hemisphere. In part, however, the axones from the dorsal nuclei enter the cerebellum by the inferior peduncle of the same side, and we shall refer to this when considering the cerebellum.

Cranial Nerves.—We shall next consider briefly the relations of the several afferent cranial nerves, beginning with the vagus and working cephalad.

Nervus Vagus (*Tenth Nerve*).—The nucleus of termination for the afferent fibres of the tenth nerve (vagus) are shown in Fig. 91. The afferent fibres of this nerve are found to convey impulses which arise in the pharynx, œsophagus, stomach, liver, pancreas, spleen, larynx, bronchi, and lungs. Further, this nerve contributes afferent fibres to the nervus laryngeus superior. The location of the nucleus of termination (N. alæ cineræ) falls within the area of the *nœud vital.* Concerning the axones of the neurones forming the nucleus of termination, it can only be said that they are continued cephalad in the medial lemniscus and the fasciculus longitudinalis medialis.

Nervus Glossopharyngeus (*Ninth Nerve*).—The ninth nerve (glossopharyngeus, Fig. 91) is represented in the bulb by the tractus solitarius, the fibres of which find their principal nucleus of termination in the cell-group lying just to the medial side of the tract. The neurones of this nucleus send their axones cephalad by way of the medial lemniscus. The afferent fibres of N. glossopharyngeus mediate general sensations for the tonsils and pharynx, the tympanic cavity and Eustachian tube, while by way of the ramus lingualis it innervates the taste-organs of the posterior part of the tongue and those in the pharynx. In addition to these fibres mediating the sense of taste, pathological evidence points to some additional fibres with the same function (not belonging to the ninth nerve) which reach the bulb by way of the fifth nerve and the nervus intermedius. The nuclei of termination for these three nerves are very close to one another in the bulb, and hence the innervation of a special sense-organ from three cranial nerves, which, in the first instance, seems anomalous, becomes more intelligible when it is recognized that the nuclei concerned are practically continuous.

Nervus Intermedius.—In this connection the afferent fibres in the nervus intermedius (of Wrisberg) should be mentioned. These fibres arise from the cell-bodies of the ganglion geniculatum, enter the bulb between the superficial origin of the seventh and the vestibular root of the eighth nerve, and, running caudad along the dorso-medial tip of the ascending root of the fifth, finally terminate with the fibres of the glossopharyngeus in the cells of termination found along the tractus solitarius. The longitudinal extension of these fibres of the nervus intermedius in the bulb closely matches that of the nucleus of the eighth nerve, and at the periphery the fibres from the geniculate ganglion are distributed, in part at least, with those of the seventh nerve.[1]

Nervus Auditorius (*Eighth Nerve*).—*A. Cochlear Root.*—The eighth nerve

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[1] Van Gehuchten: "Recherches sur la Terminaison centrale des Nerfs sensible périphériques—le Nerf intermédiare de Wrisberg." *Le Névraxe*, Mars, 1900, t. i. fasc. 1.

goes to the inner ear. The cochlear portion of the inner ear mediates sensations of sound and is connected with the bulb by means of the nervus cochleæ; the cochlear branch of the eighth nerve. The cell-bodies of the nervus cochleæ are located in the spiral ganglion of the cochleæ, which is homologous with the dorsal root ganglion of a spinal nerve. The ganglion cells are bipolar or diaxonic, one axone passing toward the organ of Corti in the cochlea, and the other toward the bulb.

On reaching the bulb, the nerve formed by the latter axones enters in a large measure the nucleus nervi cochleæ ventralis,[1] and to a less extent the nucleus nervi cochleæ dorsalis. According to Held,[2] some of the root-fibres entering the ventral nucleus may be continuous as far as the superior quadrigemina, reaching that level by way of the trapezoideum, the superior olive, the lateral lemniscus, and the colliculus inferior; to all of which gray masses, including the nucleus nervi cochleæ dorsalis, these axones may give collaterals. Further, some fibres may terminate in any of the localities reached by the collaterals. Besides the direct continuations of the afferent axones by way of the ventral nucleus, each one of the localities mentioned above, including both the dorsal and ventral cochlear nuclei, contains cell-bodies forming, on the one hand, nuclei of termination, and on the other by their axones continuing the auditory pathway even to the cerebral cortex (Held). A group of central cells with their bodies in the nucleus nervi cochleæ dorsalis send their axones across the floor of the fourth ventricle, forming the striæ acusticæ. These axones in part decussate with the corresponding fibres—the crossing occurring in the raphé—and then either as direct or crossed fibres find their way cephalad by the same path (with some additions) as that described in connection with the ventral nucleus.

B. Vestibular Root.—Quite separate from the cochlear is the vestibular division of the eighth nerve, and this separateness is a strong argument against the suggestion sometimes made that the portions of the labyrinth innervated by the vestibular nerve, may also mediate sensations of sound. The best evidence shows the nerve to convey those impulses from the macula acustica utriculi and the cristæ ampullares, which are largely utilized in the maintenance of the equilibrium and in arousing the sensations of the movement of the body as a whole. The peripheral neurones which give rise to the vestibular fibres have their cell-bodies collected in the vestibular ganglion. The peripheral axones of the ganglion-cells end among sensory epithelium of the parts just named, while the central axones, forming a larger root than that associated with the cochlea, join the bulb at the caudal edge of the pons, the vestibular root lying to the cephalic side of the cochlear root. Having entered the bulb, the axones divide, after the manner of dorsal root fibres, into an ascending and a descending branch, which find their nuclei of termination in[3] (1) the nucleus nervi vestibuli spinalis (the radix descendens); (2) in

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[1] Barker: *The Nervous System and its Constituent Neurones*, 1899, pp. 544–555.

[2] Held: *Archiv für Physiologie*, Anat. Abth., Leipzig, 1893.

[3] Barker: *The Nervous System and its Constituent Neurones*, 1899, p. 627, *et seq.*

the nucleus nervi vestibuli medialis; (3) the nucleus nervi vestibuli lateralis (nucleus of Deiters); and (4) the nucleus nervi vestibuli superior. Finally, among other connections are to be specially mentioned those with the cerebellum (nuclei fastigii, nucleus dentatus, and the cerebellar cortex). Nothing definite is known concerning the pathways by which the impulses entering over the radix vestibularis reach the cortex.

Nervus Trigeminus (*Fifth Nerve*).—The neurones of this nerve have their cell-bodies located in the ganglion semilunari (Gasseri), and the peripheral axones act as the nerves of common sensation for the skin of the face and tongue and the mucous membranes of the mouth. The central axones which branch on reaching the bulb send their shorter divisions cephalad for a little distance, and the longer caudad, in both cases finding cells of reception in the region of the substantia gelatinosa, and in the latter instance extending caudad at least as far as the first segment of the spinal cord. Possibly, one set of neurones of the fifth passes directly into the cerebellum. The pathway from the nucleus of termination to the cortex has not been determined.

Second Nerve, Optic.—As has long been recognized, the optic nerve, so called, is a cerebral tract morphologically equivalent to such tracts as connect any portion of the cerebral cortex with a primary centre, the retina being in part the representative of the cerebrum; and the pulvinares, the quadrigemina, and geniculata externa being the primary centres.

At the chiasma where the two optic nerves come together their fibres intermingle, and then emerge as the optic tracts, which contain not only the fibres connected with the retina, but others added from the superposed parts of the brain, and forming the commissures of Meynert and von Gudden.

In the rabbit it was shown by von Gudden[1] that in the chiasma the majority of the fibres forming one optic nerve pass to the tract of the opposite side, but that a portion of the fibres remains in the tract of the same side.

This was inferred because removal of one eyeball caused in young rabbits a degeneration in the associated optic nerve and also in *both* optic tracts—most marked, however, in the tract of the side opposite to the lesion. Conversely, the section of one optic tract causes a degeneration in both optic nerves, the nerve of the side opposite to the lesion being most affected, and a smaller degeneration appearing in the nerve of the same side (see Fig. 98).

In the fish, amphibia, reptiles, and birds—except the owls[2]—the decussation appears to be complete.[3] For the partial decussation in the owls the evidence is physiological. This distribution of the optic fibres was associated by von Gudden with the position of the eyes in the head. The extreme lateral position of the eyes as it occurs in the lower mammals permits of but little combination of the two visual fields; whereas the position in man, in a

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[1] von Gudden: *Gesammelte und hinterlassene Abhandlungen*, Wiesbaden, 1889.

[2] Ferrier: *The Croonian Lectures on Cerebral Localization*, London, 1890, p. 70.

[3] Singer and Munzer: *Denkschriften der math.-naturwiss. Classe der kais. Akademie der Wissenschaften*, 1888, Bd. iv.

frontal plane, permits a combination of the fields to a much greater degree. It was in accordance with this principle that partial decussation of these nerves was anticipated by von Gudden in the owl, although the histological evidence for it was not obtained by him.

The most recent researches on mammals have so increased the number in which a partial decussation occurs that we are justified in regarding this arrangement as the rule, although the proportion of the uncrossed fibres is small in those mammals in which the eyes are placed laterally.[1]

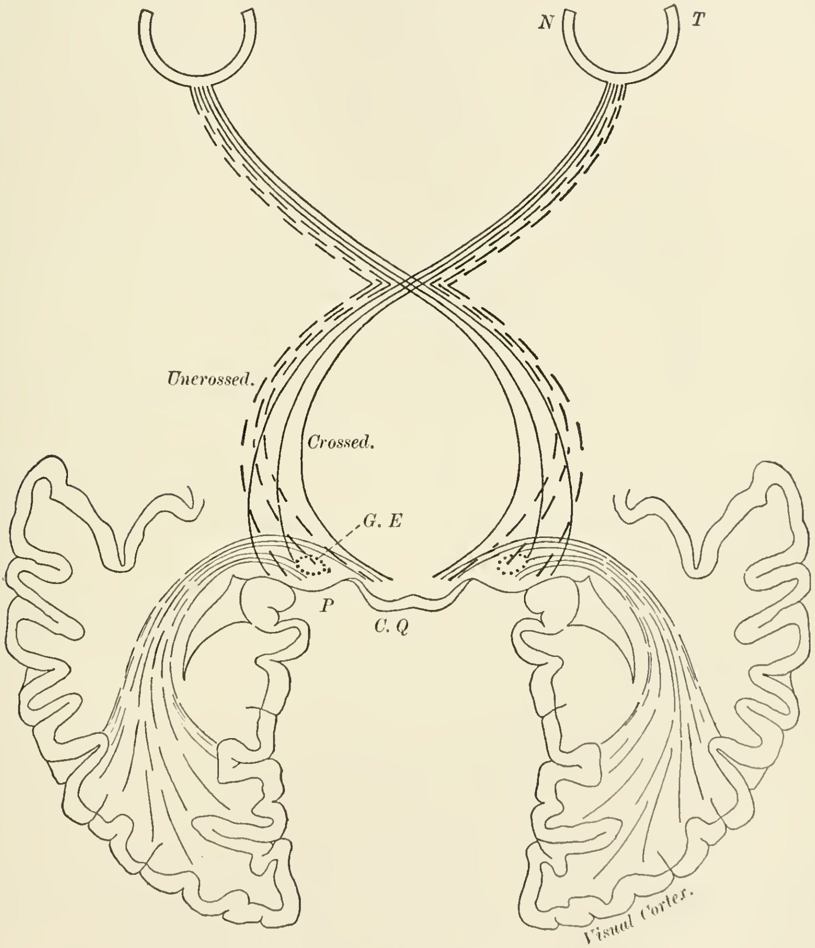

Fig. 98.—Illustrating the relations of the afferent fibres in the optic nerve. The crossed fibres are indicated by solid lines, the uncrossed fibres by broken lines: *N*, nasal side of the right eye; *T*, temporal side of the same; *G. E*, geniculatum externum; *P*. pulvinar; *C. Q*. quadrigeminum anterius.

In man the evidence from degeneration in the optic nerve points to the presence of a crossed and an uncrossed bundle of fibres in each optic nerve, the uncrossed being much the smaller of the two bundles. The contrary

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[1] Cajal: *Die Structur des Chiasma opticum nebst einer Allgemeinen Theorie der Kreuzung der Nervenbahnen*, Leipzig, 1899.

view of complete decussation has been maintained by Michel.[1] The central ends of the afferent optic fibres forming an optic tract are for the most part distributed between the anterior quadrigeminum, the geniculatum externum, and the pulvinar of the same side. By central cells located in these latter structures the pathway is continued to the occipital cortex of the hemisphere of the same side, their axones passing in the occipital end of the internal capsule and forming the optic radiation. It must be remembered, however, that between the cortex and the primary centres, and again between these centres and the retina, there are pathways conducting *from* the cortex to the primary centres, and also *from* the primary centres to the retina.[2]

As the result of partial decussation it will be seen that the relations of the two retinæ to the cortex is this: The nasal or crossed bundle of the contralateral retina and the temporal or uncrossed bundle of the retina of the same side come together in the optic tract of one side and are associated with the occipital lobe of that side. Hence it would appear that hemianopsia or blindness in the corresponding halves of the two eyes following a lesion of the optic pathway anywhere behind the chiasm would be, in some measure, explained by this anatomical arrangement. If strictly interpreted, an approximately equal number of fibres would be expected for each half of the retina. Such, however, has not been established as the relation between the areas of the bundles. It is to be added, nevertheless, that anatomical arrangements such as decussations are probably open to wide individual variations, and hence that many more observations are required before we can say what is the *usual* relation between these two bundles.

With a view to determining the exact location of the cortical centres in man, many observations have been made. The cuneus and immediately surrounding parts of the cortex are those most concerned. Henschen[3] indicates the calcarine fissure and its immediate neighborhood as the most important locality. Observations on the arrest in the development of the cortex due to early blindness following destruction of the retina in the case of the blind deaf-mute Laura Bridgman, show the entire cuneus to be the central and fundamental portion, while the associated portions extend some distance on to the convex surface of the hemisphere.[4]

First Nerve.—Comparative anatomy indicates that the parts of the encephalon mediating the sense of smell are most closely connected with the cerebral hemispheres, in the sense that phylogenetically the first development of the cortex was in connection with the central terminations of the olfactory tracts.[5] It happens in man, however, that although the cerebral hemispheres are proportionately much more massive than in the lower mammals, yet the olfactory bulbs and tracts are at the same time but poorly developed. The pathway

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[1] *Kölliker's Festschrift*, Würtsburg, 1887.

[2] von Monakow: *Archiv für Psychiatrie*, 1890, Bd. xx. H. 3.

[3] Henschen: *Klinische und anatomische Beiträge zur Pathologie des Gehirns*, Upsala, 1890–92.

[4] Donaldson: *American Journal of Psychology*, 1892, vol. iv. No. 4.

[5] Sir William Turner: *Journal of Anatomy*, 1890; Edinger: *Anatomischer Anzeiger*, 1893.

of the olfactory impulses is from the olfactory area in the nose to the olfactory bulb of the same side, thence *via* the olfactory tract to its termination in front of the anterior perforated space, one branch of the tract passing directly into the substance of the gyrus fornicatus at this point, and the other going into the more lateral portion represented in man by the temporal end of the gyrus hippocampi. The cortical areas, together with the olfactory lobe and tract, form the rhinencephalon of the comparative anatomists. It has been shown, nevertheless, by Hill[1] that in anosmic mammals the fascia dentata alone varies with the development of the olfactory apparatus. The experimental pathological evidence is very meagre in relation to these nerves, but, on the other hand, the anatomical evidence is of the best.[2]

D. LOCALIZATION OF CELL-GROUPS IN THE CEREBRAL CORTEX.

The foregoing section has brought to light the fact that groups of incoming impulses find their way to the cerebral cortex. The significance of this is evident only when in response to those impulses arriving at the cortex others leave it, and finally affect some expressive tissue or instrument by the aid of which we can interpret them. Since the cerebral hemispheres with their cortex become increasingly developed as we pass up the mammalian series, it naturally follows that the pathways connecting the cortex with the lower parts of the system are correspondingly increased. Using the reactions of the expressive tissues as a guide, it is our present purpose to trace the impulses in those cases in which the cortex forms part of the path. We turn, therefore, to the study of those parts of the cerebral cortex the direct stimulation of which produces impulses that pass to cell-groups lying more or less caudad in the central system.

Earlier Observations.—It was demonstrated by Fritsch and Hitzig in 1870[3] that if a constant current is applied to the surface of the dog's cerebrum, it is possible, by interrupting it, to obtain movements of the limbs and face when the electrodes are placed on the parts of the cerebral cortex about the sulcus cruciatus. The reaction varies according to the place of stimulation, a constant relation subsisting between the two. From this time on, active investigations of the relations thus suggested have been pursued, both by stimulating small areas in the cortex of various animals, including the monkey and man, and by the removal of various parts of the cerebral hemispheres and cortex, together with the study of the effects of pathological lesions in man. The results following removal of the parts are complicated by the transitory effects of the lesion, and can best be treated by themselves later on. The results following the stimulation of the cortex are the simplest, and will next be described.

Stimulation of the Cortex.—The common method of experiment is to

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[1] *Philosophical Transactions of the Royal Society*, 1893, vol. clxxxiv.

[2] For a description of the very complicated pathways associating the olfactory bulb with the other portions of the cerebrum, the reader is referred to Barker's *The Nervous System*, 1899.

[3] *Archiv für Anatomie und Physiologie*, 1870.

apply the faradic current by means of fine but blunt electrodes, the ends of which are but two or three millimeters apart, to the exposed surface of the cerebral hemispheres, the pia being undisturbed. Rabbits, dogs, and monkeys have been the animals most commonly studied.

If the current be slight, its application for one or more seconds causes a response in the shape of movements of muscles, which are thrown into co-ordinated contraction. The contraction continues for some time after the stimulus has been removed. When the stimulus is very strong, instead of a limited and co-ordinated response, there may be a widespread contraction of many muscles, resembling an epileptic convulsion. This, however, occurs more commonly in the lower than in the higher mammals. On the other hand, the irritability of the cortex is easily reduced, so that it becomes irresponsive, and often immediately after the first exposure of the brain there is a time during which no response can be obtained.

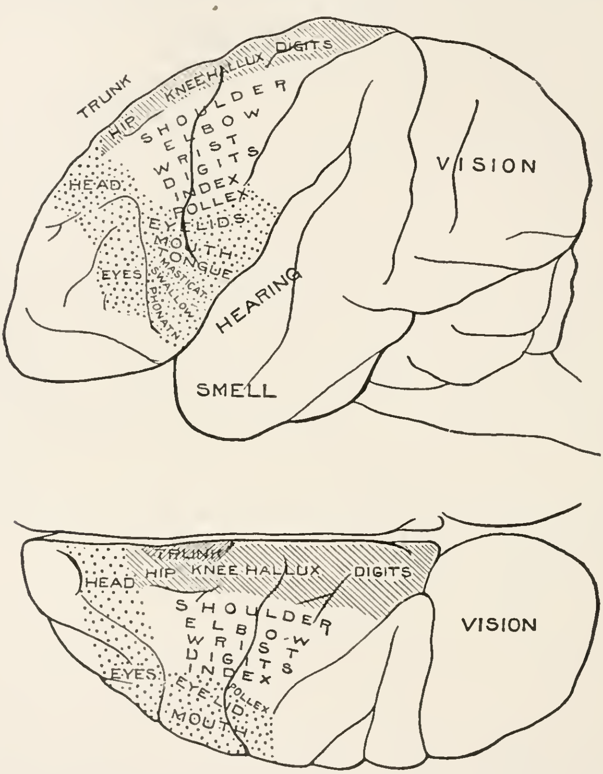

Fig. 99.—Brain of the macaque monkey, showing the sensory and motor areas. In the sensory region the name of the sensation is over the locality most closely associated with the corresponding sense-organ; in the motor region the name of the part is written over the portion of the cortex which controls it. The upper figure gives a lateral view of the hemisphere, and the lower a dorsal view (Beevor and Horsley).

Deferring for a moment the evidence by which the sensory characters of the several areas have been established, and also the arrangements within the cortex by which any group of muscles can be made to respond to stimuli arriving at any sensory area, we shall follow out the distribution of those cortical cells which, on direct stimulation, cause contractions of the skeletal muscles.

The results here presented were obtained from the electrical stimulation of the monkey's brain by Beevor and Horsley[1] (see Figs. 99, 100). These experimenters explored the exposed surface of the hemisphere with the electrodes, moving them two millimeters at a time, and at each point noting the muscle-group first thrown into contraction.

As the result of many observations on the monkey, it is possible to map out the cerebral cortex in the following way: The surface of the hemispheres is divided into regions (motor and sensory regions), which are the largest subdivisions. These are subdivided into areas for the muscle-groups belonging to different members of the body—arms, head, trunk, etc.—as well as those areas within which all the impulses from a given sense-organ reach the cortex. The areas in turn are subdivided into centres, comprising the groups of cells, which, for example, control the smaller masses of muscle belonging to a given segment of a limb, or in the visual area constitute those cells especially connected with one part of the retina. There is thus a motor region, the stimulation of which gives rise to the more evident bodily movements. Within this are several subdivisions, the stimulation of one of which is followed by movements of groups of muscles—for instance, those controlling the arm—and within such an area in turn come the smaller centres, or those the stimulation of which is first followed by movements at one joint only.

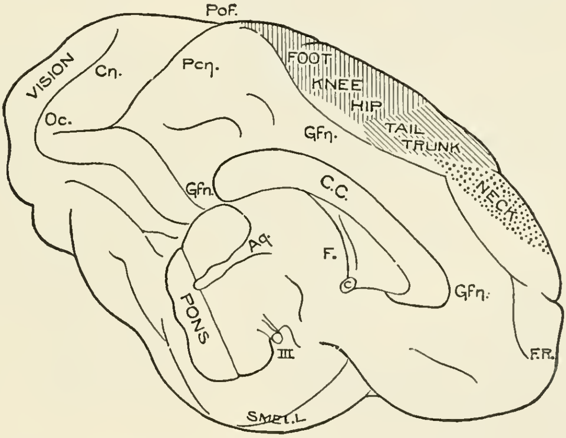

Fig. 100.—Mesial surface of the brain (monkey). The localization of motor functions is indicated along the shaded portion of the marginal gyrus. The location of the visual area is indicated at the tip of the occipital lobe, and the location of the olfactory area at the tip of the temporal (Horsley).

The physiological characters of these cortical motor centres have been determined by the following observations:

If a vertical incision be carried around such a centre so as to isolate it from the other parts of the cortex, the characteristic reactions still follow the stimulation of it, indicating that the special effect can be produced by the

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[1] Beevor and Horsley: *Philosophical Transactions of the Royal Society*, 1888-90.

passage of impulses from the point of stimulation toward the infracortical structures. If, in addition, a cut be made below the cortex and parallel with its surface, then stimulation of the cortex above this section is ineffective, thus indicating that the impulses pass from the cortex directly into the substance of the hemisphere along certain nerve-tracts, which by this operation were sectioned. Further, if the bit of cortex thus separated from the underlying white substance be removed and the faradic current be applied to the white substance beneath, a reaction of the same type and involving the same muscles can be obtained, although it differs from that to be gotten from the cortex itself, in the first place by being less co-ordinated, in the second by continuing only so long as the stimulus lasts, and in the third place by giving rise to less intense electrical changes connected with the passing impulse. By careful exploration the bundle of fibres which is thus picked out can be followed, as the brain substance is cut away, through the internal capsule and the cerebral peduncles.

These facts taken together lead to the conclusion that when the cortex is stimulated the impulses concerned in producing the muscular contractions traverse cell-bodies at the point of stimulation, and are transmitted thence through the underlying fibres. We shall see later that this direct course probably does not represent the sole pathway for these impulses.

Course of the Descending Impulses.—The course of the impulses is next inferred from the relation between the removal of different parts of the cortex and the consequent secondary degenerations throughout the length of the central nervous system. When the part of the cortex removed is taken from the motor area then the degeneration occurs in the internal capsule and in the callosum. The path of the fibres forming outgrowths of the cortical cells can be followed thence through the crusta and pyramids to the spinal cord.

After removal of the motor region of one cerebral hemisphere the degeneration is mainly in the internal capsule and crusta of the same side, though by way of fibres crossing in the callosum it may be traced to the other side also. At the decussation of the pyramids the fibres occupying the internal capsule of the same side as the lesion for the most part cross the middle line. The portion which remains uncrossed passes as the direct pyramidal tract of the ventral columns in man, while the crossed bundle, which is much the larger, lies in the dorsolateral field of the lateral column, forming the crossed pyramidal tract. Since the observations of Pitres[1] in 1881-82 evidence has been accumulating to show that in man a lesion of the motor cortex of one cerebral hemisphere is followed by a degeneration of the crossed pyramidal tract on both sides of the cord. Of course, the degeneration in the heterolateral tract is much the larger of the two. That the fibres degenerating in the homolateral tract remain on the same side throughout their entire course is shown by the physiological experiments of Wertheimer and Lapage[2] on

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[1] *Progrès médicale*, Paris, 1882, x. 528.

[2] *Archives de Physiologie*, 1897, No. 1, p. 168.

dogs, and by the studies of Mellus[1] on secondary degenerations occurring in the cord after very limited lesions of the motor cortex of monkeys.

The direct pyramidal tracts are well marked only in man. They usually disappear in the mid-thoracic region, having entered the gray substance by way of the ventral commissure, in which they undergo decussation. The crossed pyramidal tract shows the greatest diminution in area after passing caudad of the cervical and lumbar enlargements respectively, and hence it is inferred that the pyramidal fibres largely terminate at these levels of the cord.

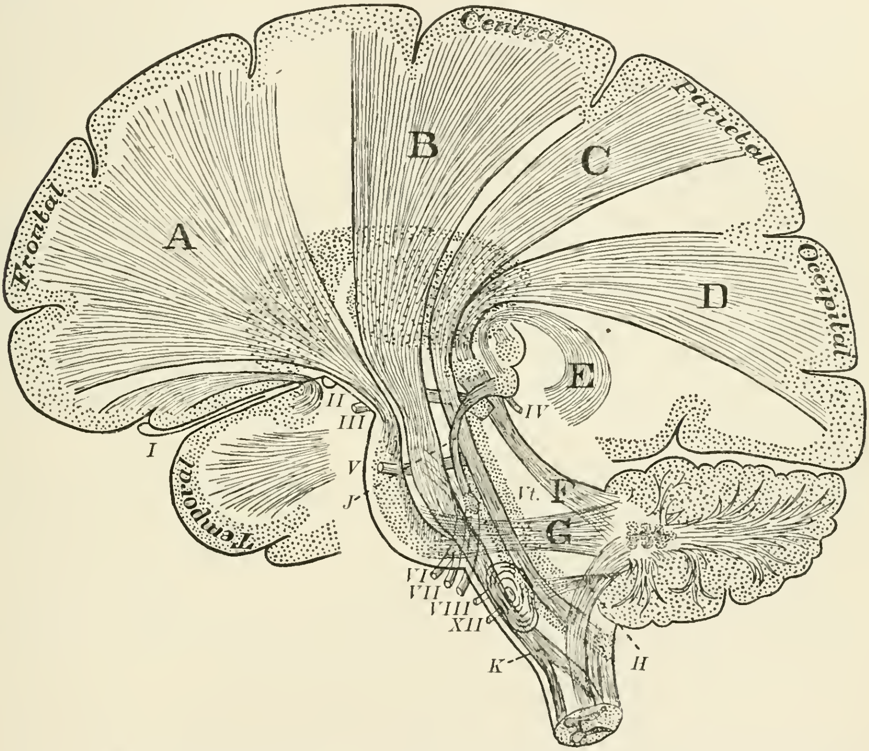

FIG. 101.—Schema of the projection-fibres within the brain (Starr); lateral view of the internal capsule: *A*, tract from the frontal gyri to the pons nuclei, and so to the cerebellum; *B*, motor tract; *C*, sensory tract for touch (separated from *B* for the sake of clearness in the schema); *D*, visual tract; *E*, auditory tract; *F*, *G*, *H*, superior, middle, and inferior cerebellar peduncles; *J*, fibres between the auditory nucleus and the inferior quadrigeminal body; *K*, motor decussation in the bulb; *Vt*, fourth ventricle. The numerals refer to the cranial nerves. The sensory radiations are seen to be massed toward the occipital end of the hemisphere.

Sherrington has put forward the view that the pyramidal fibres recross in the cord, these recrossing fibres being derived in large part from a division of the pyramidal fibres into two branches, one of which may cross to the opposite side of the cord, while the other continues its first course. Such dividing fibres he designates as "geminal fibres;" and the number of them is by no means small.

The observations of Sherrington were made on monkeys (Macacus) and

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[1] *Proceedings of the Royal Society*, London, 1894 and 1895.

dogs, and probably the arrangement of these fibres in man is similar. The observations are particularly significant as giving another anatomical basis for the control of the movements in both halves of the body from each cerebral hemisphere.

The continuous degeneration, coupled with the histological evidence for the absence of intervening nerve-cells, indicates that the cell-bodies in the cortex have axones that extend all the way to the cell-groups of the spinal cord, even as far as the sacral region. The usual picture of the final connections of the pyramidal fibres shows the collaterals as coming into contact with the large cells in the ventral horns of the cord. On the ground of recent experiments on monkeys and cats, Schäfer[1] denies the existence of such a direct association of the two sets of elements. He finds that a large mass of collaterals which degenerate when the pyramidal tract is interrupted end about the large cells in the column of Clarke.

Returning to consider the arrangement of these cells in the cortex, we find that the axones of one group of these cortical cells pass to the cell-groups in the cervical enlargement, while those from others pass to the groups in the lumbar enlargement. It thus happens that if the spinal cord be cut across in the middle of the thoracic region, and then the leg area (see Fig. 78) be stimulated, an electrometer applied to the cut end of the cord will show the passage of nerve-impulses, because the electrometer is applied to a tract of fibres on their way to the lumbar enlargement, and the fibres originate from cortical cells within the region stimulated.

When, however, the cortical stimulus is made in the arm-area, the electrometer being applied as before, no electric change occurs, for the axones of the cells in the arm terminate in the part of the cord containing the cell-groups which control the muscles of the arm, and these groups all lie cephalad to the point of section of the cord. It is evident, therefore, that the arrangement is a comparatively simple one—namely, an extension of the axones of the several groups of cortical cells from the different areas for the leg, arm, face, etc., to the axial cell-groups which control the muscles of these parts, and which are situated in the cord.

The cortical cells in the motor region belong to the group of central cells —*i. e.*, their axones never leave the central system—and hence they are engaged in distributing impulses within it. To the axial cell-groups in the cord they bring impulses, and therefore, from the standpoint of these latter, may be considered as afferent, whereas, owing to the fact that they carry impulses away from the cortex, they are sometimes called efferent. Just how these two sets, the cortical and the cord elements, are numerically related still requires to be worked out. According to one estimate, there are for the arm, trunk, and leg, in man, 79,111 pyramidal fibres in each half of the cord, or 158,222 in the entire cord.[2] The number of fibres in the pyramidal tracts indicates that there certainly is not one fibre for each cell in the axial cell-

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[1] *Journal of Physiology*, vols. xxiii. and xxiv.; Proceedings of the Physiological Society.

[2] Blocq et Ozanoff: *Gaz. des Hôpit.*, 1892.

groups, because the number of pyramidal fibres is very much less than is the number of cells which they control. This discrepancy is in some measure relieved by the formation of "geminal" fibres already described. Moreover, the branching of the pyramidal fibres near their termination is very probable, and the most plausible view at present is that each pyramidal fibre by means of its collaterals controls, perhaps indirectly, a considerable number of cord cells, and probably the cells controlled by any one fibre form a more or less compact group.

Mapping of the Cortex.—Having sketched the relations of the pyramidal cells forming the motor region of the cerebral cortex to the parts lying below, we turn to study the arrangement, size, subdivisions, and comparative anatomy of this region, and then to examine the relation of it to the other parts of the cortex. The observations here quoted are those on the monkey only.

On glancing at Fig. 99 it is evident, first, that the areas for the face and leg are widely separated from each other, that the arm-area lies between them, and that the area for the trunk, though less schematically placed, is located between that for the arm and leg. This arrangement is more typically represented on the mesial (Fig. 100) than on the convex surface of the hemisphere, and in the former locality the serial order of the cortical areas corresponds with the order of the muscle-groups which they control.

The Size of the Cortical Areas.—Evidently there is no direct relation between the extent of a cortical area and the mass of muscles which it controls. Certainly in man the mass of muscles in the leg is three times greater than that in the arm, and this latter many times greater than that of the face and head; yet it is for the last area that the greatest cortical extent is found. Mass of muscle and extent of cortical area do not therefore go together.

When the movements effected by the muscles represented in these several areas are considered, we find that such movements become more complex and more accurate as we approach the head, and it therefore accords with the facts to consider the extent of the motor areas as correlated with the refinement of the movements which they control—a relation which may depend even more on the multiplication of the pathways bringing in impulses than on those which send them out.

Subdivision of Areas.—The areas which have been described are further subdivided, the subdivisions in the arm-area being the clearest. Here it is found that the stimulation of the upper part of the arm-area gives rise to movements which start at the shoulder, while stimulation at the lower part of this area gives rise to movements first involving the fingers, and especially the thumb. The centres from which these several reactions may be obtained occupy, as Fig. 99 shows, narrow fields across the cortex in a fronto-occipital direction. Moreover, the centre for the most proximal joint of the arm is farthest removed from that for the most distal, while the intermediate joints are represented by their several centres lying in regular order between these two. A similar arrangement appears in the subdivisions of the cortex controlling the leg, and in the face-area as well.

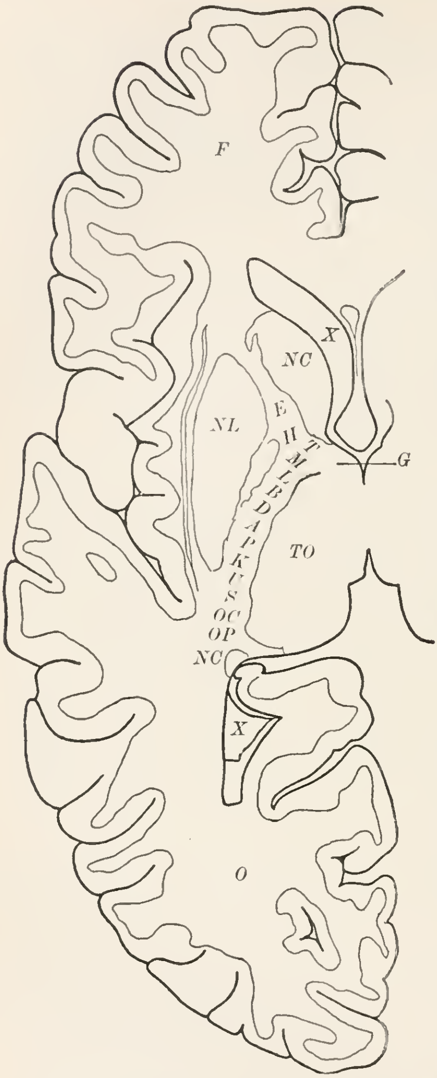

Fig. 102.—Horizontal section of the human cerebrum, showing the internal capsule on the left side: *F*, frontal region: *G*, knee of the capsule; *NC*, *NC'*, caudate nucleus; *NL*, lenticular nucleus; *O*, occipital lobe; *TO*, thalamus; *X*, *X*, lateral ventricle. In the internal capsule the letters indicate the probable position of the bundles of fibres which upon stimulation give rise to movements of the parts named or which convey special sets of incoming impulses: *E*, eyes; *H*, head; *T*, tongue; *M*, mouth; *L*, shoulder; *B*, elbow; *D*, digits; *A*, abdomen; *P*, hip; *K*, knee; *U*, toes; *S*, temporo-occipital tract; *OC*, fibres to the occipital lobe; *OP*, optic radiation (based on Horsley).

Interpreting these facts in the terms of nerve-cells and their arrangement, it appears that in the shoulder-centre the axones of the cortical cells that discharge downward affect predominantly the efferent cell-groups which in the spinal cord directly control the muscles of the shoulder, and that a similar arrangement obtains for the other centres in this region with the corresponding cell-groups in the cord. The stimulation of the different portions of the internal capsule where it is composed of bundles of fibres coming from the motor region shows (observations on orang-utang) that the fibres running to the several lower centres are there aggregated and arranged in the same order as the cortical centres from which they arise (see Fig. 102).

Separateness of Areas and Centres.—As we ascend in the mammalian series there is an increase in the perfection with which cells forming the several centres are segregated, though the areas in the different orders tend to hold the same relative positions.[1]

Figs. 103, 104 give the localizations obtained in the rabbit's brain by stimulation (Mann). The various areas occupy a large proportion of the cortex, and in some cases come very close together, so that they are not easily separated by experiment.

In the lower monkeys (*Macacus sinicus*) these cell-groups are segregated, so that those associated with the cervical portion of the cord and forming the arm-area are much more together and quite separate from those associated with the lumbar region, the leg-area. In the orang-utang,[2] and to a greater extent in man, a further sepa-

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[1] Mann: *Journal of Anatomy and Physiology*, 1895, vol. xxx.

[2] Beevor and Horsley: *Proceedings of the Royal Society*, London, 1890-91, vol. xlviii.

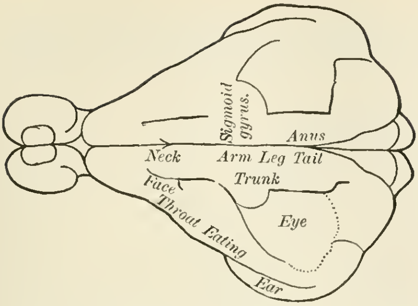

Fig. 103.—Rabbit's brain, dorsal view. The areas indicated are those the stimulation of which causes a movement of the parts named (Mann).

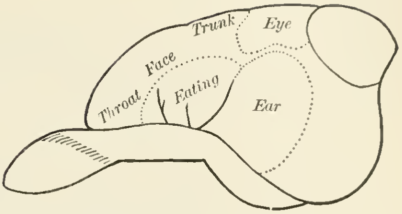

Fig. 104.—Rabbit's brain, lateral view. The areas indicated are those the stimulation of which causes a movement of the parts named (Mann).

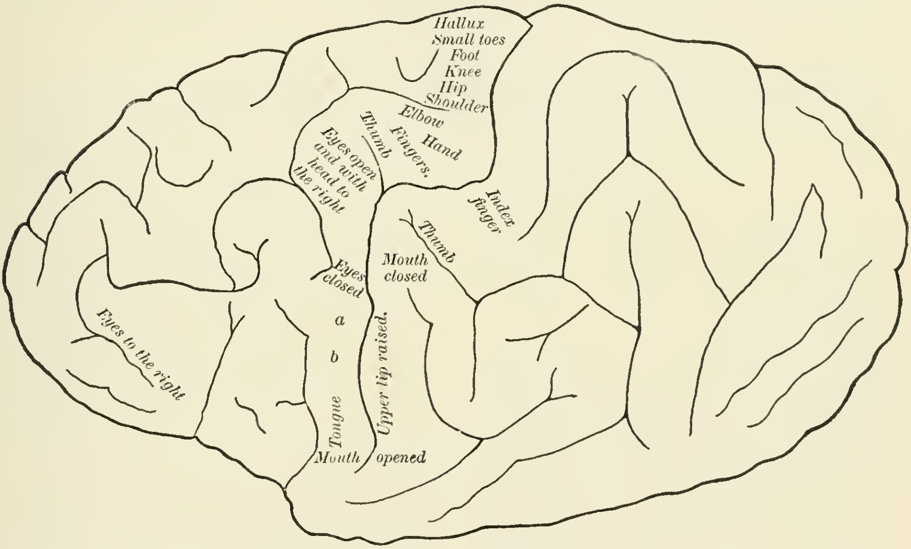

Fig. 105.—Lateral view of the left hemisphere of an orang-utang, showing the motor area about the central fissure (Beevor and Horsley).

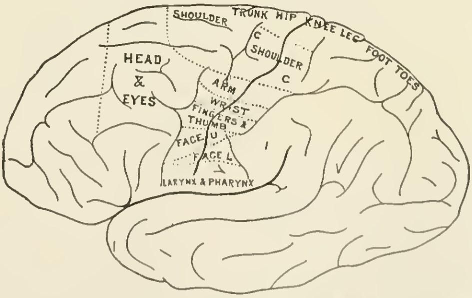

Fig. 106.—Lateral view of a left human hemisphere, showing the motor areas in man. The schema is based on the observations on the monkey, on pathological records (human), and on direct experiments on man. It is to be remembered that in the human brain the excitable localities are surrounded by rather extensive areas not directly excitable (Dana).

ration occurs, so that these centres come to be surrounded by parts of the cortex from which no response can be obtained upon direct stimulation (see Fig. 105).

By a few direct experiments and by many pathological observations something is known of the motor centres in the human cerebral cortex. When the results are plotted they give a distribution such as is shown in Fig. 106. At the same time all such figures are largely based on results obtained from the monkey. It is here seen that the two central gyri are the principal seat of these areas, and that it is only along the great longitudinal fissure separating the hemispheres that the motor areas extend beyond this limit in a cephalo-caudad direction. Perhaps the relation most worthy of remark is the comparatively small fraction of the cortex concerned with the direct control of the spinal cord cells. The motor areas in man are elaborated not so much by the increase in the number of the cells controlling the lower centres, as by an increase in the number of those cells under the influence of which these areas react. According to the estimates of Miss Thompson,[1] there are in man 9200 millions of cells in the entire cerebral cortex of both hemispheres. In the motor region about the central fissures there appear to be only 159,600 cells concerned in the production of pyramidal fibres going to the cord. The relation of the areas in a frontal section is shown in Fig 108.

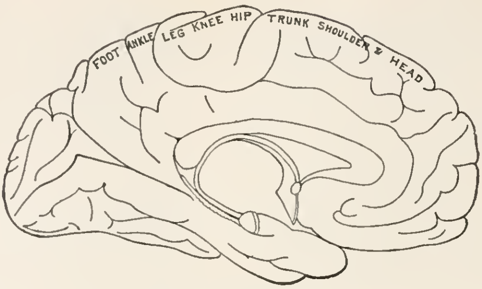

Fig. 107.—Mesial view of a human hemisphere, showing motor areas. Formed in the same way as Fig. 106.

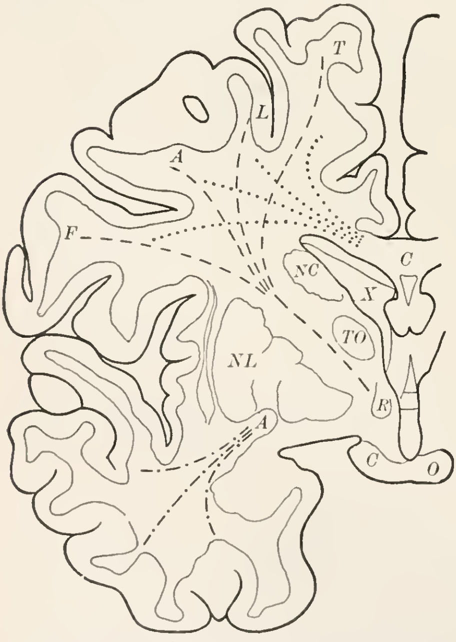

Fig. 108.—Frontal section of human cerebrum on the left side. The fibres forming the internal capsule (— — —), the callosum (. . . . .), and the anterior commissure (. — . — . —) have been indicated : *T*, cortical area for the trunk ; *L*, cortical area for the leg ; *A*, cortical area for the arm ; *F*, cortical area for the face ; *A*, anterior commissure ; *C*, callosum ; *CO*, optic chiasma ; *NC*, caudate nucleus ; *NL*, lenticular nucleus ; *R*, fornix ; *TO*, thalamus ; *X*, lateral ventricle.

Multiple Control from the Cortex.—It has been found that stimulation

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[1] Helen B. Thompson : *Journal of Comparative Neurology*, 1899, vol. ix. No. 2.

of the cortex in the region of the frontal lobes marked "eye" (Fig. 99) was followed by movements of the eye. Schäfer[1] has shown that very precise movements of the eye also follow the stimulation of the temporal and various parts of the occipital cortex. Since the efferent fibres which control the muscles concerned start from the cell-groups forming the nuclei of the third, fourth, and sixth cranial nerves, it would appear most probable that in both parts of the cortex there are located cells the axones of which pass to those groups and are capable of exciting them. An alternative hypothesis —namely, that the cortical impulse always travels *first* to the cortical cells in the frontal lobe and thence, by way of them, to the efferent cell-groups—was at one time considered, for the latent period of contraction of the eye muscles was less by several hundredths of a second when the stimulus was applied in the frontal region than when applied elsewhere. The experiments of Schäfer show, however, that when the occipital and frontal lobes are separated from one another by a section severing all the association-fibres the reactions can still be obtained by stimulation in the former locality—showing that the connections of the two cortical areas with the cell-groups controlling the muscles of the eye are independent of each other.

This instance of the direct control of the same efferent cell-groups from different areas of the cortex is analogous to the control of efferent cell-groups in the spinal cord, either by impulses coming down from the cerebrum or by those entering the cord through the dorsal roots, and the instance here cited is typical of a general arrangement.

Cortical Control Crossed.—Where the stimulation of the cerebral cortex causes a response on one side only, that response is on the side opposite to the stimulated hemisphere. It sometimes happens, however, that two groups of symmetrically placed muscles both respond to the stimulus applied to one hemisphere only; but these cases—the conjugate movements of the eyes, movements of the jaw muscles or those of the larynx—usually depend on the response of muscles which are naturally contracted together.

This last reaction must be determined by the arrangement of the fibres in the cord, since in lower mammals (dog and rabbit, for example) it is not seriously disturbed by the removal of one hemisphere.

Here should be added the very important observations of Sherrington[2] already mentioned on p. 224, which show that a stimulus which applied to the cortex will cause one set of muscles, the flexors of the arm, for example, to contract, causes at the same time a relaxation of the antagonistic muscles, thus rendering co-ordination possible in the movements of the limb.

Course of Impulses Leaving the Cortex.—In the higher mammals, as well as in man, it is by way of the pyramidal fibres that impulses travel from the cortex to the efferent cell-groups of the cord. The pyramidal tracts by definition form, in part of their course, the bundles of fibres lying on the ventral aspect of the bulb, caudad to the pons, ventrad to the trapezium, and

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[1] *Proceedings of the Royal Society*, 1888, vol. xliii.

[2] Sherrington: *Journal of Physiology*, 1897–1898, vol. xxii.

between the olivary bodies. According to Spitzka,[1] these bundles are absent in the case of the elephant and porpoise, a condition which is correlated with the slight differentiation of the limbs, which are not modified either for fine movements or for tactile purposes. It has been pointed out, too, that removal of a hemisphere causes in the dog and most rodents a degeneration of other parts of the cord (dorsal columns) than those occupied by the pyramidal tracts in man.[2] The fibres passing from the cortex to the efferent cell-groups in the cord do not, therefore, hold exactly the same position in various mammals.

Size of Pyramidal Tracts.—It has been clearly shown that if the cross-sections of the cords of the dog, monkey, and man be drawn of the same size, the pyramidal fibres being indicated, then the area of this bundle is proportionately greatest in man and least in the dog, the monkey being intermediate in this respect. The relations thus indicated are evident—namely, that the number of fibres controlling the cell-groups in man is the largest, and also is much larger than that in the lower animals.

The relative areas of the pyramidal tract at corresponding levels, the area of the entire cord being taken as 100 per cent., are given by v. Lenhossek[3] for the following animals:

Mouse	1.14 per cent.
Guinea-pig	3.0 "
Rabbit	5.3 "
Cat	7.76 "
Man	11.87 "

This relation is to be carefully noted, for with it is correlated the degree of the disturbances in the reactions of the entire nervous system following removal of parts of the cerebrum, the effect being slight when the cerebrum is connected with the cord by a small number of fibres, and serious when the connection is by many fibres, as in the case of man and the highest mammals.

E. LOCALIZATION IN THE CEREBRAL CORTEX OF THE CELL-GROUPS RECEIVING THE AFFERENT IMPULSES.

Sensory Regions.—If an attempt is made to unify the construction of the entire cortex by bringing the motor and sensory areas under a common law, it must be based on the fact that the system of axones bringing impulses to the motor region forms part of the pathway for conducting the afferent impulses from the skin and muscles back to some organ controlled by the efferent nerves. To Munk[4] is due the credit of having from the first looked upon the responsive cortex as marked off into areas within which certain groups of these fibres terminate, so that apart from the sensory areas named from the special senses, he calls the area which controls the skeletal muscles the "Fuhlsphäre" or body-sense area, on the assumption that in it end the

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[1] *Journal of Comparative Medicine and Surgery*, 1886, vol. vii.

[2] von Lenhossek: *Anatomischer Anzeiger*, 1889.

[3] *Die feiner Bau des Nervensystems im Lichte neuester Forschungen*, Basel, 1893.

[4] *Ueber die Functionen der Grosshirnriude*, 1881.

fibres bringing in impulses which arise through the stimulation of the skin and muscles. It has been suggested, to be sure, that separate localities form the seat for the dermal and muscular sensations. Ferrier indicated the limbic lobe, especially the hippocampal gyrus, while Horsley and Schäfer argued for the gyrus fornicatus. At present, the weight of evidence is in favor of the location of the centres for dermal and muscular sensations in the central gyri, a part just caudad to and a part overlapping the area stimulation of which causes the muscles of the trunk and limbs to contract. Both in monkeys and in man defects in sensation are not permanent after limited lesions of the cortex, but, as suggested by Mott, the wide distribution of the incoming impulses would explain this result.

Thus the entire portion of the cortex to which a definite function can be assigned must be looked upon as containing fibres which bring impulses into it, and cell-bodies which by their discharge send impulses to other divisions of the central system as well as to other parts of the cortex itself. All parts of the cortex having assigned functions give rise on stimulation to movements; but in the case of the sensory areas, so called, they involve the contractions of only those muscles controlling the external sense organ, as the eyeball, external ear, tongue, and nostrils.[1] Though physiologically important, and in the case of the eye reaching a high degree of refinement, they are quantitatively very insignificant when compared with the responses to be obtained from stimulating the "motor region," from which contractions of the larger skeletal muscles are obtained. Hence the usual terms "sensory" and "motor" do not completely characterize the corresponding regions, though they emphasize their most striking features.

Determination of the Sensory Areas.—Using as a guide the appearance of the medullary sheaths upon the projection-fibres of the cerebral cortex of man during the last months of fœtal life and shortly after birth, Flechsig[2] has been able to outline the sensory areas in the cortex with great clearness.

The illustrations from Flechsig (Figs. 109, 110) show the parts of the brain where the projection-fibres can be determined at a time when these fibres constitute all or almost all the medullated fibres connecting the cortex with the stem and basal ganglia. By thus marking out in color on the developing cortex the portions concerned, there are seen to be four main areas: First, the area connected with the olfactory tract (olfactory area), involving the uncinate gyrus, the gyrus hippocampi, and the part of the gyrus fornicatus nearest the callosum. Second, the area connected with the optic radiation (visual area), where the fibres in question are most abundant about the calcarine fissure. They appear, however, all through the cuneus and extend to the cortex which surrounds it on the ventral and lateral aspects of the occipital lobe. Third, we have (auditory area) the portion of the cortex which covers the transverse gyri in the Sylvian fissure and the first temporal gyrus where the former join it. This area is occupied by the projection-

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[1] Ferrier: *Functions of the Brain*, 1876.

[2] Flechsig: *Gehirn und Seele*, Leipzig, 1896.

fibres which convey the impulses arriving over the auditory nerve (the cochlear branch of the eighth). Finally the fourth area is seen (area for "body-sense"), which is most richly supplied with projection-fibres about the central fissure, in the two central gyri—but also extends forward on the lateral sur-

FIG. 109.—The colored portion about the cuneus, especially that more deeply colored about the calcarine fissure, shows the *visual area* as seen from the mesial surface. The portion comprising the deeply colored tip of the hippocampal gyrus, the dorsal portion of the hippocampal gyrus, and the edge of the gyrus fornicatus through its entire extent, marks the *olfactory area*. The remaining portion, occupying the paracentral gyrus and the mesial aspect of the first frontal gyrus, marks the mesial extension of the *body-sense area*. The uncolored portions of the cortex form the *association centres* of Flechsig. F, pes; HS, crura; Z, pineal body; 1, corpus albicans; 2, chiasma; 3, anterior commissure; 4, quadrigemina; 5, callosum; 6, fornix; 7, septum lucidum (from Flechsig).

FIG. 110.—The colored portion at the tip of the occipital lobe represents the postero-lateral extension of the *visual area*. The colored portion about the central fissure and the neighboring parts of the frontal lobe represents the lateral extension of the *body-sense area*. The colored portion about the caudal end of the first temporal gyrus, and extending over the transverse gyri within the Sylvian fissure, represents the *auditory area*. In all three areas the portions most deeply colored represent the areas where the projection-fibres are most abundant. The uncolored portions of the cortex form the *association centres* of Flechsig (from Flechsig).

face to include part of all the frontal gyri, while on the mesial surface the cortex concerned extends forward from the precuneus over more than half of the mesial surface. In this last area are delivered the afferent impulses from the skin, muscles, joints, viscera, and the lining walls of the alimentary tract. Flechsig points out that the projection-fibres, according to which these areas have been defined, are composed of axones bringing impulses to the cortex, and hence are sensory, in the usual terminology. The areas thus bounded are found to coincide with the areas which (in animals) respond to direct stimulation by the contraction of definite groups of muscles.

The earlier determinations of the sensory areas in man were made from the study of brains modified by destructive lesions or congenital defects.

The cortical centre for smell, inferred from comparative anatomy and physiology to be closely connected with the hippocampal and fornicate gyri and the uncus, has been similarly located in man on the basis of pathological observations; but the evidence lacks precision. Concerning the location of taste sensations, very little is known. Both of these senses, it must be remembered, are insignificant in man, and hence their central connections are not easily studied.

On the other hand, the cortical areas for hearing and sight have been located with much more precision and certainty.

Damage to the posterior third of the first temporal gyrus and the associated gyri transversi causes in man deafness in the opposite ear, and concordantly conditions of the ear which early in life lead to deafness and deafmutism are accompanied by a lack of development in these gyri.[1] Destruction of this area on one side causes slight deafness mainly in the opposite ear, while complete deafness follows a cortical lesion only when it is double.

In the case of the visual areas in man there is the same sort of evidence, but somewhat more exact. The destruction of the area represented by the cuneus and the surrounding cortex (Figs. 109 and 110) always injures vision, the maximum disturbance following injury to the cortex of the calcarine fissure. Conversely, the failure of the eyes to grow, arrests the development of this portion of the hemisphere.

Hemianopsia.—It is found, moreover, that injury to the visual area in one hemisphere usually produces a hemianopsia or partial defect of vision in both retinæ. The homonymous halves are affected on the same side as the lesion and the dividing line is usually vertical. The clinical picture corresponds to a semi-decussation of the optic tract and the representation of the homonymous halves of each retina in both hemispheres. At the same time the relation is much more complicated than at first sight appears, for the point of most acute vision is often unaffected in such cases. This peculiarity depends apparently on the fact that there is a binocular centre for macular vision in the cortex lining the sides and bottom of the posterior portion of the calcarine fissure.[2]

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[1] Donaldson: *American Journal of Psychology*, 1891–2, vol. iv.

[2] Laqueur and Schmidt: *Virchow's Archiv*, 1899, Bd. 158, Heft 3, S. 467.

In the case of neither vision nor hearing do we find in man any subcortical cell-groups capable of acting as centres; that is, after the destruction of the appropriate cortical region the corresponding sensations and reactions to the stimuli which arouse these sensations are completely and permanently lost.

From these facts, therefore, it appears that the impulses which give rise to visual and auditory sensations are delivered in certain parts of the cerebral cortex, and unless they arrive there the appropriate sensations are wanting.

Association Fibres and Association Centres.—Common experience shows us that we can voluntarily contract any group of muscles in response to any form of stimulus—dermal, gustatory, olfactory, auditory, or visual. When, therefore, the hand is extended in response to a visual stimulus, the nerve-impulses pass first to the visual area, and then in an indirect manner arouse the cortical cells controlling the muscles of the hand. This connection of the two areas is accomplished through the so-called association-fibres of the cortex. These fibres are formally defined as those which put into connection different parts of one lateral half of any subdivision of the central system (see Fig. 111).

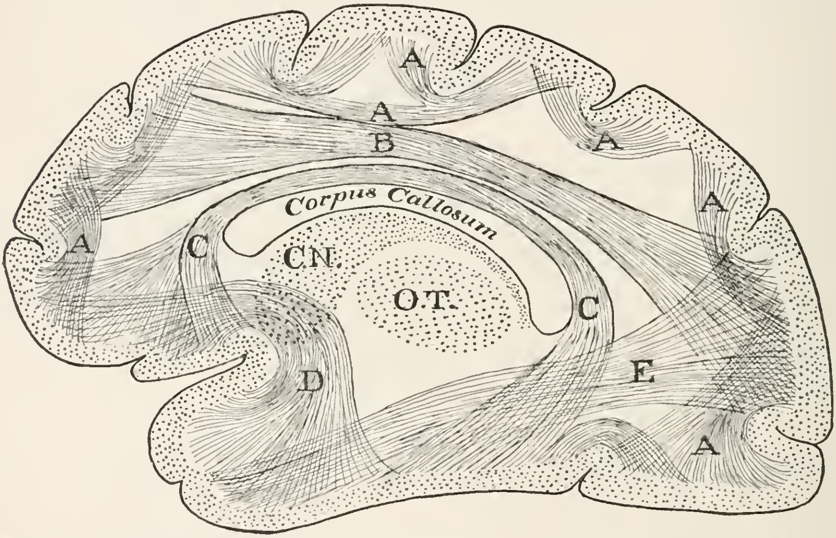

FIG. 111.—Lateral view of a human hemisphere, showing the bundles of association-fibres (Starr): *A*, *A*, between adjacent gyri; *B*, between frontal and occipital areas; *C*, between frontal and temporal areas, cingulum; *D*, between frontal and temporal areas, fasciculus uncinatus; *E*, between occipital and temporal areas, fasciculus longitudinalis inferior; *C*, *N*, caudate nucleus; *O*, *T*, optic thalamus.

The bundles which are thus shown in the cerebral hemisphere must be looked upon as typical of the arrangement throughout the entire cortex, and, further, the arrangement in the cortex is typical of that in other parts of the central system. Anatomy would suggest, and pathology would bear out the suggestion, that it is by these tracts that the impulses travel from one area to another.

The term "association centres" is applied by Flechsig[1] to those portions of the cerebral cortex that lie between the sensory centres which he has been able to demonstrate. The functions of the association centres are first to furnish pathways, more or less intricate, between the several centres, and second, to retain as memories previous sense impressions, so that in acting they also modify the impulses sent into them, and by these modifications shade and adjust to an almost infinite degree the form of the final response.

On looking at Figs. 109, 110, we note two well-defined areas: (1) that occupying the frontal lobe and forming the great anterior association centre, and (2) the area in the parieto-temporal region which forms a second, the posterior association centre. The third, the middle association centre coincides with the Island of Reil, and is much less in evidence. On comparison it will be seen that these regions correspond to what have been called the "latent areas" of the cortex, because no evident response follows the direct stimulation of them. When we compare the extent of these association centres in man with that in other mammals, even the apes, we find the human brain characterized by the high development of these portions. Thus Flechsig feels justified in speaking of these association centres as the "organs of thought," and in pointing out how by means of them the incoming sense impressions are made to interact on one another, and in combination with the memory images which are thus aroused give rise to new ideas.

The association processes carried on by these several centres, are modified by their location, so that the several centres have different and distinct values. With the disturbance of these association centres are correlated the several sorts of mental defects which have been gathered under the term aphasia.

Aphasia.—The development of the ideas bearing on this subject has been slow. After the publication of the great work of Gall and Spurzheim (1810–19) on the brain, some pathologists (Bouillaud, 1825; Dax, 1836), especially in France, were in seach of evidence touching the doctrine of the localization of function. At the same time the subject of phrenology, as put forward by Gall and Spurzheim, was not in good repute, and anything which looked that way, even in a slight degree, was generally scouted. Broca, however, published (1861) the important observation that when the most ventral or the third frontal convolution in the left hemisphere (often designated Broca's convolution) was thrown out of function, the power of expression by spoken words was lost. For this reason, the name of "speech-centre" has been applied to this convolution.

Since this discovery which links the neurology of the first part of the century with that of to-day, and also forms a fundamental observation in the modern doctrine of cerebral physiology, many steps have been taken.

It was early observed that although in such cases the capacity for spoken language was lost, nevertheless the muscles which were used in the act of phonation were by no means paralyzed. This relation is due probably to the fact that the muscles are innervated from both hemispheres and possibly also

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[1] Flechsig: *Loc. cit.*

from localities outside the third frontal gyrus. Experiments show that in animals stimulation of the cortex in the region corresponding to the third frontal gyrus causes contractions of many of the muscles employed in speech.[1]

The interesting observation was also made that in the normal right-handed person the muscles of phonation could not be co-ordinated for speech from the right hemisphere alone. Thus the symmetrical portion of the right hemisphere has not the same physiological value.

Besides this lesion, which involves the cortex in front of the motor region proper, numerous other lesions—namely, those which involve the tracts running between the areas of special sensation (vision and hearing, for example), and the motor or expressive region—produce corresponding disturbances (see Fig. 112).

An individual in whom the association tracts between the visual and motor areas have been interrupted can, for instance, see an object presented to him in the sense that he gets a visual impression ; but because of the interruption of the association fibres the object is not recognized, and the impulses reaching this sensory area elicit no response from those muscles the motor centres for which are located outside of the receiving cortex.

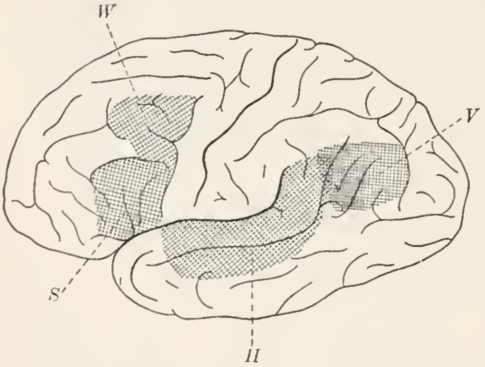

FIG. 112.—Lateral view of a human hemisphere; cortical area *V*, damage to which produces "mind-blindness"; cortical area *H*, damage to which produces "mind-deafness"; cortical area *S*, damage to which causes the loss of audible speech; cortical area *W*, damage to which abolishes the power of writing.

Upon attempting to picture the anatomical arrangement in anything like the completeness demanded by the physiological reactions, it is necessary to postulate the existence of association pathways between each area, whether sensory or motor, and all the others. This arrangement is to be regarded as modified in several ways.

In the first place, the connection between a given sensory and a given motor area differs widely according to the areas concerned. The connection, for example, between the visual area and the motor area for the arm is probably represented by more nerve-elements, and these better organized, than the connection between the gustatory area and that for the movements of the leg.

When, therefore, it is said that such connections exist, it must be added always that the nexus is different for the several regions concerned, and what is more, that in man, at least, it is different for the two hemispheres.

Relative Importance of the Two Hemispheres.—The cerebral cortex

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[1] Semon and Horsley : *Philosophical Transactions of the Royal Society*, 1890, vol. 181. Also *Deutsche medicinische Wochenschrift*, No. 31, 1890.

is always active during our periods of consciousness, and it is to be thought of as a region over which the focal point of intensest activity is continually shifting—this focal point, wherever it may be, having about it a halo of less active cells as extensive as the cortex itself.

When the subject is right-handed, it appears that injury to the left cerebral hemisphere is productive of more disturbance than injury to the right hemisphere. At the same time, lesion of the left hemisphere is far more frequent than that of the right. So far as can be judged from experiments on man, the higher sense-organs, the eye and the ear, are more perfect, physiologically, on the right side. Since the connection of the sense-organs is largely with the cortex of the contra-lateral hemisphere, this means that the impulses going mainly to the left hemisphere are better differentiated than those going to the right, and it would appear to be easier for these impulses to reach a motor area in the same hemisphere than to reach the corresponding area on the opposite side. It is further true that in right-handed persons the cortical activities of the left hemisphere in the region of the body sense-area, must always be greater than those of the opposite hemisphere, and these two circumstances cannot fail to have a profound influence. The observations of Flechsig[1] on the pyramidal tracts also show that these tracts, before medullation at least, may be unevenly developed on the two sides of the cord, and the ease of control may thus be rendered unequal—a condition which must be dominant in the determination of the side of the body which shall be most exercised. Be this as it may, the lesions which cause aphasia or apraxia (inability to determine the meaning and use of objects), are predominantly in the left hemisphere in persons who are right-handed, while there is some evidence that the right hemisphere is more important in left-handed persons.

In the adult, damage to one hemisphere is usually followed by a permanent loss of function, to a greater or less degree, but this loss may be more transient and less serious when the lesion occurs in the very young subject, so that during the growing period the sound hemisphere can in a measure replace the one that has been injured.

Assuming this general plan for the arrangement of the cortex to be correct, it is evident that a given cell, the axone of which forms part of the pyramidal tract, must in the human cortex be subject to a large series of impulses coming to it over as many paths. Schematically, it would be as represented in Fig. 113.

The discharging cell may be destroyed; then, of course, the muscles controlled by it become paralyzed for voluntary movements. The discharging cell may, however, remain intact, but the pathways by which impulses arrive at it be damaged. This is the type of lesion which produces symptoms of aphasia. When an interruption of associative pathways occurs some one or more of these tracts is broken, and hence the discharging cell does not receive a stimulus adequate to cause a response.

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[1] *Leitungsbahnen im Gehrin und Rückenmark*, 1876.

The physiological complexity of the elements in any part of the central system, either when different portions of the system from the same animal or when the corresponding portions of different animals are compared, depends on the number of paths by which the impulses are brought to the discharging cells.

Composite Character of Incoming Impulses.—To these conclusions based on the anatomy are to be added others suggested by clinical observations. In order that a patient suffering from a lesion between the visual and motor areas may be able to recognize an object and to indicate its use, it is sometimes necessary that the object shall appeal to several senses. For example, the name and use of a knife, when seen alone, may not be recalled, but when it is taken into the hand—that is, when the dermal and muscular sensations are added to the visual one—the response is made, though, acting alone, any one set of sensations is inadequate to produce this result.

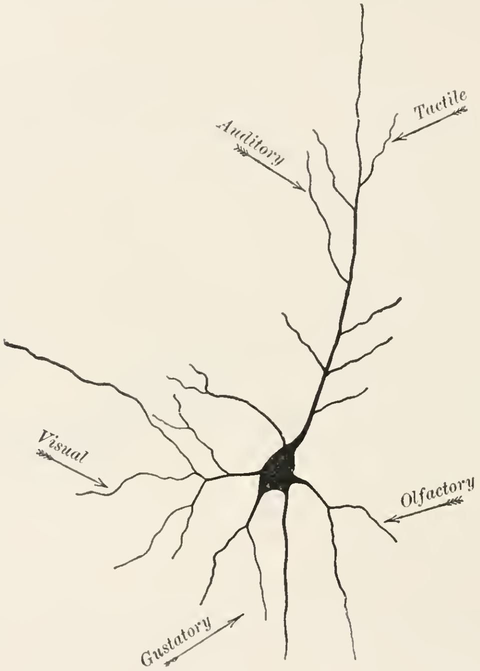

FIG. 113.—Schema showing in a purely formal manner the different sort of afferent impulses which may influence the discharge of a cortical cell.

Just where the block occurs in such a case it is not possible to say with exactness, but the lesion lies, as a rule, between the sensory and motor areas concerned, and by the damage to the pathway, it is assumed that one or more groups of impulses are so reduced in intensity that they are alone insufficient to produce a reaction ; and therefore it is only when the impulses from several sources are combined that a response can be obtained.

Variations in Association.—It is a familiar fact that individuals differ in no small degree in the acuteness of their senses—*i. e.*, in the power to discriminate small differences, and this, too, when the sense-organs are normal. Further, the powers of those best endowed are by no means to be attained by others, however conscientious their training. Moreover, the sensory pathways differ widely. The inference is fair, therefore, that those who think in terms of visual images, as compared to those who think in auditory images, do so by virtue of the fact that in the former case the central cells concerned in vision are distinctly the better organized, while in the latter case it is those concerned in hearing.

In the same way, the power of expression varies in an equally marked degree, and the capacity for the expression of ideas by means of the hand, in writing, is by no means necessarily equal to the power of expression by means of spoken words. In the former case we have the results of the play of impulses from the several sensory centres on the motor area for the hand, and this is reinforced by the sight of that which has been written, whereas in the latter case impulses from these same sensory centres play upon the area which controls the muscles of phonation, and this reaction is reinforced by the sound of the words uttered. Of course, in the case of a defective, like a blind-deaf-mute, the expression of thought is by movements of the fingers, and this is reinforced by the tactile and muscular sensations which follow these movements.

It is not by any means to be expected that the anatomical connections which render such reactions possible will be equally perfect for the different sensori-motor combinations, or the same combinations in different persons, and hence the powers of the individual will be modified by the varying perfection of these paths. From this it also follows that the same lesion as grossly determined, will not produce identical results in the two persons, for it will not effect the damage of structural elements which are strictly comparable.

Latent Areas.—It has been plain from an examination of the foregoing figures, as well as from the descriptions, that there must be a large portion of the cortex which, so far as has been observed, may be called latent. These areas, which include nearly the entire ventral surface of the hemispheres, a large part of the mesial surface, and on the dorsal and lateral aspects a large portion of the frontal, parietal, and temporal lobes together with the island, certainly require a word.

These last correspond with the "association centres" as described by Flechsig. To direct stimulation they give no response. From any one portion of the latent area the connections are not massive enough to permit of impulses which will cause a muscular contraction, and hence these impulses coming from one locality to a discharging cell form only a fraction of the impulses which control it. For this reason the significance of these parts fails to be clearly evident upon direct experiment.

The cortex of the frontal lobes has some connections with the nuclei of the pons, and so with the cerebellum. The more recent experiments on the functions of this region are by Bianchi[1] and Grosglik,[2] the former on monkeys and dogs and the latter on dogs alone.

These experimenters found that the removal of one frontal lobe is comparatively insignificant in its effects, while when both are removed the change is profound. On removing the frontal lobe on one side only there is no disturbance of vision, hearing, intelligence, or character. There do occur both sensory and motor disturbances, but these are for the most part transient. On the side opposite to the lesion there is in the limbs a blunting of all sensations and some paresis. Moreover, there is a hyperæsthesia combined with a paresis of the muscles of the neck and trunk which move these parts *away* from the side of the lesion.

These several effects of the operation tend to pass off, and if then the remaining frontal lobe be removed from a dog or monkey, not only do the symptoms just described appear on the other side of the body, but still more fundamental changes occur. A ceaseless wandering to and fro, such as Goltz[3] observed in those dogs in which the anterior half of the brain had been removed, characterizes the animals; curiosity, affection, sexual feeling, pleasure, memory, and the capacity to learn are at the same time abolished, and the expressions of the animal are those of fear and excessive irritability. That, therefore, the frontal lobes play an important rôle in the total reactions of the central system is amply evident, but this by no means justifies the conclusion that they are the seat of the intelligence.

F. COMPARATIVE PHYSIOLOGY OF THE DIVISIONS OF THE ENCEPHALON.

For the better comprehension of the conditions found in man and the monkeys, it will be of importance to briefly review the comparative physiology of the parts of the encephalon in vertebrates below the monkeys. The encephalon in the lower vertebrates is usually composed of a very much smaller number of cells than is found in that of man, and also the massing of the elements toward the cerebral cortex and in connection with the principal sense-organs has gone on to a far less extent.

For the determination of the functions of the several parts of the encephalon it is possible to employ in animals the method of removal as well as the method of stimulation. The doctrine of cerebral localization was at one time crudely expressed by the statement that a cortical centre was one the stimulation of which produced a given reaction, and the removal of which abolished this same reaction. Goltz soon showed that in the dog the removal of even an entire hemisphere did not cause a paralysis of the muscles on the opposite side of the body, although others had shown that a stimulation of certain portions of the cortex of the hemisphere would cause the muscles to contract. It was argued, therefore—and quite rightly—that the cortical centres of the dog did not completely answer to the definition.

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[1] *Archives italiennes de Biologie,* 1895, t. xii.

[2] *Archiv für Anatomie und Physiologie,* 1895.

[3] *Ueber die Verichtungen des Grosshirns,* 1881.

From the experimental work of the strict localizationists like Hitzig,[1] Munk,[2] and Ferrier,[3] and from the work of those who, like Goltz[4] and Loeb,[5] denied a strict localization in the cerebral cortex, several important points of view have been developed.

In the first instance, anatomy indicates that in the central system there are but few localities which consist only of one set of cell-bodies, together with the fibres coming to these bodies and going from them. Almost every part has both more than one set of connections with other parts and also fibres passing through it, or by way of it, to other localities. Hence in removing any part of the hemispheres, for instance, not only are groups of cell-bodies taken away, but a number of other pathways are interrupted at the same time, and thus the damage extends beyond the limits of the part removed. Moreover, when any portion of the central system has been removed there is a greater or less amount of disturbance of function following immediately after the operation; but this disturbance partially passes away. There are thus "temporary" as contrasted with "permanent" effects of the lesion, and these require to be sharply distinguished, because it is a permanent loss which is alone significant in these experiments. Finally, it has been made clear that neither the relative nor the absolute value of any division of the central system is fixed, but depends on the degree to which centralization has progressed, or, to use the more common measure, the grade of the animal in the zoölogical series, both expressions implying an increase in the connections between the cerebrum and the lower centres. The age of the animal on which the operation has been made is also of no small importance in this respect. These relations can be illustrated by reference to several experiments.

Removal of Cerebral Hemispheres.—If from a bony fish the cerebral hemispheres (including the corpora striata as well as the mantle) be removed, the animal apparently suffers little inconvenience. The movements are undisturbed; such fish play together in the usual manner, discriminate between a worm and a bit of string, and among a series of colored wafers to which they rise always select the red ones first.[6] In these fish the eye is the controlling sense-organ, and, as will be recognized (see Fig. 114), the operation has by no means damaged the primary centres of vision.

Quite different is the result when the cerebrum is removed from a shark.[7] In this case, although the eyes are intact, the animal is reduced to complete quiescence; yet, on the whole, the nervous system of the shark is rather less well organized and more simple than that of the bony fish.

The astonishing effect produced is explained by a second experiment (see Fig. 115).

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[1] *Untersuchungen ueber das Gehirn*, Berlin, 1874.

[2] *Ueber die Functionen der Grosshirnrinde*, Berlin, 1881.

[3] *The Functions of the Brain*, London, 1876.

[4] *Ueber die Verichtungen des Grosshirns*, Bonn, 1881.

[5] *Archiv für die gesammte Physiologie*, 1884, Bde. 33 u. 34.

[6] Steiner: *Die Functionen der Centralnervensystems*, 1888.

[7] Steiner: *Loc. cit.*

If the olfactory tract be severed on one side, no marked disturbance in the reactions of the shark is to be noticed; when, however, both tracts are severed, the shark acts as though deprived of its cerebrum. From this it appears that the removal of the principal sense-organ, that of smell, is the real key to the reactions, and that the responsiveness of the fish is reduced in the first instance, because in this case it has been deprived of the impulses coming through the principal organs of sense, and in the second, the removal of the cerebrum contains the pathway for the impulses from the olfactory bulbs to the cell-groups which control the cord.

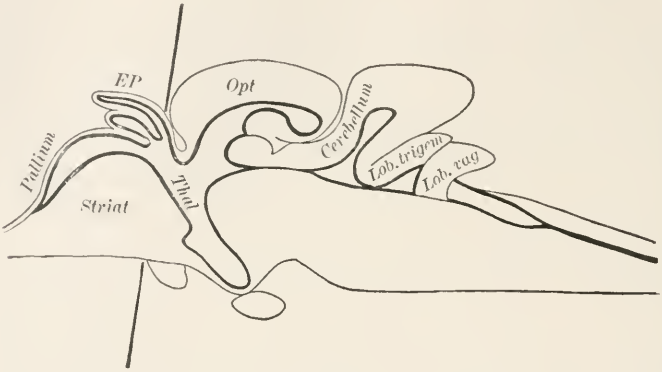

FIG. 114.—Schema of the encephalon of a bony fish—embryonic (Edinger). The vertical black line marks off the structures in front of the thalamus.

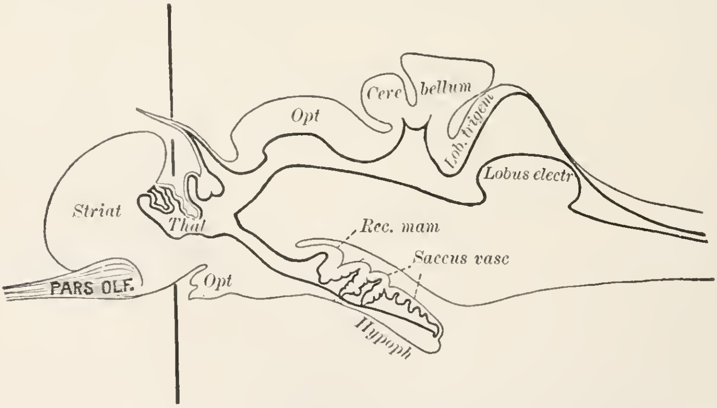

FIG. 115.—Schema of the encephalon of a cartilaginous fish (Edinger). The vertical black line marks off the striatum and pars olfactoria which lie in front of the thalamus.

Passing next to the amphibia as represented by the frog, there are several series of observations on the physiological value of the divisions of the central system. Schrader[1] finds the following: Removal of the cerebral hemispheres *only*, the optic thalami being uninjured, does not abolish the spontaneous activity of the frog. It jumps on the land or swims in the water, and

[1] *Archiv für die gesammte Physiologie*, 1887, Bd. xli.

changes from one to the other without special stimulation. It hibernates like a normal frog, retains its sexual instincts, and can feed by catching passing insects, such as flies (see Fig. 116). A frog without its hemispheres is therefore capable of doing several things apparently in a spontaneous way. Such frogs balance themselves when the support on which they rest is slowly turned, moving forward or backward as the case demands, in order to maintain their equilibrium. In doing this the frog tends first to move the head in the direction opposite to the motion of the support, and then to follow with movements of the body. If the optic thalami are removed (Fig. 116, *C*), the power of balancing is lost, because, although movements of the head still occur, those of the body are abolished. A frog thus operated on and deprived of the hemispheres and thalami exhibits the lack of spontaneity which is usually described as following the loss of the hemispheres alone, but which is not a necessary consequence of this operation, as the preceding experiments show.

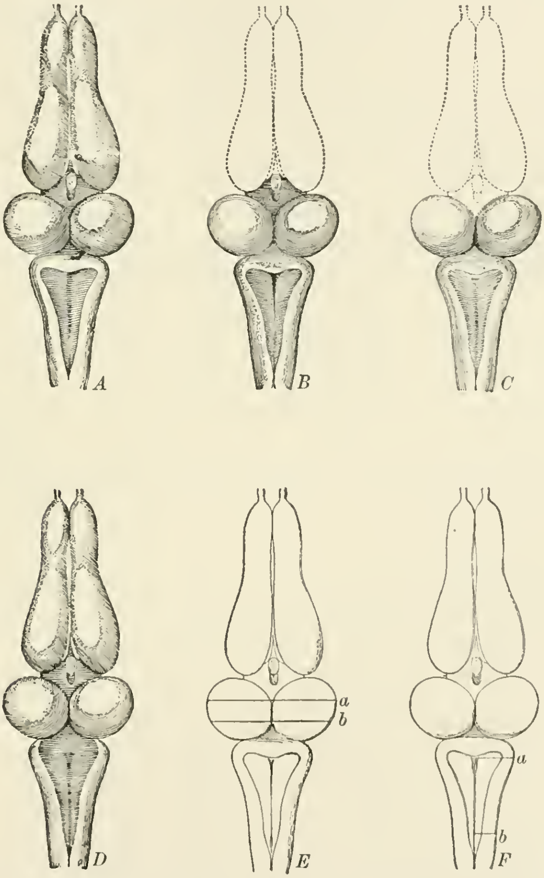

FIG. 116.—Frog's brain; the parts in dotted outline have been removed: *A*, brain intact; *B*, cerebral hemispheres removed; *C*, cerebral hemispheres and thalami removed; *D*, cerebellum removed; *E*, two sections through the optic lobes; *F*, two sections through the right half of the bulb (Steiner).

A frog possessed of the mid-brain and the parts behind it (Fig. 116, *C*) will croak when stroked on the back. When the optic lobes have been removed this reaction becomes more difficult to obtain, but it is not necessarily abolished, neither is the characteristic fling of the legs in swimming. At the same time, a frog with its optic lobes can direct both its jumping and swimming movements according to light stimuli acting through the eye, jumping around and over obstacles which form a shadow in its path, and climbing out of the swimming tank on the lighter side. This power is lost when the optic lobes have been removed.

When the anterior end of the bulb (pars commissuralis—Stieda) has been also removed then the frog becomes incessantly active, creeping about and not coming to rest until he has run himself into some corner. Schrader found such frogs capable of clambering over the edge of a box eighteen centimeters high. They are at a loss when the edge of the box has been finally attained, and vainly reach into space from this position. In the water they swim "dog-fashion," but only upon special stimulation do they make a spring.

If more of the bulb is removed, the bearing of the frog departs more and more from the normal, and is only temporarily regained in response to strong stimulation; nevertheless, co-ordinated movements can be obtained when the bulb down to the calamus scriptorius has been removed, and only when the movements of the arms are directly affected by the damage of the upper end of the cord does the inco-ordination become constant.

A section through the optic lobes at *a* (Fig. 116, *E*) puts the frog in a condition similar to that following the isolated removal of the lobes, while a section at *b* has the curious effect of causing the animal to move backward upon stimulation of the toes.

When the small ridge which forms the cerebellum in the frog has been removed a slight tremor of the leg-muscles and a loss of precision in jumping are the only defects noted (Fig. 116, *D*). These results hold for symmetrical removal of the divisions of the encephalon. When the removal is unsymmetrical in the inter-brain, mid-brain, or bulb (Fig. 116 *F*, *a* and *b*), there is more or less tendency to forced positions or forced movements.

As a rule, action is most vigorous on the side of the body associated with the greater quantity of nerve-tissue. This relation appears as a natural result of the greater effectiveness of the incoming impulses when entering a larger group of central cells. Indeed, the removal of the different portions of the central system in the frog is accompanied by a progressive loss in responsiveness, stronger and stronger stimuli being required to induce a reaction. This holds true down to the anterior end of the bulb, the removal of which, on the contrary, sets free the lower centres, so that the frog becomes incessantly active. Just how this release is effected is not easy to explain, but further removal is again followed by the loss of responsiveness.

Passing next to the bird, as represented by the pigeon, the observations of Schrader are the most instructive.[1] The removal of the hemispheres from the bird involves taking away the mantle and the basal ganglia, the chiasma

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[1] *Archiv für die gesammte Physiologie*, 1888, Bd. xliv.

and the optic nerves being left intact. For the first few days after the operation the bird is in a sleep-like condition. Next the sleep becomes broken into shorter and shorter periods, and then the bird begins walking about the room. From the beginning its movements are directed by vision; slight obstacles it surmounts by flying up to them, larger ones it goes around. In climbing, its movements are co-ordinated by the sense of touch, and the normal position of the body is maintained with vigor. The birds which walk about by day remain quiet and asleep during the night. In flying from a high place the operated pigeon selects the point where it will alight, and prefers a perch or similar object to the floor.

A reaction to sound is expressed by a start at a sudden noise, like the explosion of a percussion-cap.

Pigeons without the cerebrum do not eat voluntarily, though the presence of the frontal portions of the hemispheres is sufficient to preserve the reaction.

In a young hawk slight damage to the frontal lobes abolished for the time the use of the feet in the handling of food, and thus abolished in this way the power of feeding as well as that of standing.

With the loss of the cerebrum the pigeon does not lose responsiveness to the objects of the outer world, but they all have an equal value. The bird is neither attracted nor repelled, save in so far as the selection of the points toward which it will fly is an example of attraction. Sexual and maternal reactions both disappear, and neither fear nor desire is evident.

In ascending the mammalian series, the removal of the cerebrum becomes a matter of increasing difficulty. The reasons for this are several, and reside in the increasing size of the blood-vessels and the nutritive complications dependent on the increase in the mass of the cerebrum, as well as in the greater physiological importance of this division. Goltz[1] has been able by repeated operations to remove the entire cerebrum of a dog, and still to keep the animal alive and under observation for eighteen months, at the end of which time the animal, though in good health, was killed for further examination. This dog was blind, though he blinked when a very bright light was suddenly flashed in his face. He could be awakened by a loud sound, and when awake responded to such sounds, when intense, by shaking the head or ears. This would not, however, be complete proof that he could hear. The sense of taste was so far present that meat soaked in quinine was rejected after tasting. Tactile stimuli and those involving the muscle sense, as in the case where the animal was lifted, caused him to struggle and to bite in the direction of the irritation. These reactions were modified according to the locality of the stimulus. The power to make movements expressive of pain was still present.

On the motor side the dog was capable of such highly complicated acts as walking, standing, and eating, and in these operations was guided by the muscle-sense and that of contact. The sexual instincts were lost, but the

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[1] *Archiv für die gesammte Physiologie*, Bd. xli.

animal was excessively active, and became more and more excited when ready to defecate or when hungry.

The examination of the brain showed that in front of the mid-brain the important structures had been removed or were degenerated, only small portions of the corpora striata remained, mainly parts of the caudal portions of the nucleus caudatus. The frontal portion of the thalamus had been removed and the nuclei in the remainder were highly atrophic, so that the defects were due to a removal of rather more than the cerebrum proper.

Emotions, feelings, conscious sensations, or the capacity to learn were entirely wanting in this dog, and its reactions were those of a very elaborate machine.

If we compare, now, the effects of the removal of the cerebral hemispheres in the bony fish, the pigeon, and the dog, we see that the results of the operation are progressively more disturbing as we pass up the series. In the higher animals the effects are more often fatal, the disturbance immediately following is much more severe, the return of function slower, and the permanent loss greater. As a partial exception to the above statements is the observation that after operation the general health of pigeons always declines, and it is not possible to keep them alive more than about six weeks. On the contrary, a dog could be kept in good health for some eighteen months; but there is this difference between the experiments, that the removal in the case of the dog was made by several successive operations.

By removal of the cerebrum the higher animal tends to lose just those capacities which best serve to distinguish it from the lower forms. When, therefore, the inquiry is made why the results obtained in the dog are not obtainable in the monkey or in man, there are several replies. In the first place, no such extensive experiments have been made on monkeys of the right age and under equally favorable conditions. If the mature animal is taken, the secondary degenerations are so massive that they certainly cause great disturbance in the remaining part of the system. This is not equivalent to an assertion that the same results could be obtained in the monkey by more extensive experiments, but a suggestion of one difference behind the results thus far reported. There is no reason for assuming any deep-seated difference in the arrangement of the central system of the highest mammals as compared with that in the lower. Indeed, in some human microcephalic idiots the proportion of sound and functional tissue in the encephalon is less than one-fourth that found in a normal person; yet, on the other hand, no normal adult could lose anything like the amount of tissue which is out of function in these microcephalic brains and at the same time live.

The central system, therefore, even in man, is to be looked upon as possessed of some power to adapt itself when portions have been lost, but this is most evident when the defect begins early and develops slowly.

Keeping the cerebrum still in view, it is possible to go into further details. In forms below the monkey the loss of portions of the cerebral cortex from the motor area is accompanied by a greater or less paralysis of the muscles represented. This, however, is an initial symptom only, and gradually disappears, though not always with the same completeness. In man, of course, the tendency to recover is least.

The anatomical relations behind this difference are the following: The efferent cells in the ventral horns are dominated principally by two sets of impulses, those arriving directly over the dorsal roots of that segment in which they are located, and those coming over the long paths by way of the cerebral cortex and pyramidal tracts. In the lower mammals this second pathway is insignificant, and when interrupted, therefore, the disturbance in the control of the ventral-horn cells is but slight. Passing up the series, however, this pathway tends to become more and more massive and important, as the figures previously given show (see p. 252), until in man and the monkey a damage of it such as is effected by injury to the cortex causes a high degree of paresis if not permanent paralysis, because by this injury a large proportion of the impulses is thus cut off from the efferent cells.

It has been previously shown that the cortical areas do not vary according to the mass of the muscles which they control. Experiments also show that it is the fore-limbs which are most disturbed in their reactions when the lesion involves the cortical centres for both fore- and hind-limbs, and this falls under the law that the more highly adaptable movements (*i. e.*, those of the fore-limb as contrasted with those of the hind-limbs) are most under the control of the cortex. If the examination be restricted to the fore-limb alone, it is found that the finger and hand movements or those of the more distal segments are in turn the ones most disturbed. Thus, in the limbs the more distal groups of muscles are those best controlled from the cortex. It follows, then, that for the arm, paralysis of shoulder movements as the result of cortical lesion is least complete, while as we travel toward the extremity of the arm the liability to disturbance of its function as the result of cortical injury increases steadily.

Turning now to the "sensory" areas of the cortex, the principles underlying their physiological significance and connections appear to be similar. The lower the animal in the vertebrate series the more probable that its reactions can be controlled by the afferent impulses which have not passed through the cerebral cortex.

None of the senses except vision can be analyzed sufficiently to bring out the significance of the subdivisions of the cortical area; hence the illustrations are taken from that sense alone.

It has already been shown that without cerebral hemispheres a bony fish can distinguish the colors of wafers thrown on water and discriminate between a bit of string and a worm. In the same case, a frog is able to direct its movements and to catch flies—*i. e.*, to detect objects in motion and react to them normally. A pigeon can direct its movements in some measure, and even select a special object as a perch; but it is not able to respond to the sight of food or its fellows, or those objects which might be supposed to excite the bird to flight. In the dog the vision which remains permits only the response of blinking when the eye is stimulated by the flash of a strong light. The progressive diminution in the response which follows visual stimuli in these animals is open to the interpretation that the path by which the impulses may pass over to the cells forming the primary centres intermediate between the sense-organ and the cortex is progressively diminished. Thus, as the pathway to the cortex becomes more permeable, the impulses arriving at the primary optic centres are in a less and less degree reflected toward the cord. When, therefore, the cortex has been removed, the reactions taking place by way of it are disturbed in proportion to their normal importance.

In the first instance, when the reflection occurs in the primary centres the incoming impulses are distributed toward the cord by paths not known, while in the second they pass from the cortex along the pyramidal tracts.

In the cortex of the dog subdivisions of the visual area have been made by Munk.[1] He found that the more anterior portions of the visual area were associated with the superior parts of the retina, and the more posterior portions with the inferior, while the area in one hemisphere corresponded with the nasal portion of the retina of the opposite eye, and to a less degree with the temporal portion of the retina of the same side. The determination of these relations was made by the removal of parts of the visual area (dogs) and the subsequent examination of the field of vision. It appears, therefore, that the incoming impulses from certain portions of the retina are delivered at definite parts of the cortex, and that when the parts are injured in the dog or higher mammals these impulses are blocked. By stimulation, it will be remembered, Schäfer determined similar relations in the monkey.

Before leaving the cerebral hemispheres, mention of the fact should be made that still other functions, control of the sphincter ani (Fig. 103), secretion of saliva, and micturition, can be roused by the stimulation of the cortex in the appropriate region—namely, in the region where the muscles and glands concerned might be expected to have representation if they followed the general law of arrangement. Changes in the production and elimination of heat from the body follow interference with the motor region of the cerebrum, and the removal of portions of the cortex in this region is followed by a rise in the temperature of the muscles affected and an increased blood-supply to them.

In the encephalon, the cerebrum, and especially its outer surface, is the portion the functions of which have been studied. The significance of the other portions of the encephalon can be far less well determined. The disturbances caused by the section and stimulation of the callosum have been studied by Koranyi[2] and by Schäfer.[3] It was found that complete section of the corpus callosum was not followed by any perceptible loss of function. On the other hand, stimulation of the uninjured callosum from above gave symmetrical bilateral movements, while if the cortex on one side was removed stimulation of the callosum gave unilateral movements on the side controlled

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[1] *Ueber die Functionen der Grosshirnrinde*, Berlin, 1881.

[2] *Archiv für Anatomie und Physiologie*, Bd. xlvii.

[3] *Brain*, 1890.

by the uninjured hemisphere. These results seem to corroborate the conclusion derived from histological work to the effect that the system of the callosum is composed only of commissural fibres, and that it sends no fibres directly into the internal capsule of either side. Concerning the corpora striata and the optic thalami, very little is known. In the case of the corpora striata injury causes in man no permanent defect of sensation or motion, although both forms of disturbance may at the outset be present in the case of acute lesions. Lesions of the corpora striata cause a rise in body-temperature.[1] Following a puncture of one corpus striatum there occurs in rabbits a rise amounting to some 3° C.; it begins a few minutes after the operation and may last a week, but the temperature tends to return to the normal. The most striking feature in these experiments is the very wide effects produced by an extremely small wound, like the puncture of a probe.

In the cases where lesion of the striatum on one side causes in man a rise of temperature, it appears mainly on the side of the body opposite the lesion.[2] A vaso-motor dilatation occurs over the parts of the body where the temperature is high.

In less degree a rise of temperature follows injury of the optic thalamus—at least such is the result of experiments on rabbits; but the effect of the lesion is never so marked as in the case of the striatum. Owing to the disproportion between the area of the lesion and the extent of the effects, it is difficult to conceive of the anatomical relations which permit the reaction. It is of interest to note, however, that similar relations hold for the vaso-motor centre in the bulb, in which case the vessels supplying a great area are controlled by a small group of cells.

The difficulty of an anatomical explanation is increased by the fact that Ott[3] enumerates in animals six heat-centres: 1. The cruciate, about the Rolandic fissure; 2. The Sylvian, at the junction of the supra- and post-Sylvian fissures; 3. The caudate nucleus; 4. The tissues about the striatum; 5. A point between the striatum and the thalamus, near the median line; 6. The anterior mesial end of the thalamus.

Thalamus.—In considering the thalamus, we find that the various cell-groups forming it are connected with distinct portions of the cerebral cortex by double pathways—one set of axones having their origin in cell-bodies located in the cortex, and the other in cell-bodies in the subdivisions of the thalamus. The relations between these two divisions have been specially studied by v. Monakow,[4] who finds by experiment that lesion of one part, either cortex or the thalamic nuclei, is followed by degeneration in the other part, and that the location of the degeneration depends on that of the lesion.

Further, it has been observed by Mellus[5] that the axones passing from the

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[1] Aronsohn und Sachs: *Archiv für die gesammte Physiologie*, 1885, Bd. xxxvii.; Richet: *Comptes rendus de l'Acad. des Sciences*, 1884; Ott: *Brain*, 1889, vol. xi.

[2] Kaiser: *Neurologisches Centralblatt*, 1895, No. 10.

[3] Ott: *Loc. cit.*

[4] *Archiv für Psychiatrie und Nervenkrankheiten*, 1893, Bd. xxvii.

[5] *Proceedings of the Royal Society*, London, 1894 and 1895.

motor cortex of the monkey toward the thalamus are fibres of smaller calibre than those destined for the pyramidal tracts.

Moreover, the studies of Tschermak[1] on the termination of the tracts which continue the dorsal columns of the spinal cord in the interbrain, show an abundant connection of the fibres, especially with the ventral cell-groups of the thalamus. The connection may be either an actual ending of the fibre or a termination by means of collaterals.

When these anatomical observations are considered in connection with the differences in the reactions of the frog with and without its thalami, it appears that cell-groups which increase the responsiveness of the central system must be located here. On the other hand, in the case of Goltz's dog without its fore-brain, the thalami (interbrain) were so largely damaged that it hardly seems possible that they could have been much utilized in the reactions which were made by that animal.

Human pathology throws little light on the functions of the thalami—though lesion of it is often accompanied by loss of power to express the emotions through the muscles of the face—a symptom to which attention has been repeatedly drawn.

The Cerebellum.—The only other division of the encephalon, the functions of which can properly be described apart, is the cerebellum. This portion is among vertebrates almost as variable in its development as the mantle of the cerebral hemispheres, and in many fish and mammals is asymmetrical in its gross structure.

Observation on this subdivision has been carried out in the first instance by Luciani,[2] and later by Russell[3] and by Ferrier.[4]

The cerebellum is not concerned with psychical functions. The removal of it does not cause permanently either paralysis or anæsthesia, but the immediate effects of an extensive injury are (in dogs and monkeys) a paresis and analgesia as well as anæsthesia mainly in the hind-legs, and in consequence a high degree of inco-ordination in locomotion. A distinct series of symptoms, however, follows injury to this organ, and these are modified according to the locality and nature of the lesion. Removal of one-half (cerebellar hemisphere plus half the vermis) of the cerebellum in the dog causes a deviation outward and downward of the optic bulb on the opposite side, a proptosis of the bulbs on both sides, nystagmus and contracture of the muscles of the neck on the side of the lesion, and an increase of the tendon-reflexes in the limbs. In walking the dog wheels toward the side opposite to the lesion, and tends to fall *toward* the side of the lesion.

The symptoms are chiefly unilateral, and, caudad from the cerebellum, are on the side of the lesion. The symptoms are less severe when only one hemisphere, instead of an entire half of the cerebellum, has been removed.

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[1] "Notiz betreffs des Rindenfeldes der Hinterstrangsbahnen," *Neurologisches Centralblatt*, 1898, No. 4.

[2] *Archives italiennes de Biologie*, 1891–92, xvi.

[3] *Philosophical Transactions of the Royal Society*, 1894.

[4] *Brain*, 1893, vol. xvi.

The existing symptoms are not intensified by the removal of the remaining half. The permanent condition of the muscles after operation is expressed by an atonia, or lack of tonus, in the resting muscles; an asthenia, or loss of strength, which was measured by Luciani, and was most marked in the hind-leg; an astasia, or a lack of steadiness in the muscles during action; and finally an ataxia, or a want of orderly sequence, in the contractions of the muscle-groups. The general expression of these symptom is a twist of the trunk, the concavity being toward the operated side, combined with a disorderly gait. At the same time there is no demonstrable permanent disturbance of tactile or muscular sensibility.

Though the two halves of the cerebellum are united by strong commissural fibres, the complete division of the organ in the middle line is followed by a disturbance of the gait which is only transitory. Hence it is inferred that the connections of the cerebellum are mainly with the same side of the bulb and spinal cord. Cephalad of the cerebellum the connection, however, is a crossed one, each cerebellar hemisphere being associated with the contralateral cerebral hemisphere. Throughout these connections, both cephalad and caudad to the cerebellum itself, it appears that there is always a double pathway, and the cerebellum not only sends impulses to, but receives them from, the regions with which it is associated.

One effect of removal of one-half of the cerebellum is to increase the responsiveness of the cortex of the contra-lateral cerebral hemisphere to electrical stimulation, thereby making it possible with a weaker stimulus to obtain a reaction which could be obtained from the other hemisphere only with a stronger one. When an irritative lesion is made, instead of a merely destructive one, the rotation and falling are away from the side of the lesion, instead of toward it.

The experiments altogether show the cerebellum to be closely associated with the proper contraction of the muscles, and this is so directly connected with the maintenance of equilibrium[1] that it is not surprising to find that stimulation or removal of the cerebellar cortex, besides producing nystagmus, may give rise to deviations of the eyes similar to those found on injury of the semicircular canals or stimulation of their nerves in fishes.[2]

PART III.—PHYSIOLOGY OF THE NERVOUS SYSTEM TAKEN AS A WHOLE.

A. Weight of the Brain and Spinal Cord.

In attributing a value to the mass of the nervous system we assume that the elements which compose it possess potential energy. This energy varies for any given element in accordance with a number of conditions, but for the moment it will be sufficient to point out that if the mass of the entire system is significant the masses of its respective subdivisions are also significant, as

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[1] A. Thomas: "Le Cervelet," *Étude anatomique, clinique et physiologique*, Paris, 1897.

[2] Lee: *Journal of Physiology*, 1893, vol. xv.; 1894, vol. xvii.

showing in some measure the relative physiological importance of the several parts.

Weight of the Encephalon and Spinal Cord.—When the weight of any portion of the nervous system is taken, the final record represents, in addition to the weight of the nerve-tissues proper, that of the supporting and nutritive tissues normally associated with them, together with the enclosed blood and lymph. It is, however, assumed that under normal conditions the relation between the nervous and non-nervous tissues is nearly a constant one, and that the results of different weighings are therefore comparable among themselves.

Outside of the nervous tissue proper are the pia and the fluid contained in the vessels and ventricular cavities. Sometimes the encephalon is freed from the pia and fluid, and at others they are weighed all together. According to Broca,[1] the weight of the pia covering the encephalon is, in normal males, as follows:

FIG. 117.—Showing the principal divisions of the encephalon made for the study of its weight: 1, hemisphere seen from the side, fissuration according to Eberstaller; 2, mid-brain, region of the quadrigemina; 3, pons; 4, cerebellum, or hind-brain; 5, bulb, or after-brain. Divisions 2, 3, and 5, taken together, form what is designated the "stem" in the tables of Boyd (modified from *Quain's Anatomy*).

20 to 30 years	45 gms.
31 to 40 "	50 "
60 "	60 "

The cast of the ventricles as made by Welcker displaces 26 c.c. of water, which gives an idea of the normal capacity of these cavities. In man, the gray matter of the cerebrum has, on the average, 81 per cent. of water; while the white matter from various parts of the central system has 70 per cent.[2]

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[1] Broca, quoted by Topinard: *Eléments d'Anthropologie générale*, 1885.

[2] Halliburton: *Journal of Physiology*, 1894.

The specific gravity of the entire encephalon is for the male, 1036.3, and for the female, 1036.

Weight of the Encephalon.—The encephalon is that portion of the central nervous system contained within the skull. The accompanying diagram (Fig. 117) shows the encephalon, together with one manner of subdividing it. Its weight has usually been taken while it was still covered by the pia, but after allowing the fluids to drain away for five minutes or more. Sometimes drainage has been facilitated by cutting into the brain; hence, when the brain-weight records by any observer are to be discussed, the first question concerns the method according to which the brains were examined, for the weights may be either with or without the pia and with or without drainage.

The anthropologists classify encephala according to weight in the following manner:

The Nomenclature of the Encephalon according to Weight. Weight in Grams. *(Topinard.)*

Classes.	Males.	Females.
Macrocephalic	From 1925 to 1701	From 1743 to 1501
Large	" 1700 to 1451	" 1500 to 1351
Medium	" 1450 to 1251	" 1350 to 1151
Small	" 1250 to 1001	" 1150 to 901
Microcephalic	" 1000 to 300	" 900 to 283

From the observations of Dr. Boyd, in England, on the weight of the brain the following table has been compiled:

Table showing the Weight of the Encephalon and its Subdivisions in Sane Persons, the Records being arranged according to Sex, Age, and Stature (from Marshall's tables based on Boyd's records).[1]

Males.					Females.				
Ages.	Encephalon.	Cerebrum.	Cerebellum.	Stem.	Stem.	Cerebellum.	Cerebrum.	Encephalon.	Ages.
Stature 175 cm. and upward.					Stature 163 cm. and upward.				
20–40	1409	1232	149	28	23	134	1108	1265	20–40
41–70	1363	1192	144	27	23	131	1055	1209	41–70
71–90	1330	1167	137	26	24 *a*	130	1012	1166	71–90
Stature 172–167 cm.					Stature 160–155 cm.				
20–40	1360	1188	144	28	26 *s*	137 *s*	1055	1218	20–40
41–70	1335	1164	144	27	26 *s*	131	1055	1212 *s*	41–70
71–90	1305	1135	142 *s*	28 *a s*	24	128	969 *s*	1121	71–90
Stature 164 cm. and under.					Stature 152 cm. and under.				
20–40	1331	1168	138	25	24 *s*	130	1045	1199	20–40
41–70	1297	1123	139 *a*	25	25 *a s*	129	1051 *a*	1205 *a*	41–70
71–90	1251	1095	131	25	25 *a s*	123	974	1122	71–90

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[1] *a* indicates that a record considered according to age is too large; *s* indicates that a record considered according to stature is too large.

The method of weighing the brain used by Dr. Boyd[1] was as follows: The skull-cap being removed and the pia intact, the hemispheres were sliced away by horizontal sections as far down as the tentorium. The parts of the hemispheres still remaining were then removed by a section passing in front of the quadrigemina. The cerebellum was next separated from the stem, this latter being represented by the quadrigemina, the pons, and the bulb. Each hemisphere, the cerebellum, and the stem was then weighed separately.

If groups of similar ages and corresponding statures, as entered in the Table, are compared according to sex, it is at once seen that the male possesses the heavier encephalon, and that all the subdivisions of it are likewise heavier.

When individuals of the same sex and falling within the same age-limits are compared according to stature, those having the greater stature are found to have the greater brain-weight, though in the case of the subdivisions of the encephalon, and especially among the females, there are some irregularities, but these would probably disappear could the number of observations be increased. Finally, within the groups of those having the same stature, but different ages, the weight decreases with advancing age. The middle group, forty-one to seventy years of age, is in one way unfortunate, because, while the brain is probably still growing (see curve of growth, Fig. 118) during the first third of that period, and is nearly stationary (males especially) during the second, it begins to diminish so rapidly during the last third that the average weight is lower for the cases between sixty-one and seventy years than for the twenty years between forty-one and sixty years. Between seventy-one and ninety years the involutionary changes in the central system are most marked, and the decrease in weight during this period is clearly indicated.

Before suggesting an explanation of these variations according to age, sex, and stature, it is to be noted that they occur in other mammals as well as in man. As regards the difference in the weight of the encephalon due to sex, it has been shown to obtain among the apes,[2] the male having the heavier brain; and from the general relation of size according to sex among the mammalia, where the male as a rule has the greater body-weight and larger skull, it is to be anticipated that a similar difference in the weight of the brain will be shown in other genera.

Among individuals of the same species, but of different races or of different statures and weights, the law holds good that the larger races have the heavier brains, as do the larger and heavier individuals.[3] Here, as in the case of man, it is always assumed that the differences in body-weights are mainly correlated with the active tissues like muscle, and not with fat. As to the

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[1] *Philosophical Transactions of the Royal Society*, London, 1860; see also Marshall: *Journal of Anatomy and Physiology*, 1892.

[2] Keith: *Journal of Anatomy and Physiology*, 1895.

[3] Du Bois, in the *Arch. für Anthropol.*, Bd. xxv., maintains that among forms which may be fairly compared, the formula $E = S^{0.56}$, will give the weight of the encephalon,—E being the encephalic weight and S the body-weight.

loss of the brain in weight after maturity, observations on animals are scanty, but point to decrease in weight toward the natural close of life.

Interpretations of Weight.—Assuming as the simplest case that the number of the nerve-elements composing a given portion of the central system is *constant* within the limits of the same species, then differences in the weight of these portions in different individuals imply variations in the size of the component cells. The significance of variations in the size of the nerve-elements must be, primarily, that the larger the cells, and especially the larger the cell-bodies, the greater the mass of cell-substance ready at any moment to undergo chemical change leading to the release of energy, and the more numerous the probable connections. On the other hand, if the number of elements is *variable*, an increase in the number must, in view of the law of isolated conduction, also provide a larger number of conducting pathways. Whether this increase in the number of pathways shall further add to the complication of the system depends on the localities at which it occurs.

In the absence of fuller data, the explanation of the series of differences shown in Boyd's table is in a very high degree tentative. The loss of weight in advanced years appears to be due to a general atrophy of the nerve-elements. The greater brain-weight associated with greater stature appears to depend on the variations in the size of the elements rather than in their number, and, so far as can be seen, the distinction according to sex is also susceptible of the latter explanation.

Weights of Different Portions.—A study of the proportional weights of the several subdivisions of the encephalon according to the sex, stature, and age, shows that there is very little difference caused by variations in these conditions. This, too, so far as it goes, suggests that the absolute weight is dependent rather on variations in the size than in the number of the elements, since an harmonious variation in number would be less probable than an harmonious variation in size.

Social Environment.—It is not to be expected that the weight of the brain among the least-favored classes in any community will be the same as that of those who, during the years of growth, are under favorable conditions. All extensive series of observations which we possess relate to the least-favored social classes, and hence it is not improbable that the figures in the foregoing tables, which are based on data obtained mainly at the Marylebone Workhouse in London, are decidedly below those which would be obtained from the more fortunate classes in the same community. We have a list of brain-weights which contains the records for a number of men of acknowledged eminence, and also for others who attained recognition as able persons without being exceptionably remarkable. This list shows the persons thus selected to have brains on the average heavier than the usual hospital subject.[1]

Brain-weight of Criminals.—The observations of Manouvrier have shown that among French murderers the brain-weight is similar to that of the indi-

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[1] Donaldson: *The Growth of the Brain*, 1895.

viduals usually examined in the Parisian hospitals. In the same manner, the observations on the brain-weight among the insane indicate, according to the records of Boyd and others, that the insane as a class (the microcephalics being excluded) are not characterized by a special brain-weight. When, however, the insane are grouped according to the form of disease from which they have suffered, it is evident that those in which the brain was congested at death exhibit the higher weight, while those in which the pathological processes caused destructive changes, exhibit a low weight. The differences in these cases are rather the results of disease than the cause of it.

Brain-weights of Different Races.—Concerning the weights of the brain in different races there are no extensive observations which have been made directly on the brain itself. Davis,[1] however, has determined the cranial capacities of a series of skulls belonging to different races, and the brain-weights have been calculated from these.[2] This calculation gives the largest brain-weights to the western Europeans, but for a proper interpretation of the results there are needed at least the data concerning stature and age of the cases studied, both of which are here lacking.

Weight of the Spinal Cord.—Comparatively few observations are available for the spinal cord: Mies[3] found that in adults it weighed 24 to 33.3 grams, with an average weight of 26.27 grams; this for the cord deprived of the nerve-roots but covered by the pia. The variations due to sex and stature have not been determined. It seems probable, however, that the cord, like the brain, will be found lighter in females and in short persons: Mies states that its decrease in old age is proportionately less than that of the brain.

B. GROWTH-CHANGES.

The characters of the brain and cord thus far described have been those found in the adult. Between birth and the natural end of life, however, great changes take place, and, as it is necessary to consider the functions of the central system at all times in its history, the importance of knowing the direction in which the growth-changes are probably occurring is obvious.

Growth of the Brain.—The weight of the brain from birth to the twenty-fifth year is shown in Fig. 118. The curve is based on the table of Vierordt.[4]

The curve beyond the twenty-fifth year is continued on the basis of the observations by Bischoff,[5] and for comparison the curve representing the encephalic weights of a series of eminent men, forty-five in number, is drawn in a dotted line, the averages for decennial periods being alone dotted.

These records exhibit the fact that at birth the weight of the brain is about one-third of that which it will attain at maturity. The increase is very rapid

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[1] *Journal of the Academy of Natural Sciences*, Philadelphia, 1869.

[2] Donaldson: *Growth of the Brain*, 1895, p. 115.

[3] *Neurologisches Centralblatt*, 1893.

[4] *Archiv für Anatomie und Physiologie*, 1890.

[5] *Hirngewicht des Menschen*, Bonn, 1880.

during the first year, and vigorous for the first seven or eight years, after which it becomes comparatively slow. The maximum weight is indicated in the fifth decade (males), fourth (females), although there is a "premaximum" in the middle of the second decade (at thirteen and fifteen years for males and fourteen years for females), in which the too early and too vigorous

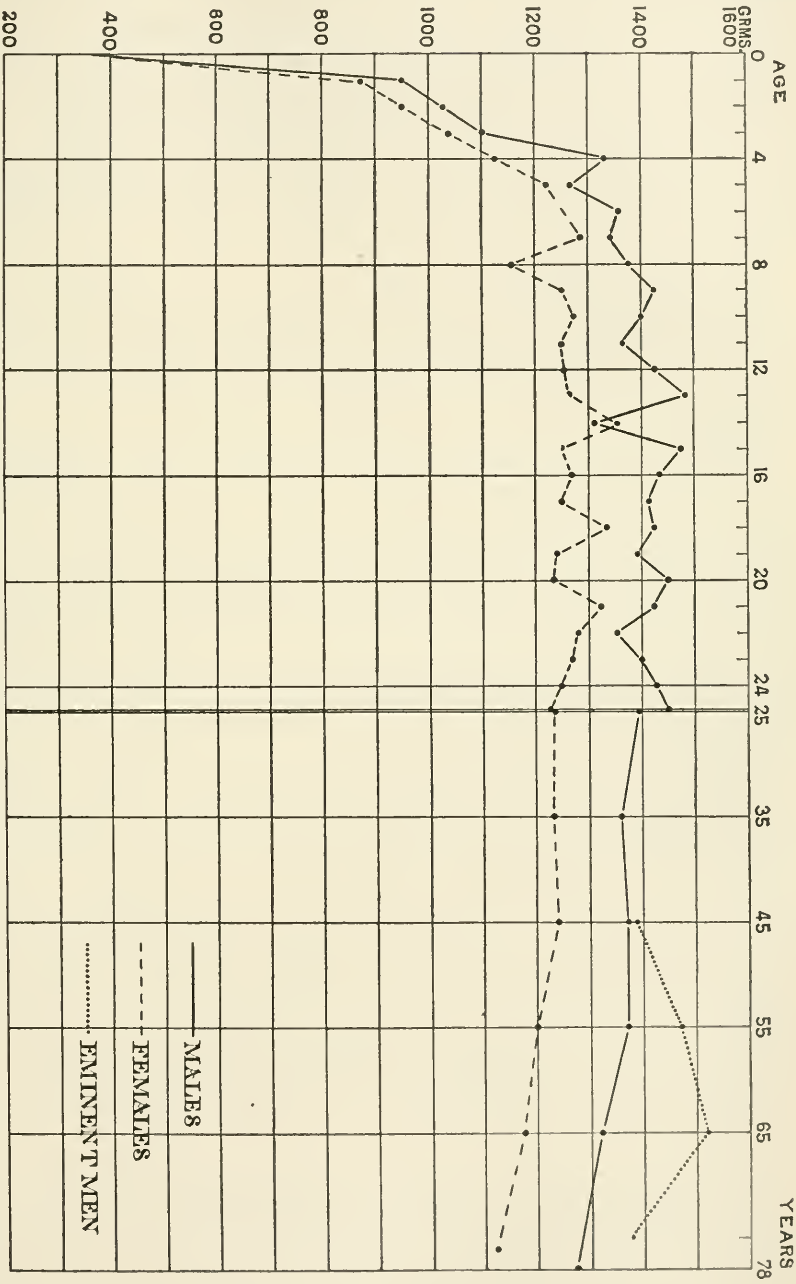

Fig. 118.—Curves for each sex, showing the weight of the brain according to age. For the first twenty-five years the curve is formed from annual averages based on the figures of H. Vierordt; from twenty-five years on, the curves are formed from decennial averages based on the observations of Bischoff. All the data are from observations on the less fortunate classes. The dotted curve for eminent men is formed from decennial averages based on forty-five observations.

growth of the encephalon appears to be an important factor in the cause of death; hence the larger brain-weight found at autopsies during these years. While, in general, the individual may be supposed to follow, in the development of his encephalon, the course here indicated by the curve, this premaximal increase must be excepted for the reasons given.

Relation between Growth of Body and that of Encephalon.—On comparing the growth of the entire body with that of the encephalon, it is evident that the growth is more rapid in the central nervous system than in the body at large, and that it is almost completed in the former at the end of the eighth year, whereas the body has at that time reached but one-third of the weight which it will attain at maturity.

A causal relation between a well-developed central system and the subsequent growth of the entire body is thus suggested, and also it is evident that conditions which influence growth will at any time find the body on the one hand, and the central system on the other, at quite different phases in their development.

The long-continued growth of the body brings it about that the central system, which at birth may form 12 per cent. of the total weight of the individual, is at maturity about 2 per cent. or less. For this change in proportion the increase of the muscular system is mainly responsible.

Further, the much smaller mass of the muscular system in the female is the chief cause of the higher percentage value of the central system in the female —a relation which has been much emphasized, but which is really not significant, since in both sexes this high percentage value of the central system is most developed at birth, and becomes steadily less marked as maturity is approached.

Increase in the Number of Functional Nerve-elements.—Having thus briefly indicated the facts of growth so far as they can be detected by the balances, it still remains to mention the series of changes which may be studied by other means, such as micrometric measurements or enumeration. The results obtained by these methods are somewhat complex, and must be treated with great care. Human embryology indicates that after the third month of fœtal life the number of cells in the central system is not increased. With the cessation in the production of new cells the only remaining means of increase in size is by enlargement of those cells already present.

How this occurs is well indicated by the accompanying table (p. 281), which shows the change in the size of cell-bodies in a given locality in man.

All vertebrates are not similar in respect to the manner of this change. Birge[1] has shown that in frogs there is a gradual increase in the number of the fibres forming the ventral and dorsal spinal roots, and that this goes on at the rate of about fifty additional fibres in the ventral roots and seventy in the dorsal, for each gram added to the total weight of the frog. The increase was still apparent in a frog weighing 112 grams. In the case of the ventral

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[1] Birge: *Archiv für Anatomie und Physiologie*, suppl., 1882.

root-fibres it was also determined that the cells of origin in the ventral horns of the spinal cord increased at a corresponding rate. Here is exemplified an instance of long-continued enlargement of the nervous system by the regular development of immature cells, a method of growth most marked probably in those animals which increase in size so long as they live.

Volumes of the Largest Cell-bodies in the Ventral Horn of the Cervical Cord of Man (based on Kaiser's records of the mean diameters).

The volume 700μ^3, in the fetus of four weeks, is taken from His, and the figures represent multiples of that volume.

Subject.	Age.	Proportional volume of the cell-bodies 1=700μ^3.	Time interval.
Fetus	4 weeks	1	36 weeks.
"	20 "	17	
"	24 "	31	
"	28 "	67	
"	36 "	81	
Child at birth	—	124	15 years.
Boy at fifteen years	—	124	
Man, adult	—	160	15 "

It is believed that in this case the *new* cells and *new* fibres are not, strictly speaking, new morphological elements, but are the result of developmental changes taking place in the cells present in the system from an early period.

A distinction is thus to be made between cell-elements which, because they are not developed, are therefore not a part of the system already physiologically active, and those cells already organized together and which are fully functional. When, therefore, it is said that the cells of origin for the ventral root-fibres increase in number, the increase refers to the latter group, and not to the total number of elements of both kinds present in the cord. In other words, the number of cells appears to increase because the number of *developed* cells becomes greater.

In support of this suggestion the observations on the growth of the fibres in the roots of the frog's spinal nerves may be cited.[1] Hardesty found the greatest number of medullated fibres in the ventral roots, nearest the cord, and in the dorsal roots, nearest the spinal ganglion. Thus in each the greatest number was nearest the cells of origin, an arrangement which is most readily explained by assuming that some of the fibres had grown but a short distance from their cells of origin at the time the frog was killed.

On the other hand, Schiller[2] counted the number of nerve-fibres in the oculo-motor nerves of cats, and found but a very slight difference in this number between birth and maturity. So far, then, as this nerve is concerned, it is found in the cat to be nearly complete at the time of birth.

In man there are very few observations on the increase in the number of

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[1] Hardesty: *Journal of Comparative Neurology*, 1899, vol. ix.

[2] Schiller: *Comptes rendus de l'Académie des Sciences*, Paris, 1889.

functional nerve-cells with age. Kaiser,[1] as is shown in the accompanying table, found in man increasing numbers of large nerve-cells in the ventral horns of the spinal cord at the ages named:

Number of Developed Cells in the Cervical Enlargement of Man at Different Ages (*Kaiser*).

Age.	Number of Nerve-cells.
Fetus, 16 weeks	50,500
" 32 "	118,330
New-born child	104,270
Boy, 15 years	211,800
Male, adult	221,200

Here, as in the frog, the apparent increase must be looked upon as due to the gradual development of elements present from an early date. And it must be further remembered that in this case the cells thus maturing after birth probably belong in a large measure to the group of "central cells," the function of which is to increase the complexity of the pathways *within* the cord.

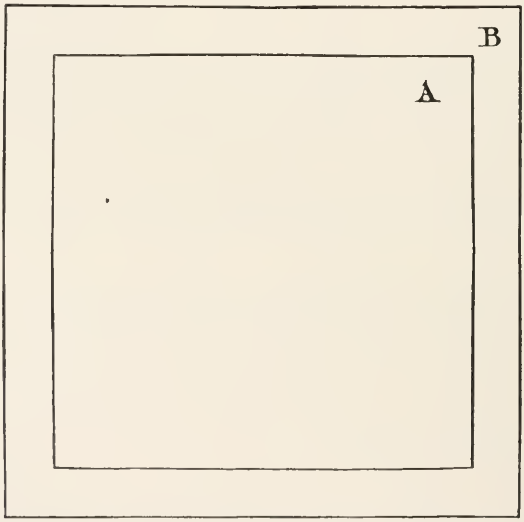

FIG. 119.—Diagram illustrating the extent of the cerebral cortex. The outer square (*B*) shows a surface approximately one-fiftieth of 2352 sq. cm. in extent; the inner square (*A*) has two-thirds of this area, and is the proportion of the cortex sunken in the fissures. 2352 sq. cm. are approximately the area of the entire cortex in a male brain weighing 1360 grams.

Increase in the Fibres of the Cortex.—The area of the cerebral cortex (see Fig. 119) varies according to several conditions, but in general the more voluminous the cerebral hemispheres the greater its extent. That which covers the walls of the sulci,—the sunken cortex—has in man about twice the extent of that directly exposed on the surface of the hemispheres.

In the cortex of the human cerebral hemispheres it has been shown by Vulpius[2] that the number of fibres in the different layers is greater in the

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[1] *Die Functionen der Ganglienzellen des Halsmarkes*, Haag, 1891.

[2] Vulpius: *Archiv für Psychiatrie und Nervenkrankheiten*, 1892.

thirty-third year than at earlier periods, but in old age this number is decreased. At exactly what age decrease sets in, is not to be determined from these observations. They show, simply, that in general the number of fibres was less at seventy-nine years than at thirty-three years.

In a similar way Kaes has shown[1] that the association fibres of the human cerebral cortex form three parallel systems. In general it is the deepest layer—*i. e.*, that farthest from the surface of each system—which first becomes medullated. The first fibres appear at about the fourth month of life in the deepest portion of the deepest layer. The middle system is the last to be completely medullated, this process continuing in it up to the forty-fifth year of life.

Passow[2] has shown that at maturity the cortex of the central gyri exhibits association fibres which increase in abundance as we pass from the great longitudinal fissure (leg area) toward the Sylvian fissure, these fibres being most abundant in the areas for the hand and fingers. On the other hand, in the central gyri of a child fifteen months of age, these fibres are equally abundant in these two localities. From this it appears that the differentiation takes place after the first year of life.

Significance of Medullation.—Two sorts of nerve-fibres are described—those with and those without a medullary sheath. Both have the power of isolated conduction, but in the peripheral system the non-medullated fibres are found in connection with the sympathetic system, where less specialized functions are carried on, and also in a large but varying degree in the central system. The wider significance of this difference in medullation is at the moment quite obscure.

The first suggestion, that absence of the medullary sheath is an immature condition which persists in various parts of the nervous system, brings us at once to the question of the physiological difference thus implied, but not explained.

It is known that the central system is at birth very imperfectly medullated, and the growth of these medullary sheaths must form a large part of the total increase in its bulk. In the mature nerve-fibre the axis-cylinder and the medullary sheath have nearly equal volumes, and therefore approximately equal weights. The medullated fibres form probably not less than 97 per cent.[3] of the total weight of the nerve-tissues composing the encephalon, and of this nearly one-half would be medullary substance.

Increase in the Mass of the Neurones.—The amount of this increase under various conditions has already been discussed, and been found to range between zero and fifty-thousand-fold (p. 176).

Number of Cells.—Any attempt to determine the entire number of nerve-cells, the bodies of which lie within the walls of the neural tube, must be open to many sources of error.

[1] Kaes: *Wiener med. Wochenschrift*, 1895, Nos. 41, 42; Kaes: *Jahrbüchern der Hamburg, Staats Krankenanstalten*, Jahrgang, 1893–94, Bd. iv.

[2] Passow: *Archiv für Psychiatrie*, Bd. 31, S. 859, 860.

[3] Thompson: *Journal of Comparative Anatomy*, 1899, vol. ix.; Donaldson: *Ibid.*, No. 2.

A careful study of the cortex[1] based on Hammarberg's records, gives 9200 million cell-bodies in this region alone. Considering the amount of gray matter present in the rest of the central system, an estimate of 13,000 million for the total number in the entire central nervous system is probably a conservative calculation.

From the foregoing facts, together with those bearing on the cell-elements, it is possible to get some conception of the growth-processes in the central system, and to see how they are due to an enlargement of the nerve-elements which have been formed at a very early stage in the life-history of the individual. In such enlargements the chief increase is due to the formation of the axones, and in them, in turn, about half the substance is represented by the medullary sheaths.

In all probability these sheaths are no exception to the rule according to which all parts of the body are variable, not only in their absolute, but also in their relative size, and therefore it is possible that the quantitative variation in this constituent is a very important factor in modifying the weight of the central system, perhaps accounting in some cases for the very heavy brains occasionally reported.

Change in Specific Gravity with Age.—During fetal life and at birth the percentage of water in the nerve-tissues is high, but becomes less at maturity. In white rats at birth the percentage of water for the encephalon is 89 per cent. and for the spinal cord 85.3 per cent. At maturity it is about 78 per cent. for the encephalon and 70.1 per cent. for the cord. This change is correlated in some measure with the development of the medullary substance.

For the gross physical changes which have thus been indicated as occurring during growth, an explanation is to be found in the changes affecting the constituent elements, and these have been set forth when describing the growth of the individual cells.

C. ORGANIZATION AND NUTRITION OF THE CENTRAL NERVOUS SYSTEM.

What is here meant by organization may be easily illustrated. When, for example, by later growth new tissue is added to the liver, or the skin is increased in area or a muscle enlarged, there is caused by the addition of new substance a change in the powers of these tissues, which is mainly quantitative. The larger organ exhibits the same capabilities that the smaller organ exhibited, but does so in a greater degree.

In the central nervous system, on the other hand, it appears that with growth the system becomes capable of new reactions in the sense that its various responses are controlled and directed by a larger number of incoming impulses, and thus the number, complexity, and refinement of the reactions are increased, and in this sense it really attains new powers.

With the change in the age of the central system there occurs from birth up to the prime of life, if we may judge from general reactions, an increase

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[1] Thompson: *Journal of Comparative Neurology*, 1899, vol. ix.

in this organization. This is maintained for a time, and then in old age it breaks down, at first gradually, and later rapidly. It becomes important, therefore, to examine the manner in which this organization is accomplished.

Organization in the Central System.—When first formed the cells composing the central system are completely separated from one another. In the mature nervous system the impulses, as has been pointed out, probably travel for the most part from the axones of one unit to the dendrites of another.

For organization the most important changes, however, are those affecting the cell outgrowths, both dendrites and axones. During growth both of these increase in the length of their main stems and of their respective branches. In picturing the approach of two elements within the central system the process is usually described as that of the outgrowth of the axone toward the dendrites or bodies of those cells which are destined to receive the impulse, but it must not be forgotten that the dendrites are also growing, and the question of the approximation of the branches of these latter to those of the axone depends in part on their own activities.

The conditions modifying this process are, however, obscure. It is evident that medullation outside of the central system is not necessary to the functional activity of a fibre, and therefore probably in the central system unmedullated fibres are also in many cases functional. Whatever may be the relation of the establishment of new pathways to the acquisition of medullary sheaths by the axone and its branches, it is also found that all fibres which when mature are medullated begin as unmedullated fibres, and that the increase in medullation throughout the central system is an index of the increase in organization. A consideration of the facts of growth in the layers of the cortex, for instance, will show them to be open to this interpretation.

Applying these ideas concerning organization to the three classes of cells, afferent, central, and efferent, which compose the nervous system, we find the following: In the central system the afferent cells contribute to organization by the multiplication of the collaterals. At the periphery the division of the branches of the axone increases the number of opportunities for excitation which such an element offers. These cells are, for the most part, without dendrites. Among the central cells all possible modes of growth are contributory; that is, the branches of both kinds add directly to the complexity of the central pathways. On the other hand, the efferent group contributes to this complexity almost solely by the formation of dendrites, the collaterals which come from the axones of these cells forming but an insignificant contribution. Not only, therefore, is organization in large part dependent on changes in the central cells by reason of their numerical preponderance, but also by reason of the fact that to them a multiplication of pathways both by elaboration of the axones and the dendrites is alone possible.

Defective Development.—In view of these facts, defective development in the nervous system may depend on failure in one or more of these several processes by which the system is organized, and it should be possible to correlate defective development involving mainly one set of elements with a distinct clinical picture. The results of defective development are not merely an absence of certain powers, but in some measure a diminution in the strength and range of those that remain (Hammarberg[1]).

Laboratory Animals.—The bearing of these facts on the conception which we form of the nervous systems of those animals commonly employed for laboratory experiments may be here mentioned. The frog, pigeon, rabbit, cat, and dog form a series in which the total mass of the central system increases from the beginning to the end of the series.

The number of cells in the largest system, that of the dog, is many times greater than that in the smallest, the frog; and it is probable that the others are in this respect intermediate. Organization is apparently more rapidly completed and more nearly simultaneous throughout the entire system in forms like the frog and pigeon, and also in these latter the organization is least elaborate. While the educability of the nervous system of the dog may depend on several conditions, the comparative slowness of organization is undoubtedly one of them, and a very important one. Where the organization is early established it is also simple, and thus portions of the system retain through life a greater capacity for acting alone. In selecting an animal, therefore, on which to make a series of experiments, these several facts must be kept in view, for the choice is by no means a matter of indifference.

Blood-supply.—For the general distribution of the blood-vessels in relation to the gross subdivision of the brain the student is referred to the works on anatomy. The finest network of vessels is, however, to be found where the cell-bodies are most densely congregated, and indeed the distinction between the masses of gray and white matter in the central system is as clearly marked by the relative closeness of the capillary network as in any other way (see p. 191). One result of this relation between the blood-supply and the cell-bodies which form the gray matter is a general arrangement of the vessels along the radii of the larger subdivisions of the brain, as the cerebral hemispheres and the cerebellum.

The conditions which control the circulation within the cranium and spinal canal are not exactly the same at all periods of life, but the variations occur in minor points only.

The studies of Huber[2] show that in the cat, dog, and rabbit at least, the vessels in the pia of the cerebral hemispheres are supplied with both medullated and unmedullated nerves. The former are probably sensory in function; the latter, possibly, vaso-motor. These latter nerves have been followed to arteries so small as to possess but two layers of muscle-cells, but were not traced by Huber to vessels actually penetrating the nervous substance of the hemispheres. von Kölliker, however, claims to have followed them even there.

These observations make the existence of a corresponding vaso-motor

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[1] Hammarberg: *Studien ueber Klinik und Pathologie der Idiotie nebst Untersuchungen ueber die normale Anatomie der Hirnrinde*, Upsala, 1895.

[2] *Journal of Comparative Neurology*, 1899, vol. ix. No. 1.

supply to the pial vessels in man probable. Nevertheless the efficiency of this vaso-motor mechanism does not appear to be great, since various authors fail to find physiological evidence for a local control of the arterioles.

The reactions of the central vessels are broadly those of a system of elastic tubes in a closed cavity. As a result, it is found that the *quantity* of blood in the central system is subject to *very slight variations only*. A rise in the arterial pressure causes a more *rapid* flow of the blood through the encephalon. It also causes a rise in the venous pressure, and with this a corresponding rise in the intracranial pressure, the last two varying in the same sense and to the same extent.[1]

The flow through the central system is subject to the influence of gravity, and takes place the more readily the more the resistance is diminished.[2] The principal controlling mechanism is in the splanchnic area. According to the condition of the vessels in this area, the intracranial blood-pressure varies.

It is to be noted in passing that when a person lying on a table is balanced on a transverse axis, this axis is about 8.77 cm. to the cephalic side of the line which joins the heads of the femurs.[3] This leaves, of course, the splanchnic area mainly on the cephalic side of this axis, and hence any inflow of blood from the extremities would tend to make the head end of the person thus balanced dip down. This dip will occur even when the splanchnic area alone is filled, and hence the dipping as such would not *necessarily* indicate an increase in the quantity of blood in the encephalon.

In the adult the cranial cavity is almost rigidly closed. There is an opportunity for the escape of a small quantity of cerebro-spinal fluid through the foramen magnum into the vertebral canal. When, as the result of increased arterial pressure, the brain has distended so as to drive out the subdural fluid, the brain is forced against the walls of the cranium and blocks the outflow into the spinal canal. On the other hand, it has been found that if a mass displacing from 2 to 3 c.c. be introduced into the subdural space of a dog, the brain will adjust itself without rise of intracranial pressure. If in this case the volume of the mass introduced is increased, there follows a rise of intracranial pressure, and this rise in every instance tends to impede the circulation through the brain. While the fontanelles are open the brain normally pulsates, and we recognize in its variations in volume all the different variations in blood-pressure with which we are familiar. The pulsation of the brain is doubtless an important aid to the movements of the fluids within, and hence tends to facilitate nutrition during the earlier stages of growth.

In pathological cases where the cranial wall has been destroyed there is a similiar variation in volume to be observed in the adult, and it is possible that the beneficial effects which in so many instances follow trephining of

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[1] Howell: *American Journal of Physiology*, 1898, i. No. 1.

[2] Hill: *Journal of Physiology*, 1895, vol. xviii.

[3] W. und Ed. Weber: *Mechanik der menschlichen Gehwerkzeuge*, 1836.

the skull may depend upon this mechanical release. Of course, in cases with a defective skull-wall an increase in arterial pressure causes a more decided increase in the *volume* of blood in the brain ; this, however, is much more marked than it would be under ordinary conditions, and is not to be regarded as the main effect, which is an increase in the quantity of the blood passed through the central system in a unit of time. Mosso[1] has found the temperature of the blood coming from the brain (dog's) slightly higher than that of the rectum and of the arterial blood. The differences are very small, but he draws the conclusion that the metabolic processes in the brain are sufficiently intense to *raise* the temperature of the blood passing through it.

As against the intensity of the metabolism in the central system, it has been observed that blood taken from the torcular Herophili of the dog was intermediate in gaseous content between arterial blood and that taken from the femoral vein, thus indicating that the arterial exchange was less intense in the brain than in the muscles of the leg. The following is a condensed statement of the figures :

Percentages of Oxygen and Carbonic Acid in various Samples of Dogs' Blood (Hill).[2]

Average of 52 arterial samples	CO_2 . .	37.64	per cent.
	O . .	18.25	"
Average of 42 torcular samples	CO_2 . .	41.65	"
	O . .	13.49	"
Average of 28 femoral vein samples	CO_2 . .	45.75	"
	O . .	6.34	"

The absolute quantity of the blood in the brain and cord is certainly small ; if we may judge from the observations on animals, it is not more than 1 per cent. of the entire blood in the body. It is to remembered, however, that the cell-bodies, which alone are well supplied with blood, probably represent less than 2 per cent. of the entire encephalic mass.

With general rise and fall of pressure elsewhere, there is a rise and a fall of pressure within the central system. During the first phases of mental activity blood is withdrawn from the limbs; the blood thus withdrawn can be shown to pass toward the trunk and head, for when a person lying on a horizontal table supported at the centre on a transverse knife-edge is just balanced, then increased activity of the cerebral centres causes the head to dip down (Mosso), and if the skull-wall is defective the brain is seen to swell.

In the later stages of fatigue the blood-supply to the nerve-centres diminishes owing to a decrease in force of the heart-beat and the tonicity of the splanchnic vessels, so that the brain in birds exhausted by a long flight has been found by Mosso to be in a high degree anæmic. There is much reason to think that in man a similar reaction occurs.

The study of the cerebral circulation in the case of those in whom the skull-wall is at some point deficient shows a bulging of the skin over the

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[1] *Die Temperatur des Gehirns*, Leipzig, 1894.

[2] *Journal of Physiology*, 1895, vol. xviii.

opening into the cranial cavity as a result of mental effort or emotion. In the normal adult this bulging cannot, of course, occur to anything like such an extent, and the space for the arterial blood must be gained both by driving out the blood from the cerebral veins within the cranium and through the expulsion of the subdural fluid.

Influence of Glands.—In the growth of the nervous system it is not only the quantity, but the peculiar qualities of the blood that are important, and among the various glands the activity of which is so necessary for the growth of the nervous, as well as the other systems, and is also needed for its full maintenance, the thyroid appears as very important. In sporadic cretinism, associated as it is with atrophy of the thyroid, the feeding of sheep's thyroids has produced remarkable growth-changes in all parts of the body—the nervous system included.

At the same time, experimental extirpation of the thyroid is followed by destructive changes in the central system, caused by disturbances in its nutrition. The future will doubtless reveal other forms of internal secretion which also have a significance for the activity of the central system.

Starvation.—In starving animals the nervous system loses but very little in weight.[1] This small loss is most striking in view of the fact that extensive histological changes occur in the cell-bodies. However, if we consider the cell-bodies as the part mainly affected during starvation, then the small mass of the cell-bodies would go far toward explaining the result, but it does not explain why the myeline is so resistant.

Fatigue.—The histological basis of fatigue as expressed by the changes in the individual cells, has already been discussed. The fatigue of the system as a whole is but the expression of fatigue in large numbers of its elements, but the manner in which the changes show themselves is somewhat complicated.

When the attempt is made to raise a weight by the voluntary contractions of the muscles of the index finger at regular intervals, say once a second, it is found that if the weight be heavy the power of the finger decreases, and the weight soon ceases to be lifted as high as at first. Finally a point is reached when the voluntary effort produces little or no elevation of the weight. If, however, despite this failure, the effort is still made at regular intervals, it happens, in some persons, that this power returns gradually, and a few seconds later the contractions are very nearly as high as at the beginning of the experiment (Mosso). This phenomenon may repeat itself many times, giving a record formed by groups of contractions most extensive near the centre of each group, these latter being separated by portions of the curve in which the contractions are very small or wanting (see Fig. 120). (See General Physiology of Nerve and Muscle, p. 135.)

Daily Rhythms.—Within the cycle of the astronomical day the progress of events leading to fatigue is not a steady one. Lombard[2] found that if the capacity for voluntary effort was measured by the amount of work which

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[1] Voit: *Zeitschrift für Biologie*, 1894, Bd. xxx.

[2] *Journal of Physiology*, 1892, vol. xiii.

could be done by voluntarily contracting the flexor muscles of the index finger *before the first failure* to respond to a voluntary stimulus appeared, then the curve expressing this capacity for voluntary work throughout the day was represented as in Fig. 121. Briefly, the curve shows two maxima, at 10 P. M., and 10 A. M., with two minima midway between them. In general the immediate effect of taking food is to increase the work done by the subject. Alcohol has the same effect, while smoking produces a decrease.

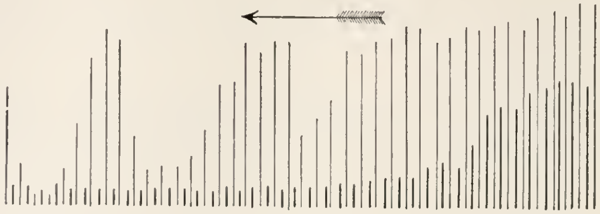

FIG. 120.—A record of the extent of the flexions of the forefinger lifting a weight at regular intervals. The light lines are those for the voluntary contraction; the heavy lines, those for contractions following the direct stimulation of the flexor muscles by electricity. In the former there are periods, in the latter none. The arrow shows the direction in which the record is to be read (Lombard).

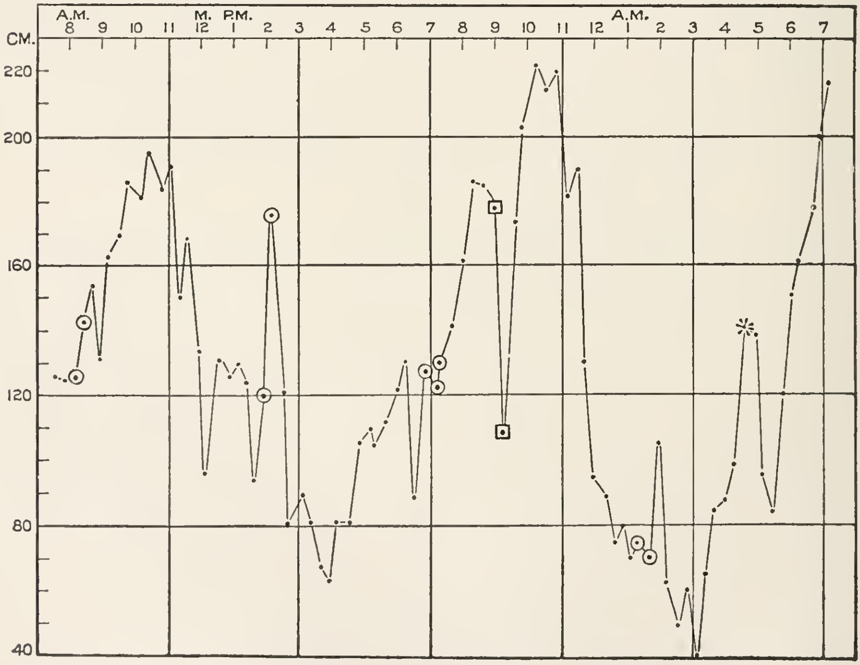

FIG. 121.—Showing at each hour of the day and night how many centimeters a weight of 3000 grams could be raised by repeated voluntary contractions of the forefinger before fatigue sets in. The curve is highest at 10 to 11 A. M., and 10 to 11 P. M.; lowest, 3 to 4 P. M., and 3 to 4 A. M. Circle with dots, observation made just after taking food; square with dot, smoking; *, work done 8 minutes after drinking 15 c.c. of whisky (Lombard).

Further, from day to day this capacity for work is influenced by a number of external conditions—temperature, barometric pressure, etc.

Time Taken in Central Processes.—All processes in the nervous system take time, and are for the most part easy to measure. The rate of the nerve-impulse has already been given. When, however, it passes from one element to another, the delay is even more marked, and it is plausible to assume that this detention occurs at the juncture of the elements. Thus in those parts of the central system where the cell-elements and also the cell-junctions are most numerous, the time taken is longest.

Fig. 122 shows this very well. Between the middle of the cerebral hemisphere and the optic lobes, although the distance is short, the impulse takes twice as long to travel as between the bulb and the lumbar enlargement. When this time is measured in the conscious individual it is, of course, open to a long series of modifying conditions, and these appear to be in part the same conditions which modify the muscular endurance of the individual at different portions of the day. Thus it has been determined that the speed with which reactions can be made as indicated by the reaction time, is subject to variations, and does not steadily decrease from the morning to the evening.

FIG. 122.—To show the rate at which impulses pass through the nervous system of a frog. At the extreme left the vertical has the value of 0.5 second and the other verticals are compared with it; thus between the cerebrum and the optic lobe requires about 0.25 second; between the bulb and the lumbar enlargement a greater distance—only about half the time; and for the still greater distance represented by the length of the sciatic nerve even less time is needed (Exner).

It has been the purpose of the paragraphs just preceding to indicate that through the day it is not possible to demonstrate a steady decline of power in the nervous system. We begin the morning, to be sure, feeling fresh, and are fagged in the evening, but the course by which this condition has been attained is not a simple or direct one.

D. SLEEP.

Conditions Favoring Sleep.—To recover from fatigue sleep is required. The prime condition favoring sleep is the diminution of nerve-impulses passing through the central system. This is accomplished in two ways. In the first instance it is usual to reduce all incoming stimuli to a minimum. This is most directly under our own control. On the other hand, the permeability of the nervous system and the intensity with which it responds are decreased as the result of the beginning fatigue. How these conditions are brought about has been a matter of much speculation and some experiment.

The parts played by the sensory and that by the central cells vary somewhat at different times of life, for impulses are much less widely diffused in early years than at maturity. Moreover, in childhood the amount of stored material is small, large at maturity, and small again in old age, and this holds true for all the groups of cells. Hence the cells would, by reason of this fact, have the greatest capability for work in the middle period. Between childhood and old age there is, however, this difference—that while in the former the non-available substances in the cell are developing, not yet having matured, those in the latter have in some way become permanently useless. The degree to which the blood-supply can be controlled varies with age, and the amounts of substance capable of yielding energy at various periods of life are different; so that, considering these factors alone, though there are probably others, it may be easily appreciated that the sleep of childhood, maturity, and old age should be quite distinguishable.

Cause of Sleep.—It is recognized that local exercise is capable of producing general fatigue, and the fatigued portions give rise to afferent impulses which, reaching the central system, cause some of the sensations of fatigue; moreover, the active tissues (nerve-cells and muscles) yield as the result of their activity some by-product which is carried by the blood through the central system and becomes the chief cause of sleep. It has been shown by Mosso that if a dog be thoroughly fatigued, giving all the signs of exhaustion, and the blood from this dog be transfused to one that has been at rest, then after the transfusion, the dog which has received the blood from the exhausted animal will exhibit the symptoms of fatigue in full force. The inference is that from the tired animal certain by-products have thus been transferred, and that these are responsible for the reactions. We know, further, that we can distinguish in ourselves different forms of the feeling of fatigue, and that the sensations which follow the prolonged exercise of the muscular system differ from those following the exercise of the higher nerve-centres.

Two things appear as highly probable: First, that there is a wide individual variation in the condition designated as normal sleep. Second, that normal sleep is the result of several sets of influences which need not necessarily be active to the same degree during each period of sleep. Excluding the factor represented by diminution of the external stimuli, sleep has been attributed more or less exclusively to one of the three following influences:

1. *Chemical Influences.*—The theories emphasizing the chemical factor point out that during the normal activity of the body there are formed and taken up by the blood substances which may directly diminish the activity of the nerve-cells and directly or reflexly affect the circulation so as to diminish the supply of blood to the brain, and especially to the cerebral cortex.

2. *Circulatory Influences.*—The vaso-motor theories look upon the changes in the blood-supply as a prime cause of sleep; these changes to be referred in the last instance to the fatigue of the vaso-motor centre in the bulb.

3. *Histological Influences.*—These are made dependent on the shrinkage of nerve-cells during fatigue, the retraction of the dendrites of the cortical cells interrupting the nerve-pathways, or the mechanical separation of the nerve-elements through the intrusion of the neuroglia-cells between them (Cajal). The vaso-motor and chemical theories combined are at present most

worthy of attention, and Howell,[1] after carefully reviewing the several theories of sleep, emphasizes the fatigue of the vaso-motor centre in the bulb as the important cause of the diminished blood-supply to the brain, this fatigue in turn being caused by the continuous activity of this centre during the waking hours.[2]

Cessation of stimuli, decreased responsiveness of the active tissues, a change in the composition of the blood, and a diminution of the blood-supply to the brain are the preliminaries to sleep.

A condition superficially resembling sleep can be induced in various ways. Removal of all external stimuli, extreme cold, anæsthetics, hypnotic suggestion, compression of the carotids, a blow on the head, loss of blood, all produce a state of unconsciousness which, in so far, has the similitude of sleep. These conditions produce this state, however, by mechanically decreasing the blood-supply or cutting off the peripheral stimuli.

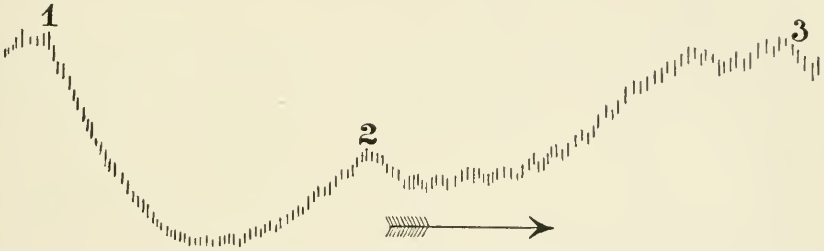

FIG. 123.—Plethysmographic record taken from the arm of a person sleeping in the laboratory. A fall in the curve indicates a decrease in the volume of the arm. The curve is to be read in the direction of the arrow. 1. The night watchman entering the laboratory, waking the subject, who shortly fell asleep again; 2, the watchman spoke; 3, watchman went out; these changes (2 and 3) occurred without awakening the subject (from experiments made by Messrs. Bardeen and Nichols, Johns Hopkins Medical School).

Normal sleep is tested by the fact that during its progress the changes that occur in the central system are recuperative, whereas this feature may be almost absent in the states which nearly resemble it.

Condition of the System During Sleep.—It appears that during sleep the capacity of the central system to react is never lost. Were such the case it would not be possible to awaken the sleeper. The reactions most depressed during sleep are those which require the full activity of the cerebral cortex for their occurrence. Conversely, it is the spinal cord which is least affected. Moreover, the sleeping person is far more responsive to stimuli from without than at first might be thought. The close relations between dreams and external stimuli have been recognized, and plethysmographic studies show still more clearly how the matter stands.

It was found that when a subject fell asleep with the arm in a plethysmograph, various stimuli which did not waken the sleeper still served to cause a diminution in the volume of the arm which was certainly due to the

[1] Howell: *Journal of Experimental Medicine*, 1897.

[2] De Manaceïne: "Sleep: Its Physiology, Pathology, Hygiene, and Psychology," *Contemporary Science Series*, London, 1897.

withdrawal of blood from it, the blood supplied to the brain being probably at the same time increased (see Fig. 123).

This experiment shows that during sleep the nervous system is capable of reactions which are not remembered in any way, but which naturally form a feature of the condition intermediate between full consciousness and deep slumber.

The depth of sleep as determined by the strength of the stimulus necessary to elicit an efficient response has been measured. The stimulus in these experiments was the sound caused by the fall of a ball upon a plate, and the measure was the height from which the ball must fall in order to produce a sound loud enough to awaken a sleeping person. The results of the observations are shown in Fig. 124.

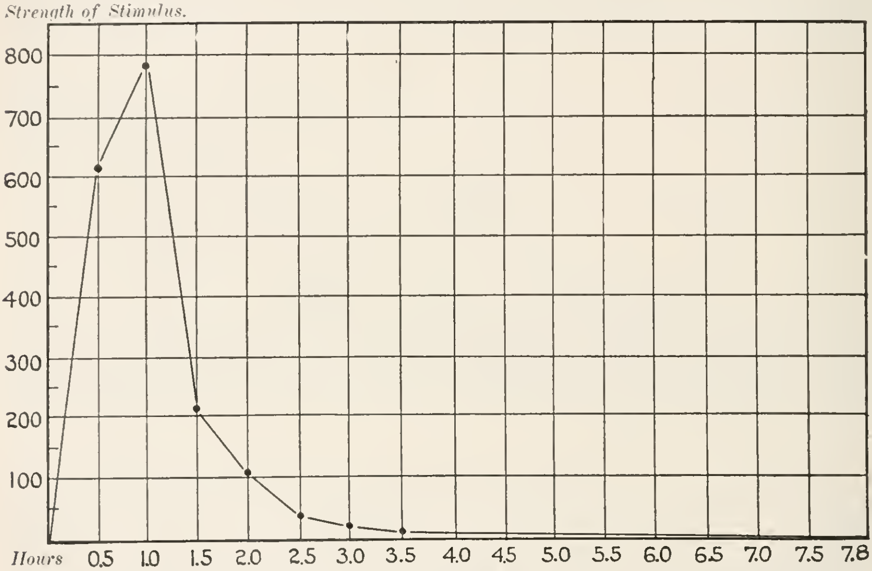

FIG. 124.—Curve illustrating the strength of an auditory stimulus (a ball falling from a height) necessary to waken a sleeping person. The hours marked below. The tests were made at half-hour intervals. The curve indicates that the distance through which the ball required to be dropped increased during the first hour, and then diminished, at first very rapidly, then slowly (Kolschütter).

It is seen from this that the period of deep slumber is short, less than two hours; and is followed by a long period, that of an average night's rest, during which a comparatively slight stimulus is sufficient to awaken. A somewhat different curve has been more recently obtained by Mönninghoff and Piesbergen.[1]

It is evident that the effectiveness of such a stimulus is, however, no measure of the recuperative processes in the central system. Repair is by no means accomplished during the interval of deep sleep, and experience has shown, as in the case of persons undertaking to walk a thousand miles in one thousand hours that although such an arrangement left the subject with two-

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[1] *Zeitschrift für Biologie*, 1893, Bd. xix.

thirds of the total time for rest and refreshment, yet the feat was most difficult to accomplish by reason of the discontinuity in the sleep.

The changes leading to recuperation needed longer periods than those permitted by the conditions of the experiment.

Loss of Sleep.—Loss of sleep is more damaging to the organism as a whole than is starvation. It has been found (Manaceïne) that in young dogs which can recover from starvation extending over twenty days, loss of sleep for five days or more was fatal. Toward the end of such a period the body-temperature may fall as much as 8° C. below the normal and the reflexes disappear. The red-blood-corpuscles are first diminished in number; to be finally increased during the last two days, when the animal refuses food. The most widespread change in the tissues is a fatty degeneration, and in the nervous system there were found capillary hemorrhages in the cerebral hemispheres, the spinal cord appearing abnormally dry and anæmic.

Patrick and Gilbert[1] have studied the effects of loss of sleep in man (three subjects, young men, observed during ninety hours without sleep). All the subjects gained slightly in weight during the period, but lost this excess in the course of the first sleep following the experiment. The excretion of nitrogen and phosphoric acid was increased during the period, the increase being relatively greater in the case of the phosphoric acid. There was a marked tendency to a decrease in the pulse-rate, and some tendency for the body-temperature to fall. During these ninety hours the subjects were tested at intervals of six hours (the tests required some two hours on each occasion), to determine variations in the muscular and mental powers.

In brief, it may be said that most tests revealed a loss, which early appeared in the reactions of the muscular system, and later in those of the nervous system. In the test for the acuteness of vision (measured by the distance at which the subject could read a printed page illuminated by the light of one standard candle at a distance of 25 cm.) there was, however, an *increase* in capability in *all* the subjects. At the end of the experiment a small number of hours of sleep in excess of that customarily taken appeared to bring about a complete restoration of the subject. The disproportion between this amount of extra sleep and the amount lost during the period of experiment is noted by the authors, though it still lacks satisfactory explanation.

E. OLD AGE OF THE CENTRAL SYSTEM.

Metabolism in the Nerve-cells.—Connected closely with fatigue are those alterations both of the constituent nerve-cells and of the entire system found in old age. The picture of the changes in the living cells is that of anabolic and catabolic processes always going on, but varying in their absolute and relative intensity according to several conditions. Of these conditions one of the most important is the age of the individual. In youth and during the growing period of life the anabolic changes appear within the daily cycle of activity and repose to overbalance the katabolic, the total expenditure of

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[1] Patrick and Gilbert: *Psychological Review*, 1896, vol. iii. No. 5.

energy increasing toward maturity. During middle life the two processes are more nearly in equilibrium, though the total expenditure of energy is probably greatest then ; and finally in old age the total expenditure of energy diminishes, while at the same time the anabolic processes become less and less competent to repair the waste. The question why in the nervous system the energies wane with advanced age is but the obverse of the question why they wax during the growing period. The essential nature of these changes is in both instances equally obscure.

Decrease in Weight of the Brain.—Between the fiftieth and sixtieth years of life there is a decrease in the bulk of the encephalon in those persons belonging to the classes from which the greater number of the records have been obtained. So far as can be seen from the present records, there is no marked change in the proportional development of the encephalon in old age, though the loss appears to be slightly greater in the cerebral hemispheres than in the other portions.

Changes in the Encephalon.—The thickness of the cerebral cortex diminishes in harmony with the shrinkage of the entire system. In large measure this must depend on the loss of volume in the various fibre-systems, which, according to the observations of Vulpius, show a senile decrease in the number of fibres composing them. This decrease is more marked in the motor than in the sensory areas. The time at which it commences cannot, however, be accurately stated, owing to the small number of records after the thirty-third year. Where records have been made between this and the seventy-ninth year it appears that there is no decided diminution until after the fiftieth year, though at the seventy-ninth year the decrease is clearly shown. Engel has shown that the branches of the arbor vitæ of the human cerebellum decrease in size and number in old age.[1]

Changes in the Cerebellum.—In the case of a man dying of old age (Hodge) some cells in the cerebellum were found shrunken and others (cells of Purkinje) had completely disappeared. In the antennary ganglion of bees a very striking difference appears between those dying of old age and the adult just emerged from its larval skin. These changes are comparable with those described in mammals, and it further appears that in passing from the youngest to the oldest forms cells have disappeared from the ganglia, and that in the young form of the bee there are some twenty-nine cells present for each one found at a later period.

To the anatomy of the human nervous system in old age contributions have been made by studies on the pathological anatomy of paralysis agitans.[2]

In subjects suffering from this affection the bodies of the nerve-cells are shrunken, pigmented, and show in some cases a granular degeneration ; the fibres in part are atrophied and degenerated ; the supporting tissues increase, and the walls of the small blood-vessels are thickened. These changes have been found principally in the spinal cord, being most marked in the lumbar

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[1] Engel: *Wiener medicinische Wochenschrift*, 1863.

[2] Ketcher: *Zeitschrift für Heilkunde*, 1892; Redlich: *Jahrbüch für Psychiatrie*, 1893.

region. But the cords of aged persons who do not exhibit the symptoms of paralysis agitans show similar changes, though usually they are not so evident, and hence the pathological anatomy of this disease resolves itself into a somewhat premature and excessive senility of the central system.

Shrinkage, decay, and destruction mark the progress of senescence, and the nervous system as a whole becomes less vigorous in its responses, less capable of repair or extra strain, and less permeable to the nervous impulses that fall upon it; and it thus breaks down, not into the disconnected elements of the fetus, but into groups of elements, so that its capacities are lost in a fragmentary and uneven way.

III. THE SPECIAL SENSES.

A. Vision.

The Physiology of Vision.—The eye is the organ by means of which certain vibrations of the luminiferous ether are enabled to affect our consciousness, producing the sensation which we call "light." Hence the essential part of an organ of vision is a substance or an apparatus which, on the one hand, is of a nature to be stimulated by waves of light, and, on the other, is so connected with a nerve that its activity causes nerve-impulses to be transmitted to the nerve-centres. Any animal in which a portion of the ectoderm is thus differentiated and connected may be said to possess an eye—*i. e.* an organ through which the animal may consciously or unconsciously react to the existence of light around it.[1] But the human eye, as well as that of all the higher animals, not only informs us of the existence of light, but enables us to form correct ideas of the direction from which the light comes and of the form, color, and distance of the luminous body. To accomplish this result the substance sensitive to light must form a part of a complicated piece of apparatus capable of very varied adjustments. The eye is, in other words, an optical instrument, and its description, like that of all optical instruments, includes a consideration of its mechanical adjustments and of its refracting media.

Mechanical Movements.—The first point to be observed in studying the movements of the eye is that they are essentially those of a ball-and-socket joint, the globe of the eye revolving freely in the socket formed by the capsule of Tenon through a horizontal angle of almost 88° and a vertical angle of about 80°. The centre of rotation of the eye (which is not, however, an absolutely fixed point) does not coincide with the centre of the eyeball, but lies a little behind it. It is rather farther forward in hypermetropic than in myopic eyes. The movements of the eye, especially those in a horizontal direction, are supplemented by the movements of the head upon the shoulders. The combined eye and head movements are in most persons sufficiently extensive to enable the individual, without any movement of the body, to receive upon the lateral portion of the retina the image of an object directly behind his back. The rotation of the eye in the socket is of course easiest and most extensive when the eyeball has an approximately spherical shape, as in the normal or emmetropic eye. When the antero-posterior diameter is very much longer than those

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[1] In certain of the lower orders of animals no local differentiations seem to have occurred, and the whole surface of the body appears to be obscurely sensitive to light. See Nagel: *Der Lichtsinn augenloser Thiere*, Jena, 1896.

at right angles to it, as in extremely myopic or short-sighted eyes, the rotation of the eyeball may be considerably limited in its extent. In addition to the movements of rotation round a centre situated in the axis of vision, the eyeball may be moved forward and backward in the socket to the extent of about one millimeter. This movement may be observed whenever the eyelids are widely opened, and is supposed to be effected by the simultaneous contraction of both the oblique muscles. A slight lateral movement has also been described.

The movements of the eye will be best understood when considered as referred to three axes at right angles to each other and passing through the centre of rotation of the eye. The first of these axes, which may be called the longitudinal axis, is best described as coinciding with the axis of vision when, with head erect, we look straight forward to the distant horizon; the second, or transverse, axis is defined as a line passing through the centres of rotation of the two eyes; and the third, or vertical, axis is a vertical line necessarily perpendicular to the other two and also passing through the centre of rotation. When the axis of vision coincides with the longitudinal axis, the eye is said to be in the *primary position.* When it moves from the primary position by revolving around either the transverse or the vertical axis, it is said to assume *secondary positions.* All other positions are called *tertiary* positions, and are reached from the primary position by rotation round an axis which lies in the same plane as the vertical and horizontal axis—*i. e.* in the "equatorial plane" of the eye. When the eye passes from a secondary to a tertiary position, or from one tertiary position to another, the position assumed by the eye is identical with that which it would have had if it had reached it from the primary position by rotation round an axis in the equatorial plane. In other words, every direction of the axis of vision is associated with a fixed position of the whole eye—a condition of the greatest importance for the easy and correct use of the eyes. A rotation of the eye round its antero-posterior axis takes place in connection with certain movements, but authorities differ with regard to the direction and amount of this rotation.

Muscles of the Eye.—The muscles of the eye are six in number—viz: the superior, inferior, internal and external recti, and the superior and inferior oblique. This apparent superfluity of muscles (for four muscles would suffice to turn the eye in any desired direction) is probably of advantage in reducing the amount of muscular exertion required to put the eye into any given position, and thus facilitating the recognition of slight differences of direction, for, according to Fechner's psycho-physic law the smallest perceptible difference in a sensation is proportionate to the total amount of the sensation. Hence if the eye can be brought into a given position by a slight muscular effort, a change from that position will be more easily perceived than if a powerful effort were necessary.

Each of the eye-muscles, acting singly, tends to rotate the eye round an axis which may be called the axis of rotation of that muscle. Now, none of the muscles have axes of rotation lying exactly in the equator of the eye—*i. e.* in a plane passing through the centre of rotation perpendicular to the axis of vision.[1] But all movements of the eye from the primary position take place, as we have seen, round an axis lying in this plane. Hence all such movements must be produced by more than one muscle, and this circumstance also is probably of advantage in estimating the extent and direction of the movement. In this connection it is interesting to note that the eye-muscles have an exceptionally abundant nerve-supply—a fact which it is natural to associate with their power of extremely delicate adjustment. It has been found by actual count that in the muscles of the human eye each nerve-fibre supplies only two or three muscle-fibres, while in the muscles of the limbs the ratio is as high as 1 to 40–125.[2]

Although each eye has its own supply of muscles and nerves, yet the two eyes are not independent of each other in their movements. The nature of their connections with the nerve-centres is such that only those movements are, as a rule, possible in which both axes of vision remain in the same plane. This condition being fulfilled, the eyes may be together directed to any desired point above, below, or at either side of the observer. The axes may also be converged, as is indeed necessary in looking at near objects, and to facilitate this convergence the internal recti muscles are inserted nearer to the cornea than the other muscles of the eye. Though in the ordinary use of the eyes there is never any occasion to diverge the axes of vision, yet most persons are able to effect a divergence of about four degrees, as shown by their power to overcome the tendency to double vision produced by holding a prism in front of one of the eyes. The nervous mechanism through which this remarkable co-ordination of the muscles of the two eyes is effected, and their motions limited to those which are useful in binocular vision, is not completely understood, but it is supposed to have its seat in part in the tubercula quadrigemina, in connection with the nuclei of origin of the third, fourth, and sixth cranial nerves. Its disturbance by disease, alcoholic intoxication, etc. causes strabismus, confusion, dizziness, and double vision.

A nerve termination sensitive to light, and so arranged that it can be turned in different directions, is sufficient to give information of the direction from which the light comes, for the contraction of the various eye-muscles indicates, through the nerves of muscular sense, the position into which the eye is normally brought in order to best receive the luminous rays, or, in other words, the direction of the luminous body. The eye, however, informs us not only of the direction, but of the form of the object from which the light proceeds; and to understand how this is effected it will be necessary to consider the refracting media of the eye by means of which an optical image of the luminous object is thrown upon the expanded termination of the optic nerve—viz. the retina.

Dioptric Apparatus of the Eye.—For the better comprehension of this portion of the subject a few definitions in elementary optics may be given. A

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[1] The axes of rotation of the internal and external recti, however, deviate but slightly from the equatorial plane.

[2] P. Tergast: "Ueber das Verhältniss von Nerven und Muskeln," *Archiv für mikr. Anat.*, ix. 36–46.

dioptric system in its simplest form consists of two adjacent media which have different indices of refraction and whose surface of separation is the segment of a sphere. A line joining the middle of the segment with the centre of the sphere and prolonged in either direction is called the axis of the system. Let the line $A P B$ in Figure 125 represent in section such a spherical surface the centre of which is at N, the rarer medium being to the left and the denser medium to the right of the line. Any ray of light which, in passing from the rarer to the denser medium, is perpendicular to the spherical surface will be unchanged in its direction—*i. e.* will undergo no refraction. Such rays are represented by the lines $O P$, $M D$, and $M' E$. If a pencil of rays having its origin in the rarer medium at any point in the axis falls upon the spherical surface, there will be one ray—viz. the one which coincides with the axis of the system, which will pass into the second medium unchanged in its direction. This ray is called the *principal ray* ($O P$), and its point of intersection (P) with the spherical surface is called the *principal point.* The centre of the sphere (N) through which the principal ray necessarily passes is called the *nodal point.* All the other rays in the pencil are refracted toward the principal ray by an amount which depends, for a given radius of curvature, upon the difference in the refractive power of the media, or, in other words, upon the retardation of light in passing from one medium to the other. If the incident rays have their origin at a point infinitely distant on the axis—*i. e.* if they are parallel to each other—they will all be refracted to a point behind the spherical surface known

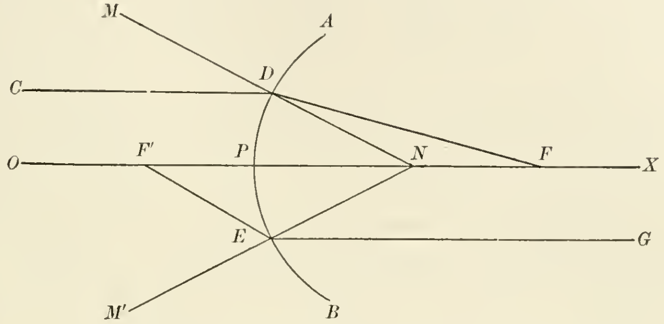

FIG. 125.—Diagram of simple optical system (after Foster).

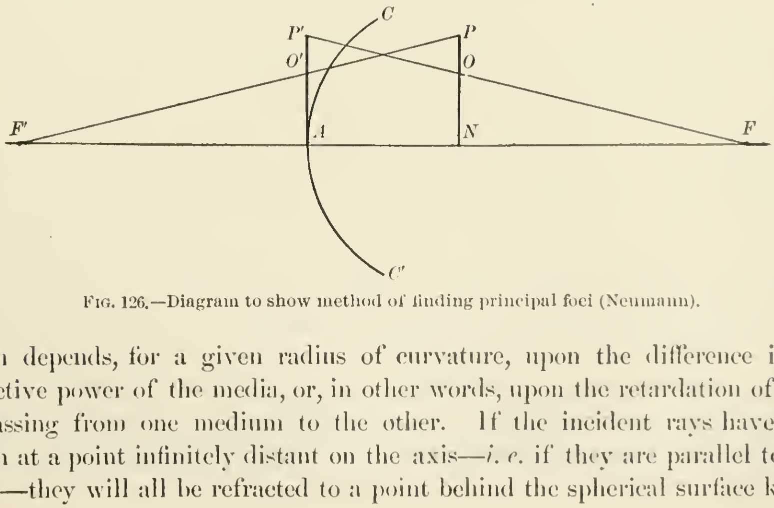

FIG. 126.—Diagram to show method of finding principal foci (Neumann).

as the *principal focus*, *F*. There is another *principal focus* (*F′*) in front of the spherical surface—viz. the point from which diverging incident rays will be refracted into parallelism on passing the spherical surface, or, in other words, the point at which parallel rays coming from the opposite direction will be brought to a focus. The position of these two principal foci may be determined by the construction shown in Figure 126. Let *C A C′* represent a section of a spherical refracting surface with the axis *A N*, the nodal point *N*, and the principal point *A*. The problem is to find the foci of rays parallel to the axis. Erect perpendiculars at *A* and *N*. Set off on each perpendicular distances *No*, *Np*, *A o′*, *A p′* proportionate to the rapidity of light in the two media (*e. g.* 2 : 3). The points where the lines *p′ o* and *p o′* prolonged will cut the axis are the two principal foci *F* and *F′*—*i. e.* the points at which parallel rays coming from either direction are brought to a focus after passing the spherical refracting surface. If the rays are not parallel, but diverging—*i. e.* coming from an object at a finite distance—the point where the rays will be brought to a focus, or, in other words, the point where the optical image of the luminous object will be formed, may be determined by a construction which combines any two of the three rays whose course is given in the manner above described. Thus in Figure 127 let *A N* be the axis, and *F* and *F′* the principal foci of the spherical refracting surface *C A C′*, with a nodal point at *N*. Let *B* be the origin of a pencil of rays the focus of which is to be determined. Draw the line *B C* representing the course of an incident ray parallel to the axis. This ray will necessarily be refracted through the focus *F*, its course being represented by the line *C F* and its prolongation. Similarly, the incident ray passing through the focus *F′* and striking the spherical surface at *C′* will, after refraction, be parallel to the axis—*i. e.* it will have the direction *C′ b*. The principal ray of the pencil will of course pass through the spherical surface and the nodal point *N* without change of direction. These three rays will come together at the same point *b*, the position of which may be determined by constructing the course of any two of the three. The points *B* and *b* are called conjugate foci, and are related to each other in such a way that an optical image is formed at one point of a luminous object situated at the other. When the rays of light pass through several refracting surfaces in succession their course may be determined by separate calculations for each surface, a process which is much simplified when the surfaces are "centred"—*i. e.* have their centres of curvature lying in the same axis, as is approximately the case in the eye.

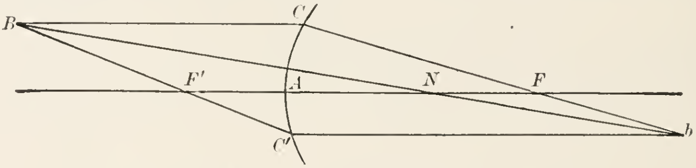

FIG. 127.—Diagram to show method of finding conjugate foci.

Refracting Media of the Eye.—Rays of light in passing through the eye penetrate seven different media and are refracted at seven surfaces. The media are as follows: layer of tears, cornea, aqueous humor, anterior capsule of lens, lens, posterior capsule of lens, vitreous humor. The surfaces are those which separate the successive media from each other and that which separates the tear layer from the air. For purposes of practical calculation the number of surfaces and media may be reduced to three. In the first place, the layer of tears which moistens the surface of the cornea has the same index of refraction as the aqueous humor. Hence the index of refraction of the cornea may be left out of account, since, having practically parallel surfaces and being bounded on both sides by substances having the same index of refraction, it does not influence the direction of rays of light passing through it. For this same reason objects seen obliquely through a window appear in their true direction, the refraction of the rays of light on entering the glass being equal in amount and opposite in direction to that which occurs in leaving it. For purposes of optical calculation we may, therefore, disregard the refraction of the cornea (which, moreover, does not differ materially from that of the aqueous humor), and imagine the aqueous humor extending forward to the anterior surface of the layer of tears which bathes the corneal epithelium. Furthermore, the capsule of the lens has the same index of refraction as the outer layer of the lens itself, and for optical purposes may be regarded as replaced by it. Hence the optical apparatus of the eye may be regarded as consisting of the following three refracting media: Aqueous humor, index of refraction 1.33; lens, average index of refraction 1.45; vitreous humor, index of refraction 1.33. The surfaces at which refraction occurs are also three in number: Anterior surface of cornea, radius of curvature 8 millimeters; anterior surface of lens, radius of curvature 10 millimeters; posterior surface of lens, radius of curvature 6 millimeters. It will thus be seen that the anterior surface of the lens is less and the posterior surface more convex than the cornea.

To the values of the optical constants of the eye as above given may be added the following: Distance from the anterior surface of the cornea to the anterior surface of the lens, 3.6 millimeters; distance from the posterior surface of the lens to the retina, 15. millimeters; thickness of lens, 3.6 millimeters.

The methods usually employed for determining these constants are the following: The indices of refraction of the aqueous and vitreous humor are determined by filling the space between a glass lens and a glass plate with the fresh humor. The aqueous or vitreous humor thus forms a convex or concave lens, from the form and focal distance of which the index can be calculated. Another method consists in placing a thin layer of the medium between the hypothenuse surfaces of two right-angled prisms and determining the angle at which total internal reflection takes place. In the case of the crystalline lens the index is found by determining its focal distance as for an ordinary lens, and solving the equation which expresses the value of the index in terms of radius of curvature and focal distance, thickness, and focal length. The refractive index of the lens increases from the surface toward the centre, a peculiarity which tends to correct the disturbances due to spherical aberration, as well as to increase the refractive power of the lens as a whole.

The curvature of the refracting surfaces of the eye is determined by an instrument known as an ophthalmometer, which measures the size of the reflected image of a known object in the various curved surfaces. The radius of curvature of the surface is determined by the following formula: $B : b = A : \frac{r}{2}$; or $r = \frac{2Ab}{B}$, in which B = the size of the object, b = the size of the image, A = distance between the object and the reflecting surface, and r = the radius of the reflecting surface. The distances between the various surfaces of the eye are measured on frozen sections of the organ, or can be determined upon the living eye by optical methods too complicated to be here described. It should be borne in mind that the above values of the so-called "optical constants" of the eye are subject to considerable individual variation, and that the statements of authors concerning them are not always consistent.

The refracting surfaces of the eye may be regarded as still further simplified, and a so-called "reduced eye" constructed which is very useful for purposes of optical calculation. This reduced eye, which for optical purposes is the equivalent of the actual eye, is regarded as consisting of a single refracting medium having an index of 1.33, a radius of curvature of 5.017 millimeters, its principal point 2.148 millimeters behind the anterior surface of the cornea, and its nodal point 0.04 millimeter in front of the posterior surface of the lens.[1] The principal foci of the reduced eye are respectively 12.918 millimeters in front of and 22.231 millimeters behind the anterior surface of the cornea. Its optical power is equal to 50.8 dioptries.[2] The position of this imaginary refracting surface is indicated by the dotted line p in Figure 128. The nodal point, n, in this construction may be regarded as the crossing-point of all the principal rays which enter the eye, and, as these rays are unchanged in their direction by refraction, it is evident that the image of the point whence they proceed will be formed at the point where they strike the retina. Hence to determine the size and position of the retinal image of any external object—*e. g.* the arrow in Figure 128—it is only necessary to draw lines from various

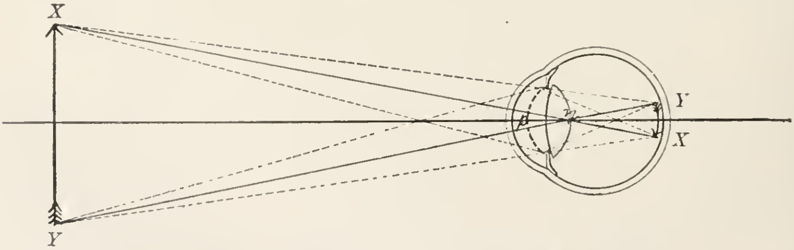

FIG. 128.—Diagram of the formation of a retinal image (after Foster).

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[1] Strictly speaking, there are in this imaginary refracting apparatus which is regarded as equivalent to the actual eye two principal and two nodal points, each pair about 0.4 millimeter apart. The distance is so small that the two points may, for all ordinary constructions, be regarded as coincident.

[2] The optical power of a lens is the reciprocal of its focal length. The dioptry or unit of optical power is the power of a lens with a focal length of 1 meter.

points of the object through the above-mentioned nodal point and to prolong them till they strike the retina. It is evident that the size of the retinal image will be as much smaller than that of the object as the distance of the nodal point from the retina is smaller than its distance from the object.

According to the figures above given, the nodal point is about 7.2 millimeters behind the anterior surface of the cornea and about 15.0 millimeters in front of the retina. Hence the size of the retinal image of an object of known size and distance can be readily calculated—a problem which has frequently to be solved in the study of physiological optics. The construction given in Figure 128 shows that from all external objects *inverted* images are projected upon the retina, and such inverted images can actually be seen under favorable conditions. If, for instance, the eye of a white rabbit, which contains no choroidal pigment, be excised and held with the cornea directed toward a window or other source of light, an inverted image of the luminous object will be seen through the transparent sclerotic in the same way that one sees an inverted image of a landscape on the ground-glass plate of a photographic camera. The question is often asked, "Why, if the images are inverted in the retina, do we not see objects upside down?" The only answer to such a question is that it is precisely *because* images are inverted on the retina that we do *not* see objects upside down, for we have learned through lifelong practice to associate an impression made upon any portion of the retina with light coming from the *opposite* portion of the field of vision. Thus if an image falls upon the lower portion of the retina, our experience, gained chiefly through muscular movements and tactile sensations, has taught us that this image must correspond to an object in the upper portion of our field of vision. In whatever way the retina is stimulated the same effect is produced. If, for instance, gentle pressure is made with the finger on the lateral portion of the eyeball through the closed lids a circle of light known as a phosphene immediately appears on the opposite side of the eye. Another good illustration of the same general rule is found in the effect of throwing a shadow upon the retina from an object as close as possible to the eye. For this purpose place a card with a small pin-hole in it in front of a source of light, and three or four centimeters distant from the eye—*i. e.* within the near point of distinct vision. Then hold some object smaller than the pupil—*e. g.* the head of a pin—as close as possible to the cornea. Under these conditions neither the pin-hole nor the pin-head can be really seen—*i. e.* they are

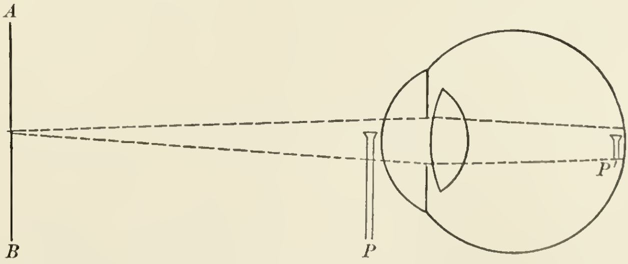

FIG. 129.—Diagram illustrating the projection of a shadow on the retina.

both too near to have their images focussed upon the retina. The pin-hole becomes itself a source of light, and appears as a luminous circle bounded by the shadow thrown by the edge of the iris. Within this circle of light is seen the shadow of the pin-head, but the pin-head appears *inverted*, for the obvious reason that the eye, being accustomed to interpret all retinal impressions as corresponding to objects in the opposite portion of the field of vision, regards the upright shadow of the pin-head as the representation of an inverted object. The course of the rays in this experiment is shown in Figure 129, in which $A\,B$ represents the card with a pin-hole in it, P the pin, and P' its upright shadow thrown on the retina.

Accommodation.—From what has been said of conjugate foci and their relation to each other it is evident that any change in the distance of the object from the refracting media will involve a corresponding change in the position of the image, or, in other words, only objects at a given distance can be focussed upon a plane which has a fixed position with regard to the refracting surface or surfaces. Hence all optical instruments in which the principle of conjugate foci finds its application have adjustments for distance. In the telescope and opera-glass the adjustment is effected by changes in the distance between the lenses, and in the photographic camera by a change in the position of the ground-glass plate representing the focal plane. In the microscope the adjustment is effected by changing the distance of the object to suit the lenses, the higher powers having a shorter "working distance."

We must now consider in what way the eye adapts itself to see objects distinctly at different distances. That this power of adaptation, or "accommodation," really exists we can easily convince ourselves by looking at different objects through a network of fine wire held near the eyes. When with normal vision the eyes are directed to the distant objects the network nearly disappears, and if we attempt to see the network distinctly the outlines of the distant objects become obscure. In other words, it is impossible to see both the network and the distant objects distinctly at the same time. It is also evident that in accommodation for distant objects the eyes are at rest, for when they are suddenly opened after having been closed for a short time they are found to be accommodated for distant objects, and we are conscious of a distinct effort in directing them to any near object.[1]

From the optical principles above described it is clear that the accommodation of the eye for near objects may be conceived of as taking place in three different ways: 1st, By an increase of the distance between the refracting surfaces of the eye and the retina; 2d, By an increase of the index of refraction of one or more of the media; 3d, By a diminution of the radius of curvature of one or more of the surfaces. The first of these methods was formerly supposed to be the one actually in use, a lengthening of the eyeball under a pres-

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[1] It has been shown by Beer (*Archiv für die gesammte Physiologie*, lviii. 523) that in fishes the eyes when at rest are accommodated for *near* objects, and that accommodation for *distant* objects is effected by the contraction of a muscle for which the name "retractor lentis" is proposed.

sure produced by the eye-muscles being assumed to occur. This lengthening would, in the case of a normal eye accommodating itself for an object at a distance of 15 centimeters, amount to not less than 2 millimeters—a change which could hardly be brought about by the action of any muscles connected with the eye. Moreover, accommodation changes can be observed upon electrical stimulation of the excised eye. Its mechanism must, therefore, lie within the eye itself. As for the second of these methods, there is no conceivable way by which a change in the index of refraction of the media can be effected, and we are thus forced to the conclusion that accommodation is brought about by a change in the curvature of the refracting surfaces—*i. e.* by a method quite different from any which is employed in optical instruments of human construction. Now, by measuring the curvature of the cornea of a person who looks alternately at near and distant objects it has been shown that the cornea undergoes no change of form in the act of accommodation. By a process of exclusion, therefore, the lens is indicated as the essential organ in this function of the eye, and, in fact, the complicated structure and connections of the lens at once suggest the thought that it is in the surfaces of this portion of the eye that the necessary changes take place. Indeed, from a teleological point of view the lens would seem somewhat superfluous if it were not important to have a transparent refracting body of *variable* form in the eye, for the amount of refraction which takes place in the lens could be produced by a slightly increased curvature of the cornea. Now, the changes of curvature which occur in the surfaces of the lens when the eye is directed to distant and near objects alternately can be actually observed and measured with considerable accuracy. For this purpose the changes in the form, size, and position of the images of brilliant objects reflected in these two surfaces are studied. If a candle is held in a dark room on a level with and about 50 centimeters away from the eye in which the accommodation is to be studied, an observer, so placed that his own axis of vision makes about the same angle (15°–20°) with that of the observed eye that is made by a line joining the observed eye and the candle, will readily see a small upright image of the candle reflected in the cornea of the observed eye. Near this and within the outline of the pupil are two other images of the candle, which, though much less easily seen than the corneal image, can usually be made out by a proper adjustment of the light. The first of these is a large faint upright image reflected from the anterior surface of the lens, and the second is a small inverted image reflected from the posterior surface of the lens. It will be observed that the size of these images varies with the radius of curvature of the three reflecting surfaces as given on p. 303. The relative size and position of these images having been recognized while the eye is at rest—*i. e.* is accommodated for distance—let the person who is under observation be now requested to direct his eye to a near object lying in the same direction. When this is done the corneal image and that reflected from the posterior surface of the lens will remain unchanged,[1]

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[1] A very slight diminution in size may sometimes be observed in the image reflected from the posterior surface of the lens.

while that reflected from the anterior surface of the lens will become smaller and move toward the corneal image. This change in the size and position of the reflected image can only mean that the surface from which the reflection takes place has become more convex and has moved forward. Coincident with this change a contraction of the pupil will be observed.

An apparatus for making observations of this sort is known as the phakoscope of Helmholtz (Fig. 130). The eye in which the changes due to accommodation are to be observed is placed at an opening in the back of the instrument at *C*, and directed alternately to a needle placed in the opening *D* and to a distant object lying in the same direction. Two prisms at *B* and *B′* serve to throw the light of a candle on to the observed eye, and the eye of an observer at *A* sees the three reflected images, each as two small square spots of light. The movement and the change of size of the image reflected from the anterior surface of the lens can be thus much better observed than when a candle-flame is used.

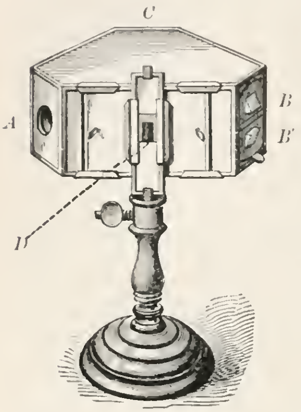

Fig. 130.—Phakoscope of Helmholtz.

The course of the rays of light in this experiment is shown diagrammatically in Figure 131. The observed eye is directed to the point *A*, while the candle and the eye of the observer are placed symmetrically on either side. The images of the candle reflected from the various surfaces of the eye will be seen projected on the dark background of the pupil in the directions indicated by the dotted lines ending at *a*, *b*, and *c*. When the eye is accommodated for a near object the middle one of the three images moves nearer the corneal image—*i. e.* it changes in its direction from *b* to *b′*, showing that the anterior surface of the lens has bulged forward into the position indi-

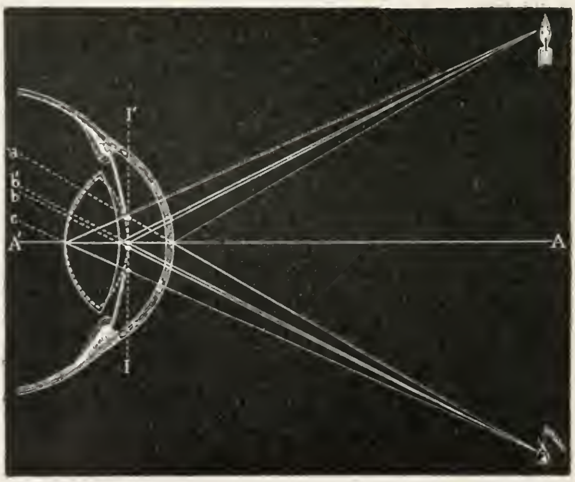

Fig. 131.—Diagram explaining the change in the position of the image reflected from the anterior surface of the crystalline lens (Williams, after Donders).

cated by the dotted line. The change in the appearance of the images is represented diagrammatically in Figure 132. On the left is shown the appearance of the images as seen when the eye is at rest, *a* representing the corneal image, *b* that reflected from the anterior, and *c* that from the posterior surface of the lens when the observing eye and the candle are in the position represented in Figure 131. The images are represented as they appear in the dark background of the pupil, though of course the corneal image may, in certain positions of the light, appear outside of the pupillary region. When the eye is accommodated for near objects the images appear as shown in the circle on the right, the image *b* becoming smaller and brighter and moving toward the corneal image, while the pupil contracts as indicated by the circle drawn round the images.

FIG. 132.—Reflected images of a candle-flame as seen in the pupil of an eye at rest and accommodated for near objects (Williams).

The changes produced in the eye by an effort of accommodation are indicated in Figure 133, the left-hand side of the diagram showing the condition of the eye at rest, and the right-hand side that in extreme accommodation for near objects.

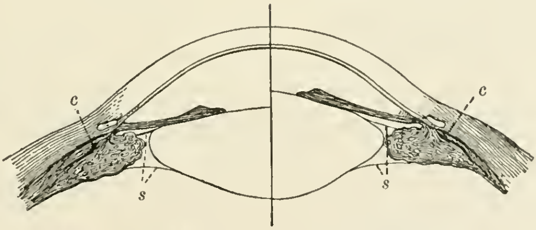

FIG. 133.—Showing changes in the eye produced by the act of accommodation (Helmholtz).

It will be observed that the iris is pushed forward by the bulging lens and that its free border approaches the median line. In other words, the pupil is contracted in accommodation for near objects. The following explanation of the mechanism by which this change in the shape of the lens is effected has been proposed by Helmholtz, and is still generally accepted. The structure of the lens is such that by its own elasticity it tends constantly to assume a more convex form than the pressure of the capsule and the tension of the suspensory ligaments (*s*, *s*, Fig. 133) allow. This pressure and tension are diminished when the eye is accommodated for near vision by the contraction of the ciliary muscles (*c*, *c*, Fig. 133), most of whose fibres, having their origin at the point of union of the cornea and sclerotic, extend radially outward in every direction and are attached to the front part of the choroid. The contraction of the ciliary muscle, drawing forward the membranes of the eye, will relax the tension of the suspensory ligament and allow the lens to take the form determined by its own elastic structure. According to another theory of accommodation proposed by Tscherning,[1] the suspensory ligament is stretched and not relaxed by the contraction of the ciliary muscle. In consequence of the pressure thus produced upon the lens, the soft external portions are moulded upon the harder nuclear portion in such a way as to give to the anterior (and to some extent to the posterior) surface a hyperboloid instead of a spherical form. A similar theory has been recently brought forward by Schoen,[2] who compares the action of the ciliary muscle upon the lens to that of the fingers compressing a rubber ball, as shown in Figure 134. These theories have an advantage over that offered by Helmholtz, inasmuch as they afford a better explanation of the presence of circular fibres in the ciliary muscle. They also make the fact of so-called "astigmatic accommodation" comprehensible. This term is applied to the power said to be sometimes gradually acquired by persons with astigmatic[3] eyes of correcting this defect of vision by accommodating the eye more strongly in one meridian than another. The theory of Tscherning is supported by Crzellitzer[4] as the result of investigations into the hyperboloid form of the lens in accommodation. On the other hand, it is maintained by Priestley Smith[5] that this form of the lens is not inconsistent with the Helmholtz theory. Moreover, it has been shown by Hess[6] and Heine[7] that in extreme accommodation the lens drops slightly toward the lower part of the eye, a movement which seems to indicate a relaxation of the suspensory ligament. The weight of evidence seems, therefore, on the whole, to be on the side of the theory of Helmholtz.

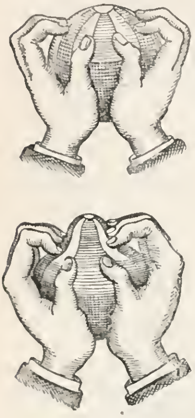

FIG. 134.—To illustrate Schoen's theory of accommodation.

Whatever views may be entertained as to the exact mechanism by which its change of shape is brought about, there can be no doubt that the lens is the portion of the eye chiefly or wholly concerned in accommodation, and it is accordingly found that the removal of the lens in the operation for cataract destroys the power of accommodation, and the patient is compelled to use convex lenses for distant and still stronger ones for near objects.

It is interesting to notice that the act of accommodation, though distinctly voluntary, is performed by the agency of the *unstriped* fibres of the ciliary muscles. It is evident, therefore, that the term "involuntary" sometimes

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[1] *Archives de Physiologie*, 1894, p. 40.

[2] *Archiv für die gesammte Physiologie*, lix. 427.

[3] See p. 317.

[4] *Archiv für Ophthalmologie*, xlii. (4) S. 36.

[5] *Ophthalmic Review*, xvii. p. 341.

[6] *Archiv für Ophthalmologie*, xlii. S. 288, and xliii. S. 477.

[7] *Ibid.*, xliv. (2) S. 299, and xlvii. (2) S. 662.

applied to muscular fibres of this sort may be misleading. The voluntary character of the act of accommodation is not affected by the circumstance that the will needs, as a rule, to be assisted by visual sensations. The fact that most persons cannot affect the necessary change in the eye unless they direct their attention to some near or far object is only an instance of the close relation between sensory impressions and motor impulses, which is further exemplified by such phenomena as the paralysis of the lip of a horse caused by division of the fifth nerve. It is found, moreover, that by practice the power of accommodating the eye without directing it to near and distant objects can be acquired. The nerve-channels through which accommodation is affected are the anterior part of the nucleus of the third pair of nerves lying in the extreme hind part of the floor of the third ventricle, the most anterior bundle of the nerve-root, the third nerve itself, the lenticular ganglion, and the short ciliary nerves (see diagram p. 323).

The mechanism of accommodation is affected in a remarkable way by drugs, the most important of which are atropia and physostigmin, the former paralyzing and the latter stimulating the ciliary muscle. As these drugs exert a corresponding effect upon the iris, it will be convenient to discuss their action in connection with the physiology of that organ.

The changes occurring in the eye during the act of accommodation are indicated in the following table, which shows, both for the actual and the reduced eye, the extent to which the refracting media change their form and position, and the consequent changes in the position of the foci :

	Accommodation for			
Actual Eye.	distant objects.		near objects.	
Radius of cornea	8	mm.	8	mm.
Radius of anterior surface of lens	10	"	6	"
Radius of posterior surface of lens	6	"	5.5	"
Distance from cornea to anterior surface of lens	3.6	"	3.2	"
Distance from cornea to posterior surface of lens	7.2	"	7.2	"
Reduced Eye.				
Radius of curvature	5.02	"	4.48	"
Distance from cornea to principal point	2.15	"	2.26	"
Distance from cornea to nodal point	7.16	"	6.74	"
Distance from cornea to anterior focus	12.918	"	11.241	"
Distance from cornea to posterior focus	22.231	"	20.248	"

It will be noticed that no change occurs in the curvature of the cornea, and next to none in the posterior surface of the lens, while the anterior surface of the lens undergoes material alterations both in its shape and position.

Associated with the accommodative movements above described, two other changes take place in the eyes to adapt them for near vision. In the first place, the axes of the eyes are converged upon the near object, so that the images formed in the two eyes shall fall upon corresponding points of the retinas, as will be more fully explained in connection with the subject of binocular vision. In the second place, the pupil becomes contracted, thus reducing the size of the pencil of rays that enters the eye. The importance of this movement of the pupil will be better understood after the subject of spherical aberration of light has been explained. These three adjustments, focal, axial, and pupillary, are so habitually associated in looking at near objects that the axial can only by an effort be dissociated from the other two, while these two are quite inseparable from one another. This may be illustrated by a simple experiment. On a sheet of paper about 40 centimeters distant from the eyes draw two letters or figures precisely alike and about 3 centimeters apart. (Two letters cut from a newspaper and fastened to the sheet will answer the same purpose.) Hold a small object like the head of a pin between the eyes and the paper at the point of intersection of a line joining the right eye and the left letter with a line joining the left eye and the right letter. If the axes of vision are converged upon the pin-head, that object will be seen distinctly, and beyond it will be seen indistinctly *three* images of the letter, the central one being formed by the blending of the inner one of each pair of images formed on the two retinas. If now the attention be directed to the middle image, it will gradually become perfectly distinct as the eye accommodates itself for that distance. We have thus an axial adjustment for a very near object and a focal adjustment for a more distant one. If the pupil of the individual making this observation be watched by another person, it will be found that at the moment when the middle image of the letter becomes distinct the pupil, which had been contracted in viewing the pin-head, suddenly dilates. It is thus seen that when the axial and focal adjustments are dissociated from each other the pupillary adjustment allies itself with the latter.

The opposite form of dissociation—viz. the axial adjustment for distance and the focal adjustment for near vision—is less easy to bring about. It may perhaps be best accomplished by holding a pair of stereoscopic pictures before the eyes and endeavoring to direct the right eye to the right and the left eye to the left picture—*i. e.* to keep the axes of vision parallel while the eyes are accommodated for near objects. One who is successful in this species of ocular gymnastics sees the two pictures blend into one having all the appearance of a solid object. The power of thus studying stereoscopic pictures without a stereoscope is often a great convenience to the possessor, but individuals differ very much in their ability to acquire it.

Range of Accommodation.—By means of the mechanism above described it is possible for the eye to produce a distinct image upon the retina of objects lying at various distances from the cornea. The point farthest from the eye at which an object can be distinctly seen is called the *far-point*, and the nearest point of distinct vision is called the *near-point* of the eye, and the distance between the near-point and the far-point is called the range of distinct vision or the *range of accommodation.* As the normal emmetropic eye is adapted, when at rest, to bring parallel rays of light to a focus upon the retina, its far-point may be regarded as at an infinite distance. Its near-point varies with age, as will be described under Presbyopia. In early adult life it is from 10 to 13 centimeters from the eye. For every point within this range there will be theoretically a corresponding condition of the lens adapted to bring rays proceeding from that point to a focus on the retina, but as rays reaching the eye from a point 175 to 200 centimeters distant do not, owing to the small size of the pupil, differ sensibly from parallel rays, there is no appreciable change in the lens unless the object looked at lies within that distance. It is also evident that as an object approaches the eye a given change of distance will cause a constantly increasing amount of divergence of the rays proceeding from it, and will therefore necessitate a constantly increasing amount of change in the lens to enable it to focus the rays on the retina. We find, accordingly, that all objects more than two meters distant from the eye can be seen distinctly at the same time—*i. e.* without any change in the accommodative mechanism—but for objects within that distance we are conscious of a special effort of accommodation which becomes more and more distinct the shorter the distance between the eye and the object.

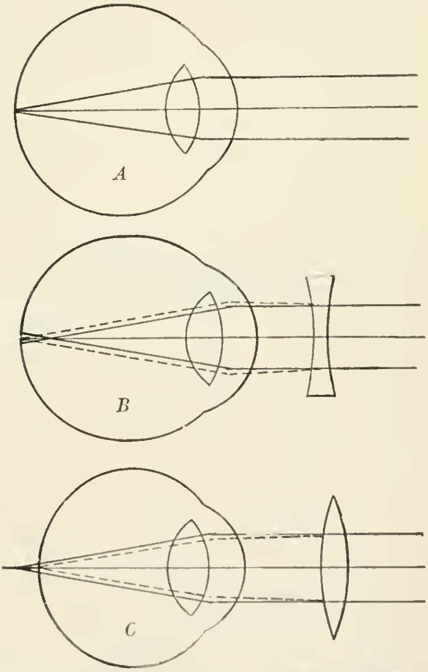

FIG. 135.—Diagram showing the difference between normal, myopic, and hypermetropic eyes.

Myopia and Hypermetropia.—There are two conditions of the eye in which the range of accommodation may differ from that which has just been described as normal. These conditions, which are too frequent to be regarded (except in extreme cases) as pathological, are generally dependent upon the eyeball being unduly lengthened or shortened. In Fig. 135 are shown diagrammatically the three conditions known as emmetropia, myopia, and hypermetropia. In the normal or emmetropic eye, *A*, parallel rays are represented as brought to a focus on the retina; in the short-sighted, or myopic, eye, *B*, similar rays are focussed in front of the retina, since the latter is abnormally distant; while in the over-sighted, or hypermetropic, eye, *C*, they are focussed behind the retina, since it is abnormally near.

It is evident that when the eye is at rest both the myopic and the hypermetropic eye will see distant objects indistinctly, but there is this important difference: that in hypermetropia the difficulty can be corrected by an effort of accommodation, while in myopia this is impossible, since there is no mechanism by which the radius of the lenticular surfaces can be increased. Hence an individual affected with myopia is always aware of the infirmity, while a person with hypermetropic eyes often goes through life unconscious of the defect. In this case the accomodation is constantly called into play even for distant objects, and if the hypermetropia is excessive, any prolonged use of the eyes is apt to be attended by a feeling of fatigue, headache, and a train of nervous symptoms familiar to the ophthalmic surgeon. Hence it is important to discover this defect where it exists and to apply the appropriate remedy—viz. convex lenses placed in front of the eyes in order to make the rays slightly convergent when they enter the eye. Thus aided, the refractive power of the eye at rest is sufficient to bring the rays to a focus upon the retina and thus relieve the accommodation. This action of a convex lens in hypermetropia is indicated by the dotted lines in Fig. 135, *C*, and the corresponding use of a concave lens in myopia is shown in Fig. 135, *B*.

The detection and quantitative determination of hypermetropia are best made after the accommodation has been paralyzed by the use of atropia, by ascertaining how strong a convex lens must be placed before the eye to produce distinct vision of distant objects.

The range of accommodation varies very much from the normal in myopic and hypermetropic eyes. In myopia the near-point is often 5 or 6 centimeters from the cornea, while the far-point, instead of being infinitely far off, is at a variable but no very great distance from the eye. The range of accommodation is therefore very limited. In hypermetropia the near-point is slightly farther than normal from the eye, and the far-point cannot be said to exist, for the eye at rest is adapted to bring converging rays to a focus on the retina, and such pencils of rays do not exist in nature. Mathematically, the far-point may be said to be at more than an infinite distance from the eye. The range of effective accommodation is therefore reduced, for a portion of the accommodative power is used up in adapting the eye to receive parallel rays.

Presbyopia.—The power of accommodation diminishes with age, owing apparently to a loss of elasticity of the lens. The change is regularly progressive, and can be detected as early as the fifteenth year, though in normal eyes it does not usually attract attention until the individual is between forty and forty-five years of age. At this period of life a difficulty is commonly experienced in reading ordinary type held at a convenient distance from the eye, and the individual becomes old-sighted or *presbyopic*—a condition which can, of course, be remedied by the use of convex glasses. According to Helmholtz, the far-point also recedes somewhat after fifty years of age. Hence emmetropic eyes may become hypermetropic and slightly myopic eyes emmetropic. Cases are occasionally reported of persons recovering their power of near vision in extreme old age and discontinuing the use of the glasses previously employed for reading. In these cases there is apparently not a restoration of the power of accommodation, but an increase in the refractive power of the lens through local changes in its tissue. A diminution in the size of the pupil, sometimes noticed in old age,[1] may also contribute to the distinctness of the retinal image, as will be described in connection with spherical aberration.

Defects of the Dioptric Apparatus.—The above-described imperfections of the eye—viz. myopia and hypermetropia—being generally (though not invariably) due to an abnormal length of the longitudinal axis, are to be regarded as defects of construction affecting only a comparatively small

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[1] The average diameter of the pupil is said to be in youth 4.1 mm. and in old age 3 mm. Silberkuhl: *Archiv für Ophthalmologie*, xlii. (3) S. 179.

number of eyes. There are, however, a number of imperfections of the dioptric apparatus, many of which affect all eyes alike. Of these imperfections some affect the eye in common with all optical instruments, while others are peculiar to the eye and are not found in instruments of human construction. The former class will be first considered.

Spherical Aberration.—It has been stated that a pencil of rays falling upon a spherical refracting surface will be refracted to a common focus. Strictly speaking, however, the outer rays of the pencil—*i. e.* those which fall near the periphery of the refracting surface—will be refracted more than those which lie near the axis and will come to a focus sooner. This phenomenon, which is called spherical aberration, is more marked with diverging than with parallel rays, and tends, of course, to produce an indistinctness of the image which will increase with the extent of the surface through which the rays pass. The effect of a diaphragm used in many optical instruments to reduce the amount of spherical aberration by cutting off the side rays is shown diagrammatically in Fig. 136.

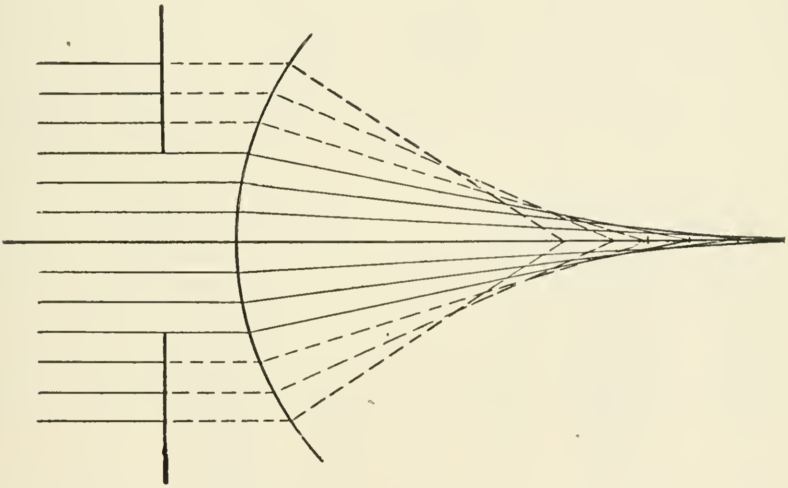


FIG. 136.—Diagram showing the effect of a diaphragm in reducing the amount of spherical aberration.

The rôle of the iris in the vision of near objects is now evident, for when the eye is directed to a near object the spherical aberration is increased in consequence of the rays becoming more divergent, but the contraction of the pupil which accompanies accommodation tends, by cutting off the side rays, to prevent a blurring of the image which otherwise would be produced. It must, however, be remembered that the crystalline lens, unlike any lens of human construction, has a greater index of refraction at the centre than at the periphery. This, of course, tends to correct spherical aberration, and, in so far as it does so, to render the cutting off of the side rays unnecessary. Indeed, the total amount of possible spherical aberration in the eye is so small that its effect on vision may be regarded as insignificant in comparison with that caused by the other optical imperfections of the eye.

Chromatic Aberration.—In the above account of the dioptric apparatus of the eye the phenomena have been described as they would occur with monochromatic light—*i. e.* with light having but one degree of refrangibility. But the light of the sun is composed of an infinite number of rays of different degrees of refrangibility. Hence when an image is formed by a simple lens the more refrangible rays—*i. e.* the violet rays of the spectrum—are brought to a focus sooner than the less refrangible red rays. The image therefore appears bordered by fringes of colored light. This phenomenon of *chromatic aberration* can be well observed by looking at objects through the lateral portion of a simple lens, or, still better, by observing them through two simple lenses held at a distance apart equal to the sum of their focal distances. The objects will appear inverted (as through an astronomical telescope) and surrounded with borders of colored light. Now, the chromatic aberration of the eye is so slight that it is not easily detected, and the physicists of the eighteenth century, in their efforts to produce an achromatic lens, seem to have been impressed by the fact that in the eye a combination of media of different refractive powers is employed, and to have sought in this circumstance an explanation of the supposed achromatism of the eye. Work directed on this line was crowned with brilliant success, for by combining two sorts of glass of different refractive and dispersive powers it was found possible to refract a ray of light without dispersing it into its different colored rays, and the achromatic lens, thus constructed, became at once an essential part of every first-class optical instrument. Now, as there is not only no evidence that the principle of the achromatic lens is employed in the eye, but distinct evidence that the eye is uncorrected for chromatic aberration, we have here a remarkable instance of a misconception of a physical fact leading to an important discovery in physics. The chromatic aberration of the eye, though so slight as not to interfere at all with ordinary vision, can be readily shown to exist by the simple experiment of covering up one half of the pupil and looking at a bright source of light *e. g.* a window. If the lower half of the pupil be covered, the cross-bars of the window will appear bordered with a fringe of blue light on the lower and reddish light on the upper side. The explanation usually given of the way in which this result is produced is illustrated in Fig. 137. Owing to the chromatic aberration of the eye all the rays emanating from an object at *A* are not focussed accurately on the retina, but if the eye is accommodated for a ray of medium refrangibility, the violet rays will be brought to a focus in front of the retina at *V*, while the red rays will be focussed behind the retina at *R*.

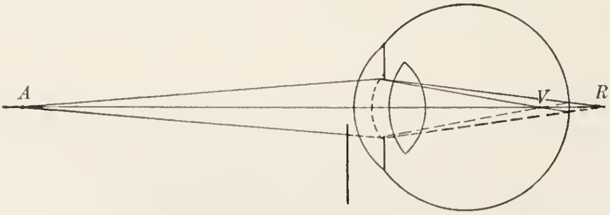


FIG. 137.—Diagram to illustrate chromatic aberration.

On the retina itself will be formed not an accurate optical image of the point *A*, but a small circle of dispersion in which the various colored rays are mixed together, the violet rays after crossing falling upon the same part of the retina as the red rays before crossing. Thus by a sort of compensation, which, however, cannot be equivalent to the synthetic reproduction of white light by the union of the spectral colors, the disturbing effect of chromatic aberration is diminished. When the lower half of the pupil is covered by the edge of a card held in front of the cornea at *D*, the aberration produced in the upper half of the eye is not compensated by that of the lower half. Hence the image of a point of white light at *A* will appear as a row of spectral colors on the retina, and all objects will appear bordered by colored fringes. Another good illustration of the chromatic aberration of the eye is obtained by cutting two holes of any convenient shape in a piece of black cardboard and placing behind one of them a piece of blue and behind the other a piece of red glass. If the card is placed in a window some distance (10 meters) from the observer, in such a position that the white light of the sky may be seen through the colored glasses, it will be found that the outlines of the two holes will generally be seen with unequal distinctness. To most eyes the red outline will appear quite distinct, while the blue figure will seem much blurred. To a few individuals the blue figure appears the more distinct, and these will generally be found to be hypermetropic.

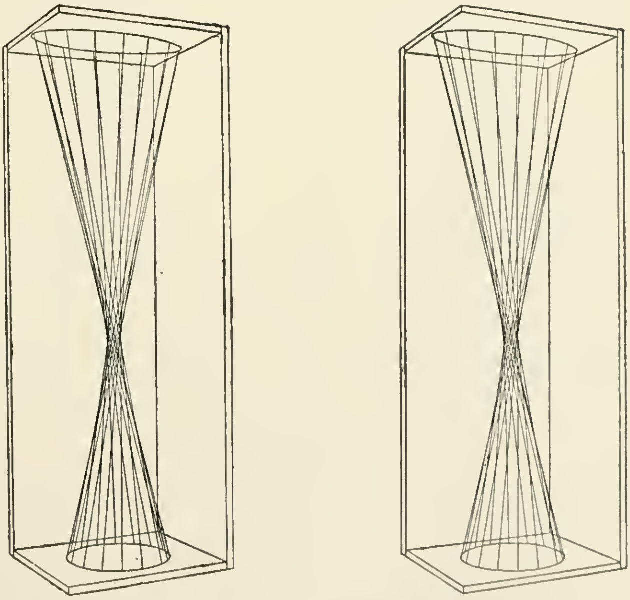


FIG. 138.—Model to illustrate astigmatism.

Astigmatism.—The defect known as astigmatism is due to irregularities of curvature of the refracting surfaces, in consequence of which all the rays proceeding from a single point cannot be brought to a single focus on the retina.

Astigmatism is said to be *regular* when one of the surfaces, generally the cornea, is not spherical, but ellipsoidal—*i. e.* having meridians of maximum and minimum curvature at right angles to each other, though in each meridian the curvature is regular. When this is the case the rays proceeding from a single luminous point are brought to a focus earliest when they lie in the meridian in which the surface is most convex. Hence the pencil of rays will have two linear foci, at right angles to the meridians of greatest and least curvature separated by a space in which a section of the cone of rays will be first elliptical, then circular, and then again elliptical. This defect exists to a certain extent in nearly all eyes, and is, in some cases, a serious obstacle to distinct vision. The course of the rays when thus refracted is illustrated in Fig. 138, which represents the interior of a box through which black threads are drawn to indicate the course of the rays of light. The threads start at one end of the box from a circle representing the cornea, and converge with different degrees of rapidity in different meridians, so that a section of the cone of rays will be successively an ellipse, a straight line, an ellipse, a circle, etc., as shown by the model represented in Fig. 139. It will be noticed that this and the preceding figure are drawn in duplicate, but that the lines are not precisely alike on the two sides. In fact, the lines on the left represent the model as it would be seen with the right eye, and those on the right as it would appear to the left eye, which is just the opposite from an ordinary stereoscopic slide. The figures are drawn in this way because they are intended to produce a "pseudoscopic" effect in a way which will be explained in connection with the subject of binocular vision. For this purpose it is only necessary to cross the axes of vision in front of the page, as in the experiment described on page 312, for studying the relation between the focal, axial, and pupillary adjustments of the eye. As soon as the middle image becomes distinct it assumes a

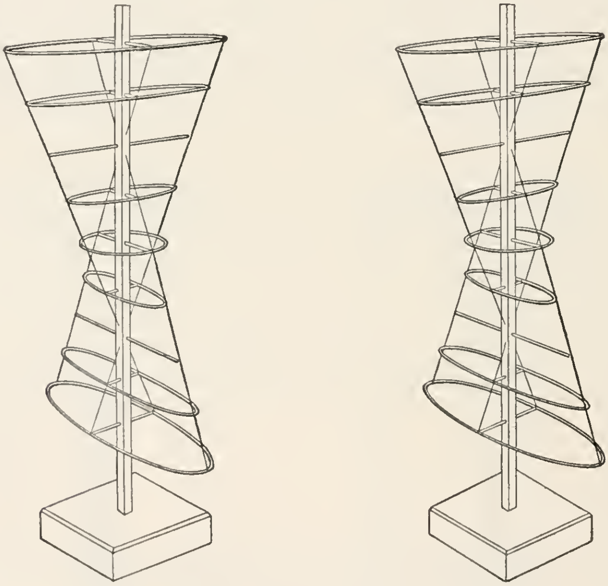


FIG. 139.—Model to illustrate astigmatism.

stereoscopic appearance, and the correct relations between the different parts of the model are at once obvious.

This imperfection of the eye may be detected by looking at lines such as are shown in Figure 140, and testing each eye separately. If the straight lines drawn in various directions through a common point cannot be seen with equal distinctness at the same time, it is evident that the eye is better adapted to focus rays in one meridian than in another—*i. e.* it is astigmatic. The concentric circles are a still more delicate test. Few persons can look at this figure attentively without noticing that the lines are not everywhere equally distinct, but that in certain sectors the circles present a blurred appearance. Not infrequently it will be found that the blurred sectors do not occupy a constant position, but oscillate rapidly from one part of the series of circles to another. This phenomenon seems to be due to slight involuntary contractions of the ciliary muscle causing changes in accommodation.

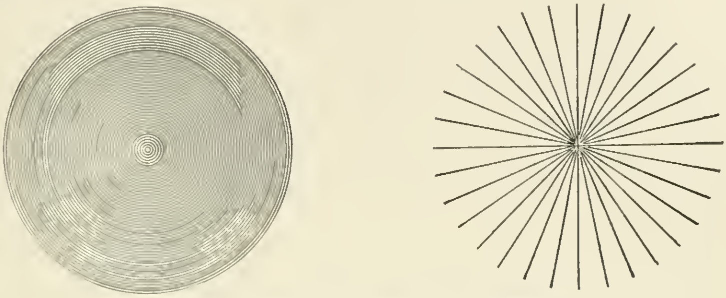


FIG. 140.—Lines for the detection of astigmatism.

The direction of the meridians of greatest and least curvature of the cornea of a regularly astigmatic eye, and the difference in the amount of this curvature, can be very accurately measured by means of the ophthalmometer (see p. 304). These points being determined, the defect of the eye can be perfectly corrected by cylindrical glasses adapted to compensate for the excessive or deficient refraction of the eye in certain meridians.

By another method known as "skiascopy," which consists in studying the light reflected from the fundus of the eye when the ophthalmoscopic mirror is moved in various directions, the amount and direction of the astigmatism of the eye as a whole (and not that of the cornea alone) may be ascertained.

Astigmatism is said to be irregular when in certain meridians the curvatures of the refracting surfaces are not arcs of circles or ellipses, or when there is a lack of homogeneousness in the refracting media. This imperfection exists to a greater or less extent in all eyes, and, unlike regular astigmatism, is incapable of correction. It manifests itself by causing the outlines of all brilliant objects to appear irregular. It is on this account that the fixed stars do not appear to us like points of light, but as luminous bodies with irregular "star"-shaped outlines. The phenomenon can be conveniently studied by looking at a pinhole in a large black card held at a convenient distance between the eye and a strong light. The hole will appear to have an irregular outline, and to some eyes will appear double or treble.

Intraocular Images.—Light entering the eye makes visible, under certain circumstances, a number of objects which lie within the eye itself. These objects are usually opacities in the media of the eye which are ordinarily invisible, because the retina is illuminated by light coming from all parts of the pupil, and with such a broad source of light no object, unless it is a very large one or one lying very near the back of the eye, can cast a shadow on the retina. Such shadows can, however, be made apparent by allowing the media of the eye to be traversed by parallel rays of light. This can be accomplished by holding a small polished sphere—*e. g.* the steel head of a shawl-pin illuminated by sunlight or strong artificial light—in the anterior focus of the eye—*i. e.* about 22 millimeters in front of the cornea, or by placing a dark screen with a pin-hole in it in the same position between the eye and a source of uniform diffused light, such as the sky or the porcelain shade of a student lamp. In either case the rays of light diverging from the minute source will be refracted into parallelism by the media of the eye, and will produce the sensation of a circle of diffused light, the size of which will depend upon the amount of dilatation of the pupil. Within this circle of light will be seen the shadows of any opaque substances that may be present in the media of the eye. These shadows, being cast by parallel rays, will be of the same size as the objects themselves, as is shown diagrammatically in Figure 141, in which *A* represents a source of light at the anterior focus of the eye, and *b* an opacity in the vitreous humor casting a shadow *B* of the same size as itself upon the retina. It is evident that if the source of light *A* is moved from side to side the various opacities will be displaced relatively to the circle of light surrounding them by an amount depending upon the distance of the opacities from the retina. A study of these displacements will therefore afford a means of determining the position of the opacities within the media of the eye.

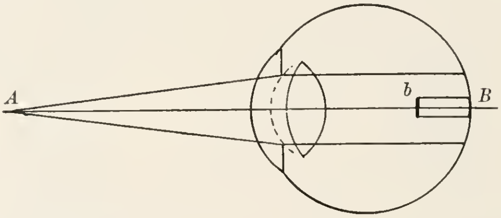


FIG. 141.—Showing the method of studying intraocular images (Helmholtz).

Muscæ Volitantes.—Among the objects to be seen in thus examining the eye the most conspicuous are those known as the *muscæ volitantes.* These present themselves in the form of beads, either singly or in groups, or of streaks, patches, and granules. They have an almost constant floating motion, which is increased by the movements of the eye and head. They usually avoid the line of vision, floating away when an attempt is made to fix the sight upon them. When the eye is directed vertically, however, they sometimes place themselves directly in line with the object looked at. If the intraocular object is at the same time sufficiently near the back of the eye to cast a shadow which is visible without the use of the focal illumination, some inconvenience may thus be caused in using a vertical microscope.

A study of the motions of the *muscæ volitantes* makes it evident that the phenomenon is due to small bodies floating in a liquid medium of a little greater specific gravity than themselves. Their movements are chiefly in planes perpendicular to the axis of vision, for when the eye is directed vertically upward they move as usual through the field of vision without increasing the distance from the retina. They are generally supposed to be the remains of the embyronic structure of the vitreous body—*i. e.* portions of the cells and fibres which have not undergone complete mucous transformation.

In addition to these floating opacities in the vitreous body various other defects in the transparent media of the eye may be revealed by the method of focal illumination. Among these may be mentioned spots and stripes due to irregularities in the lens or its capsule, and radiating lines indicating the stellate structure of the lens.

Retinal Vessels.—Owing to the fact that the blood-vessels ramify near the anterior surface of the retina, while those structures which are sensitive to light constitute the posterior layer of that organ, it is evident that light entering the eye will cast a shadow of the vessels on the light-perceiving elements of the retina. Since, however, the diameter of the largest blood-vessels is not more than one-sixth of the thickness of the retina, and the diameter of the pupil is one-fourth or one-fifth of the distance from the iris to the retina, it is evident that when the eye is directed to the sky or other broad illuminated surfaces it is only the *penumbra* of the vessels that will reach the rods and cones, the *umbra* terminating conically somewhere in the thickness of the retina. But if light is allowed to enter the eye through a pin-hole in a card held a short distance from the cornea, as in the above-described method of focal illumination, a sharply defined shadow of the vessels will be thrown on the rods and cones. Yet under these conditions the retinal vessels are not rendered visible unless the perforated card is moved rapidly to and fro, so as to throw the shadow continually on to fresh portions of the retinal surface. When this is done the vessels appear, ramifying usually as dark lines on a lighter background, but the dark lines are sometimes bordered by bright edges. It will be observed that those vessels appear most distinctly the course of which is at right angles to the direction in which the card is moved. Hence in order to see all the vessels with equal distinctness it is best to move the card rapidly in a circle the diameter of which should not exceed that of the pupil. In this manner the disfribution of the vessels in one's own retina may be accurately observed, and in many cases the position of the fovea centralis may be determined by the absence of vessels from that portion of the macula lutea.

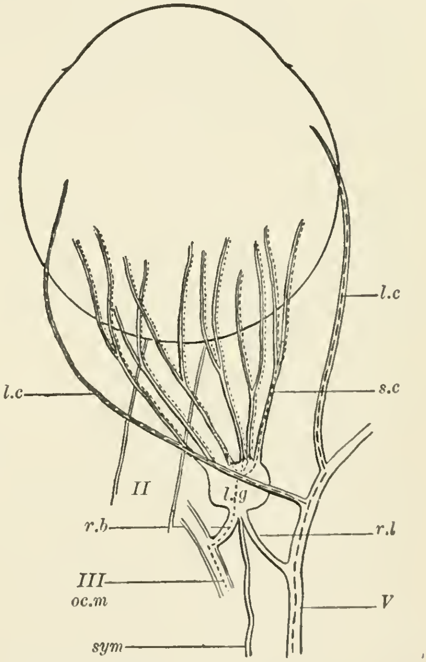
The retinal vessels may also be made visible in several other ways—*e. g.*, 1. By directing the eye toward a dark background and moving a candle to and fro in front of the eye, but below or to one side of the line of vision. 2. By concentrating a strong light by means of a lens of short focus upon a point of the sclerotic as distant as possible from the cornea. By either of these methods a small image of the external source of light is formed upon the lateral portion of the eye, and this image is the source of light which throws shadows of the retinal vessels on to the rods and cones.

Circulation of Blood in the Retina.—When the eye is directed toward a surface which is uniformly and brightly illuminated—*e. g.* the sky or a sheet of white paper on which the sun is shining—the field of vision is soon seen to be filled with small bright bodies moving with considerable rapidity in irregular curved lines, but with a certain uniformity which suggests that their movements are confined to definite channels. They are usually better seen when one or more sheets of cobalt glass are held before the face, so that the eyes are bathed in blue light. That the phenomenon depends upon the circulation of the blood globules in the retina is evident from the fact that the moving bodies follow paths which correspond with the form of the retinal capillaries as seen by the methods above described, and also from the correspondence between the rate of movement of the intraocular image and the rapidity of the capillary circulation in those organs in which it can be directly measured under the microscope. The exact way in which the moving globules stimulate the retina so as to produce the observed phenomenon must be regarded as an unsettled question.

We have thus seen that the eye, regarded from the optician's point of view, has not only all the faults inherent in optical instruments generally, but many others which would not be tolerated in an instrument of human construction. Yet with all its imperfections the eye is perhaps the most wonderful instance in nature of the development of a highly specialized organ to fulfil a definite purpose. In the accomplishment of this object the various parts of the eye have been perfected to a degree sufficient to enable it to meet the requirements of the nervous system with which it is connected, and no farther. In the ordinary use of the eye we are unconscious of its various irregularities, shadows, opacities, etc., for these imperfections are all so slight that the resulting inaccuracy of the image does not much exceed the limit which the size of the light-perceiving elements of the retina imposes upon the delicacy of our visual perceptions, and it is only by illuminating the eye in some unusual way that the existence of these imperfections can be detected. In other words, the eye is as good an optical instrument as the nervous system can appreciate and make use of. Moreover, when we reflect upon the difficulty of the problem which nature has solved, of constructing an optical instrument out of living and growing animal tissue, we cannot fail to be struck by the perfection of the dioptric apparatus of the eye as well as by its adaptation to the needs of the organism of which it forms a part.

Iris.—The importance of the iris as an adjustable diaphragm for cutting off side rays and thus securing good definition in near vision has been described in connection with the act of accommodation. Its other function of protecting the retina from an excess of light is no less important, and we must now consider how this pupillary adjustment may be studied and by what mechanism it is effected. The changes in the size of the pupil may be conveniently observed in man and animals by holding a millimeter scale in front of the eye and noticing the variations in the diameter of the pupil. It should be borne in mind that the iris, seen in this way, does not appear in its natural size and position, but somewhat enlarged and bulged forward by the magnifying effect of the cornea and the aqueous humor. The changes in one's own pupil may be readily observed by noticing the varying size of the circle of light thrown upon the retina when the eye is illuminated by a point of light held at the anterior focus, as in the method above described for the study of intraocular images.

The muscles of the iris are, except in birds, of the unstriped variety, and are arranged concentrically around the pupil. Radiating fibres are also recognized by many observers, though their existence has been called in question by others. The circular or constricting muscles of the iris are under the control of the third pair of cranial nerves, and are normally brought into activity in consequence of light falling upon the retina. This is a reflex phenomenon, the optic nerve being the afferent, and the third pair, the ciliary ganglion, and the short ciliary nerves the efferent, channel, as indicated in Figure 142. This reflex is in man and many of the higher animals bilateral—*i. e.* light falling upon one retina will cause a contraction of both pupils. This may readily be observed in one's own eye when focally illuminated in the manner above described. Opening the other eye will, under these conditions, cause a diminution, and closing it an increase, in the size of the circle of light. This bilateral character is found to be dependent upon the nature of the decussation of the optic nerves, for in animals in which the crossing is complete the reflex is confined to the illuminated eye. The arrangement of the fibres in the optic commissure is in general associated with the position of the eyes in the head. When the eyes are so placed that they can both be directed to the same object, as in man and many of the higher animals, the fibres of each optic nerve are usually found to be distributed to both optic tracts, while in animals whose eyes are in opposite sides of the head there is complete crossing of the optic nerves. Hence it may be said that animals having binocular vision have in general a bilateral pupillary reflex. The rule is, however, not without exceptions, for owls, though their visual axes are parallel, have, like other birds, a com-



Course of constrictor nerve-fibres ....
" dilator " ---------------------

FIG. 142.—Diagrammatic representation of the nerves governing the pupil (after Foster): *II*, optic nerve; *l. g*, ciliary ganglion; *r. b*, its short root from *III*, motor-oculi nerve; *sym*, its sympathetic root; *r. l*, its long root from *V*, ophthalmo-nasal branch of ophthalmic division of fifth nerve; *s. c.* short ciliary nerves; *l. c*, long ciliary nerves.

plete crossing of the optic nerves, and consequently a unilateral pupillary reflex.[1]

A direct as well as a reflex constriction of the pupil under the influence of light has been observed in the excised eyes of eels, frogs, and some other animals. As the phenomenon can be seen in preparations consisting of the iris alone or of the iris and cornea together, it is evident that the light exerts its influence directly upon the tissues of the iris and not through an intraocular connection with the retina. The maximum effect is produced by the yellowish-green portion of the spectrum.

Antagonizing the motor oculi nerve in its constricting influence on the pupil is a set of nerve-fibres the function of which is to increase the size of the pupil. Most of these fibres seem to run their course from a centre which lies in the floor of the third ventricle not far from the origin of the third pair, through the bulb, the cervical cord, the anterior roots of the upper dorsal nerves, the upper thoracic ganglion, the cervical sympathetic nerve as far as the upper cervical ganglion; then through a branch which accompanies the internal carotid artery, passes over the Gasserian ganglion and joins the ophthalmic branch of the fifth pair; then through the nasal branch of the latter nerve and the long ciliary nerves to the eye[2] (see diagram, p. 323). These fibres appear to be in a state of tonic activity, for section of them in any part of their course (most conveniently in the cervical sympathetic) causes a contraction of the pupil which, on stimulation of the peripheral end of the divided nerve, gives place to a marked dilatation. Their activity can be increased in various ways. Thus dilatation of the pupil may be caused by dyspnea, violent muscular efforts, etc. Stimulation of various sensory nerves may also cause reflex dilatation of the pupil, and since this phenomenon may be observed, though greatly diminished in intensity, after extirpation of the superior cervical sympathetic ganglion, it is probable that the dilatation depends in part upon a reflex inhibition of the constrictor nerves.

Since the cervical sympathetic nerve contains vaso-constrictor fibres for the head and neck, it has been thought that its dilating effect upon the pupil might be explained by its power of causing changes in the amount of blood in the vessels of the iris. There is no doubt that a condition of vascular turgescence or depletion will tend to produce contraction or dilatation of the pupil, but it is impossible to explain the observed phenomena in this way, since the pupillary are more prompt than the vascular changes, and may be observed on a bloodless eye. Moreover, the nerve-fibres producing them are said to have a somewhat different course. Another explanation of the influence of the sympathetic on the pupil is that it acts by inhibiting the contraction of the sphincter muscles, and that the dilatation is simply an elastic reaction. But since it is posssible to produce local dilatation of the pupil by circumscribed stimulation at or near

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[1] Steinach: *Archiv für die gesammte Physiologie*, xlvii. 313.

[2] Langley: *Journal of Physiology*, xiii. p. 575. For the evidence of the existence of a "cilio-spinal" centre in the cord, see Steil and Langendorff: *Archiv für die gesammte Physiologie*, lviii. S. 155; also Schenck: *Ibid.*, lxii. S. 494.

the outer border of the iris, it seems more reasonable to conclude that the dilator nerves of the pupil act upon radial muscular fibres in the substance of the iris, in spite of the fact that the existence of such fibres has not been universally admitted.

Whatever view may be taken of the mechanism by which the sympathetic nerves influence the pupil, there is no doubt that the iris is under the control of two antagonistic sets of nerve-fibres, both of which are, under normal circumstances, in a state of tonic activity. Therefore, when the sympathetic nerve is divided the pupil contracts under the influence of the motor oculi, and section of the motor oculi causes dilatation through the unopposed influence of the sympathetic.

The movements of the iris, though performed by smooth muscles, are more rapid than those of smooth muscles found elsewhere—*e. g.* in the intestines and the arteries. The contraction of the pupil when the retina of the opposite eye is illuminated occupies about 0.3″; the dilatation when the light is cut off from the eye, about 3″ or 4″. The latter determination is, however, difficult to make with precision, since dilatation of the pupil takes place at first rapidly and then more slowly, so that the moment when the process is at an end is not easily determined. After remaining a considerable time in absolute darkness the pupils become enormously dilated, as has been shown by flash-light photographs taken under these conditions. In sleep, though the eyes are protected from the light, the pupils are strongly contracted, but dilate on stimulation of sensory nerves, even though the stimulation may be insufficient to rouse the sleeper.

Many drugs when introduced into the system or applied locally to the conjunctiva produce effects upon the pupil. Those which dilate it are known as *mydriatics,* those which contract it as *myotics.* Of the former class the most important is atropin, the alkaloid of the Atropa belladonna, and of the latter physostigmin, the alkaloid of the Calabar bean. In addition to their action upon the pupil, mydriatics paralyze the accommodation, thus focussing the eye for distant objects, while myotics, by producing a cramp of the ciliary muscle, adjust the eye for near vision. The effect on the accommodation usually begins later and passes off sooner than the affection of the pupil. Atropin seems to act by producing local paralysis of the terminations of the third pair of cranial nerves in the sphincter iridis and the ciliary muscle. In large doses it may also paralyze the muscle-fibres of the sphincter. With this paralyzing action there appears to be combined a stimulating effect upon the dilator muscles of the iris. The myotic action of physostigmin seems to be due to a local stimulation of the fibres of the sphincter of the iris.[1]

Although in going from a dark room to a lighter one the pupil at first contracts, this contraction soon gives place to a dilatation, and in about three or four minutes the pupil usually regains its former size. In a similar manner the primary dilatation of the pupil caused by entering a dark room from a lighter one is followed by a contraction which usually restores the pupil to its original size within fifteen or twenty minutes. It is thus evident that the

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[1] See Paul Schultz: *Archiv für Physiologie,* 1898, S. 47.

amount of light falling upon the retina is not the only factor in determining the size of the pupil. In fact, if the light acts for a sufficient length of time the pupil may have the same size under the influence of widely different degrees of illumination.[1]

This so-called "adaptation" of the eye to various amounts of light seems to be connected with the movements of the retinal pigment-granules and with the chemical changes of the visual purple, to be more fully described in connection with the physiology of the retina.

The Ophthalmoscope.—Under normal conditions the pupil of the eye appears as a black spot in the middle of the colored iris. The cause of this dark appearance of the pupil is to be found in the fact that a source of light and the retina lie in the conjugate foci of the dioptric apparatus of the eye. Hence any light entering the eye that escapes absorption by the retinal pigment and is reflected from the fundus must be refracted back to the source from which it came. The eye of an observer who looks at the pupil from another direction will see no light coming from it, and it will therefore appear to him black. It is therefore evident that the essential condition for perceiving light coming from the fundus of the eye is that the line of vision of the observing eye shall be in the line of illumination. This condition is fulfilled by means of instruments known as ophthalmoscopes. The principles involved in the construction of the most common form of ophthalmoscope are illustrated diagrammatically in Figure 143.

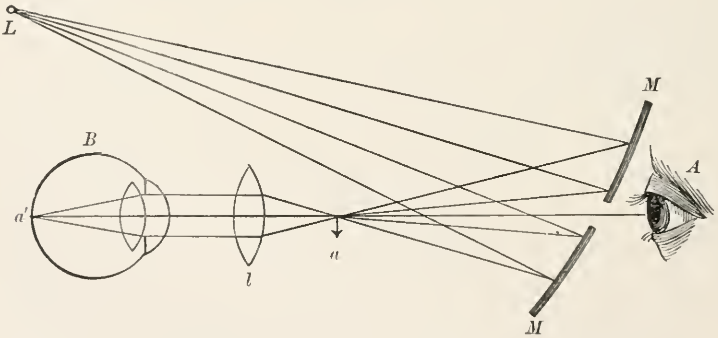

FIG. 143.—Diagram to illustrate the principles of a simple ophthalmoscope (after Foster).

The rays from a source of light *L*, after being brought to a focus at *a* by the concave perforated mirror *M M*, pass on and are rendered parallel by the lens *l*. Then, entering the observed eye *B*, they are brought to a focus on the retina at *a'*. Any rays which are reflected back from the part of the retina thus illuminated will follow the course of the entering rays and be brought to a focus at *a*. The eye of an observer at *A*, looking through the hole in the mirror, will therefore see at *a* an inverted image of the retina, the observation of which may be facilitated by a convex lens placed immediately in front of the observer's eye.

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[1] Schirmer: *Archiv für Ophthalmologie*, xi. 5.

The fundus of the eye thus observed presents a reddish background on which the retinal vessels are distinctly visible.

Retina.—Having considered the mechanism by which optical images of objects at various distances from the eye are formed upon the retina, we must next inquire what part of the retina is affected by the rays of light, and in what this affection consists. To the former of these questions it will be found possible to give a fairly satisfactory answer. With regard to the latter nothing positive is known.

The structure of the retina is exceedingly complicated, but, as very little is known of the functions of the ganglion cells and of the molecular and nuclear layers, it will suffice for the present purpose of physiological description to regard the retina as consisting of fibres of the optic nerve which are connected through various intermediate structures with the layer of rods and cones.

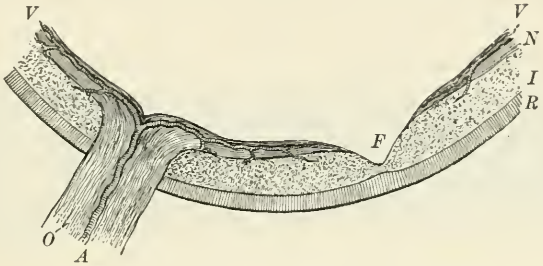

Fig. 144.—Diagrammatic representation of the retina.

Figure 144 is intended to show, diagrammatically, the mutual relation of these various portions of the retina in different parts of the eye, and is not drawn to scale. It will be observed that the optic nerve *O*, where it enters the eye, interrupts the continuity of the layer of rods and cones *R* and of the intermediate structures *I*. Its fibres spread themselves out in all directions, forming the internal layer of the retina *N*. The central artery of the retina *A* accompanying the optic nerve ramifies in the layer of nerve-fibres and in the immediately adjacent layers of the retina, forming a vascular layer *V*. In the fovea centralis *F* of the macula lutea (the centre of distinct vision) the layer of rods and cones becomes more highly developed, while the other layers of the retina are much reduced in thickness and the blood-vessels entirely disappear. This histological observation points strongly to the conclusion that the rods and cones are the structures which are essential to vision, and that in them are found the conditions for the conversion of the vibrations of the luminiferous ether into a stimulus for a nerve-fibre. This view derives confirmation from the observations on the retinal blood-vessels, for it is found that the distance between the vascular layer of the retina and the layer of rods and cones determined by histological methods corresponds with that which must exist between the vessels and the light-perceiving elements of the retina, as calculated from the apparent displacement of the shadow caused by given movements of the source of light used in studying intraocular images[1] as

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[1] "Dimmer: Verh. d. phys. Clubs zu Wien, 24 April, 1894," *Centralbl. für Physiologie*, 1894, 159.

described on p. 321. Another argument in favor of this view is found in the correspondence between the size of the smallest visible images on the retina and the diameter of the rods and cones. A double star can be recognized as double by the normal eye when the distance between the components corresponds to a visual angle of 60″. Two white lines on a black ground are seen to be distinct when the distance between them subtends a visual angle of 64″–73″. These angles correspond to a retinal image of 0.0044, 0.0046, and 0.0053 millimeter. Now, the diameter of the cones in the macula lutea, as determined by Kölliker, is 0.0045–0.0055 millimeter, a size which agrees well with the hypothesis that each cone when stimulated can produce a special sensation of light distinguishable from those caused by the stimulation of the neighboring cones. The existence of the so-called blind spot in the retina at the point of entrance of the optic nerve is sometimes regarded as evidence of the light-perceiving function of the rods and cones, but as the other layers of the retina, as well as the rods and cones, are absent at this point, and the retina here consists solely of nerve-fibres, it is evident that the presence of the blind spot only proves that the optic nerve-fibres are insensible to light. Figure 145 is intended to demonstrate this insensibility. For this purpose it should be held at a distance of about 23 centimeters from the eyes (*i. e.* about 3.5 times the distance between the cross and the round spot). If the left eye be closed and the right eye fixed upon the cross, the round spot will disappear from view, though it will become visible if the eye be directed either to the right or to the left of the cross, or if the figure be held either a greater or a less distance from the eye. The size and shape of the blind spot may readily be determined as follows: Fix the eye upon a definite point marked upon a sheet of white paper. Bring the black point of a lead pencil (which, except the point, has been painted white or covered with white paper) into the invisible portion of the field of vision and carry it outward in any direction until it becomes visible. Mark upon the paper the point at which it just begins to be seen, and by repeating the process in as many different directions as possible the outline of the blind spot may be marked out. Figure 146 shows the shape of the blind spot determined by Helmholtz in his own right eye, *a* being the point of fixation of the eye, and the line *A B* being one-third of the distance between the eye and the paper. The irregularities of outline, as at

FIG. 145.—To demonstrate the blind spot.

FIG. 146.—Form of the blind spot (Helmholtz).

d, are due to shadows of the large retinal vessels. During this determination it is of course necessary that the head should occupy a fixed position with regard to the paper. This condition can be secured by holding firmly between the teeth a piece of wood that is clamped in a suitable position to the edge of the table. The diameter of the blind spot, as thus determined, has been found to correspond to a visual angle varying from 3° 39′ to 9° 47′, the average measurement being 6° 10′. This is about the angle that is subtended by the human face seen at a distance of two meters. Although a considerable portion of the retina is thus insensible to light, we are, in the ordinary use of the eyes, conscious of no corresponding blank in the field of vision. By what psychical operation we "fill up" the gap in our subjective field of vision caused by the blind spot of the retina is a question that has been much discussed without being definitely settled.

The above-mentioned reasons for regarding the rods and cones as the light-perceiving elements of the retina seem sufficiently conclusive. Whether there is any difference between the rods and the cones with regard to their light-perceiving function is a question which may be best considered in connection with a description of the qualitative modifications of light.

The histological relation between the various layers of the retina is still under discussion. According to recent observations of Cajal,[1] the connection between the rods and cones on the one side and the fibres of the optic nerve on the other is established in a manner which is represented diagrammatically in Figure 147. The prolongations of the bipolar cells of the internal nuclear layer *E* break up into fine fibres in the external molecular (or plexiform) layer *C*. Here they are brought into contact, though not into anatomical continuity, with the terminal fibres of the rods and cones. The inner prolongations of the same bipolar cells penetrate into the internal molecular (or plexiform) layer *F*, and there come into contact with the dendrites coming from the layer of ganglion-cells *G*. These cells are, in their turn, connected by their axis-cylinder processes with the fibres of the optic nerve. The bipolar cells which serve as connective links between the rods and the optic nerve-fibres are anatomically distinguishable (as indicated in the diagram)

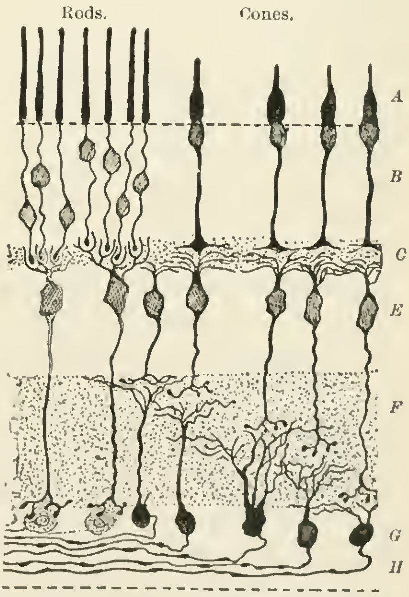

FIG. 147.—Diagrammatic representation of the structure of the retina (Cajal): *A*, layer of rods and cones; *B*, external nuclear layer; *C*, external molecular (or plexiform) layer; *E*, internal nuclear layer; *F*, internal molecular (or plexiform) layer; *G*, layer of ganglion-cells; *H*, layer of nerve-fibres.

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[1] *Die Retina der Wirbelthiere*, Wiesbaden, 1894.

from those which perform the same function for the cones. Whatever be the precise mode of connection between the rods and cones and the fibres of the optic nerve, it is evident that each retinal element cannot be connected with the nerve-centres by a separate independent nerve-channel, since the retina contains many millions of rods and cones, while the optic nerve has only about 438,000 nerve-fibres,[1] though of course such a connection may exist in the fovea centralis, as Cajal has shown is probably the case in reptiles and birds.

Changes Produced in the Retina by Light.—We must now inquire what changes can be supposed to occur in the rods and cones under the influence of light by means of which they are able to transform the energy of the ether vibrations into a stimulus for the fibres of the optic nerve. Though in the present state of our knowledge no satisfactory answer can be given to this question, yet certain direct effects of light upon the retina have been observed which are doubtless associated in some way with the transformation in question.

The retina of an eye which has been protected from light for a considerable length of time has a purplish-red color, which upon exposure to light changes to yellow and then fades away. This bleaching occurs also in monochromatic light, the most powerful rays being those of the greenish-yellow portion of the spectrum—*i. e.* those rays which are most completely absorbed by the purplish-red coloring matter. A microscopic examination of the retina shows that this coloring matter, which has been termed *visual purple*, is entirely confined to the outer portion of the retinal rods and does not occur at all in the cones. After being bleached by light it is, during life, restored through the agency of the pigment epithelium, the cells of which, under the influence of light, send their prolongations inward to envelop the outer limbs of the rods and cones with pigment. If an eye, either excised or in its natural position, is protected from light for a time, and then placed in such a position that the image of a lamp or a window is thrown upon the retina for a time which may vary with the amount of light from seven seconds to ten minutes, it will be found that the retina, if removed and examined under red light, will show the image of the luminous object impressed upon it by the bleaching of the visual purple.

FIG. 148.—Optogram in eye of rabbit (Kühne).

If the retina be treated with a 4 per cent. solution of alum, the restoration of the visual purple will be prevented, and the so-called "optogram" will be, as photographers say, "fixed."[2]

Figure 148 shows the appearance of a rabbit's retina on which the optogram of a window has been impressed.

Although the chemical changes in the visual purple under the influence of light seem, at first sight, to afford an explanation of the transformation of the vibrations of the luminiferous ether into a stimulation for the optic nerve, yet the fact that vision is most distinct in the fovea centralis of the retina, which,

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[1] Salzer: *Wiener Sitzungsberichte*, 1880, Bd. lxxxi. S. 3.

[2] Kühne: *Untersuchungen a. d. phys. Inst. d. Universität Heidelberg*, i. 1.

as it contains no rods, is destitute of visual purple, makes it impossible to regard this coloring matter as essential to vision. The most probable theory of its function is perhaps that which connects it with the adaptation of the eye to varying amounts of light, as described on p. 326.

In addition to the above-mentioned movements of the pigment epithelium cells under the influence of light, certain changes in the retinal cones of frogs and fishes have been observed.[1] The change consists in a shortening and thickening of the inner portion of the cones when illuminated, but the relation of the phenomenon to vision has not been explained.

Like most of the living tissues of the body, the retina is the seat of electrical currents. In repose the fibres of the optic nerve are said to be positive in relation to the layer of rods and cones. When light falls upon the retina this current is at first increased and then diminished in intensity.

Sensation of Light.—Whatever view may be adopted with regard to the mechanism by which light is enabled to become a stimulus for the optic nerve, the fundamental fact remains that the retina (and in all probability the layer of rods and cones in the retina) alone supplies the conditions under which this transformation of energy is possible. But in accordance with the "law of specific energy" a sensation of light may be produced in whatever way the optic nerve be stimulated, for a stimulus reaching the visual centres through the optic nerve is interpreted as a visual sensation, in the same way that pressure on a nerve caused by the contracting cicatrix of an amputated leg often causes a painful sensation which is referred to the lost toes to which the nerve was formerly distributed. Thus local pressure on the eyeball by stimulating the underlying retina causes luminous sensations, already described as "phosphenes," and electrical stimulation of the eye as a whole or of the stump of the optic nerve after the removal of the eye is found to give rise to sensations of light.

Vibrations of the luminiferous ether constitute, however, the normal stimulus of the retina, and we must now endeavor to analyze the sensation thus produced. In the first place, it must be borne in mind that the so-called ether waves differ among themselves very widely in regard to their rate of oscillation. The slowest known vibrations of the ether molecules have a frequency of about 107,000,000,000,000 in a second, and the fastest a rate of about 40,000,000,000,000,000 in a second—a range, expressed in musical terms, of about eight and one-half octaves. All these ether waves are capable of warming bodies upon which they strike and of breaking up certain chemical combinations, the slowly vibrating waves being especially adapted to produce the former and the rapidly vibrating ones the latter effect. Certain waves of intermediate rates of oscillation—viz. those ranging between 392,000,000,000,000 and 757,000,000,000,000 in a second—not only produce thermic and chemical effects, but have the power, when they strike the retina, of causing changes in the layer of rods and cones, which, in their turn, act as a stimulus to the optic nerve. The ether waves which produce these various phenomena are often spoken of as heat rays, light rays, and actinic or chemical rays, but

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[1] Engelmann: *Archiv für die gesammte Physiologie*, xxxv. 498.

it must be remembered that the same wave may produce all three classes of phenomena, the effect depending upon the nature of the substance upon which it strikes. It will be observed that the range of vibrations capable of affecting the retina is rather less than one octave, a limitation which obviously tends to reduce the amount of chromatic aberration.

In this connection it is interesting to notice that the highest audible note is produced by about 40,000 sonorous impulses in a second. Between the highest audible note and the lowest visible color there is a gap of nearly thirty-four octaves in which neither the vibrations of the air nor those of the luminiferous ether affect our senses. Even if the slowly vibrating heat-rays which affect our cutaneous nerves are taken into account, there still remain over thirty-one octaves of vibrations, either of the air or of the luminiferous ether, which may be, and very likely are, filling the universe around us without in any way impressing themselves upon our consciousness.[1]

Qualitative Modifications of Light.—All the ethereal vibrations which are capable of affecting the retina are transmitted with very nearly the same rapidity through air, but when they enter a denser medium the waves having a rapid vibration are retarded more than those vibrating more slowly. Hence when a ray of sunlight composed of all the visible ether waves strikes upon a plane surface of glass, the greater retardation of the waves of rapid vibration causes them to be more refracted than those of slower vibration, and if the glass has the form of a prism, as shown in Figure 149, this so-called "dispersion" of the rays is still further increased when the rays leave the glass, so that the emerging beam, if received upon a white surface, instead of forming a spot of white light, produces a band of color known as the solar spectrum. The colors of the spectrum, though commonly spoken of as seven in number, really form a continuous series from the extreme red to the extreme violet, these colors corresponding to ether vibrations with rates of 392,000,000,000,000 and 757,000,000,000,000 in 1 second, and wave lengths of 0.7667 and 0.3970 micromillimeters[2] respectively.

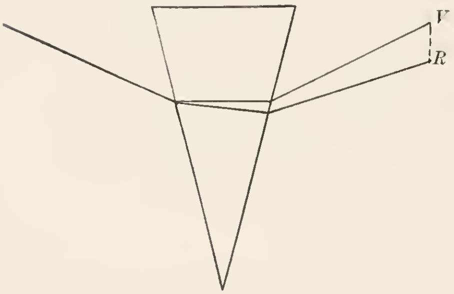

FIG. 149.—Diagram illustrating the dispersion of light by a prism.

Colors, therefore, are sensations caused by the impact upon the retina of certain ether waves having definite frequencies and wave-lengths, but these are not the only peculiarities of the ether vibration which influence the retinal sensation. The energy of the vibration, or the *vis viva* of the vibrating molecule, determines the "intensity" of the sensation or the brilliancy of the light.[3]

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[1] The vibrations of electrical energy utilized in wireless telegraphy are probably intermediate in their rate between those of sound and light.

[2] One micromillimeter = 0.001 millimeter = one μ.

[3] The energy of vibration capable of producing a given subjective sensation of intensity varies with the color of the light, as will be later explained (see p. 340).

Furthermore, the sensation produced by the impact of ether waves of a definite length will vary according as the eye is simultaneously affected by a greater or less amount of white light. This modification of the sensation is termed its degree of "saturation," light being said to be completely saturated when it is "monochromatic" or produced by ether vibrations of a single wave-length.

The modifications of light which taken together determine completely the character of the sensation are, then, three in number—viz.: 1. Color, dependent upon rate of vibration or length of the ether wave; 2. Intensity, dependent upon the energy of the vibration; 3. Saturation, dependent upon the amount of white light mingled with the monochromatic light. These three qualitative modifications of light must now be considered in detail.

Color.—In our profound ignorance of the nature of the process by which, in the rods and cones, the movements of the ether waves are converted into a stimulus for the optic nerve-fibres, all that can be reasonably demanded of a color theory is that it shall present a logically consistent hypothesis to account for the sensations actually produced by the impact of ether waves of varying rates, either singly or combined, upon different parts of the retina. Some of the important phenomena of color sensation of which every color theory must take account may be enumerated as follows:

1. Luminosity is more readily recognized than color. This is shown by the fact that a colored object appears colorless when it is too feebly illuminated, and that a spectrum produced by a very feeble light shows variations of intensity with a maximum nearer than normal to the blue end, but no gradations of color. A similar lack of color is noticed when a colored object is observed for too short a time or when it is of insufficient size. In all these respects the various colors present important individual differences which will be considered later.

2. Colored objects seen with increasing intensity of illumination appear more and more colorless, and finally present the appearance of pure white. Yellow passes into white more readily than the other colors.

3. The power of the retina to distinguish colors diminishes from the centre toward the periphery, the various colors, in this respect also, differing materially from each other. Sensibility to red is lost at a short distance from the macula lutea, while the sensation of blue is lost only on the extreme lateral portions of the retina. The relation of this phenomenon to the distribution of the rods and cones in the retina will be considered in connection with the perception of the intensity of light.

Color-mixture.—Since the various spectral colors are produced by the dispersion of the white light of the sun, it is evident that white light may be reproduced by the reunion of the rays corresponding to the different colors, and it is accordingly found that if the colored rays emerging from a prism, as in Fig. 149, are reunited by suitable refracting surfaces, a spot of white light will be produced similar to that which would have been caused by the original beam of sunlight. But white light may be produced not only by the union of *all* the spectral colors, but by the union of certain selected colors in twos, threes, fours, etc. Any two spectral colors which by their union produce white are said to be "complementary" colors. The relation of these pairs of complementary colors to each other may be best understood by reference to Figure 150.

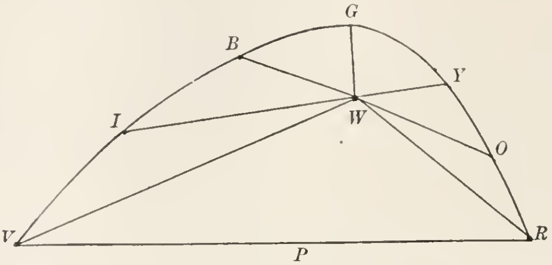

FIG. 150.—Color diagram.

Here the spectral colors are supposed to be disposed around a curved line, as indicated by their initial letters, and the two ends of the curve are united by a straight line, thus enclosing a surface having somewhat the form of a triangle with a rounded apex. If the curved edge of this surface be supposed to be loaded with weights proportionate to the luminosity of the different colors, the centre of gravity of the surface will be near the point *W*. Now, if a straight line be drawn from any point on the curved line through the point *W* and prolonged till it cuts the curve again, the colors corresponding to the two ends of this straight line will be complementary colors. Thus in Figure 150 it will be seen that the complementary color of red is bluish-green, and that of yellow lies near the indigo. It is also evident that the complementary color of green is purple, which is not a spectral color at all, but a color obtained by the union of violet and red. The union of a pair of colors lying nearer together than complementary colors produces an intermediate color mixed with an amount of white which is proportionate to the nearness of the colors to the complementary. Thus the union of red and yellow produces orange, but a less saturated orange than the spectral color. The union of two colors lying farther apart than complementary colors produces a color which borders more or less upon purple.

The mixing of colors to demonstrate the above-mentioned effects may be accomplished in three different ways:

1. By employing two prisms to produce two independent spectra, and then directing the colored rays which are to be united so that they will illuminate the same white surface.

2. By looking obliquely through a glass plate at a colored object placed behind it, while at the same time light from another colored object, placed in front of the glass, is reflected into the eye of the observer, as shown in Figure 151. Here the transmitted light from the colored object *A* and the reflected light from the colored object *B* enter the eye at *C* from the same direction, and are therefore united upon the retina.

3. By rotating before the eye a disk on which the colors to be united are painted upon different sectors. This is most readily accomplished by using

a number of disks, each painted with one of the colors to be experimented with, and each divided radially by a cut running from the centre to the circumference. The disks can then be lapped over each other and rotated together, and in this way two or more colors can be mixed in any desired proportions. This method of mixing colors depends upon the property of the retina to retain an impression after the stimulus causing it has ceased to act—a phenomenon of great importance in physiological optics, and one which will be further discussed in connection with the subject of "after-images."

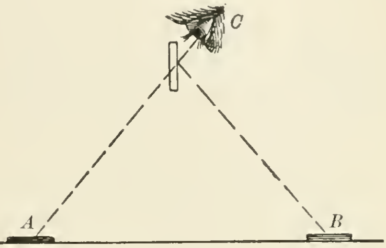

FIG. 151.—Diagram to illustrate color mixture by reflected and transmitted light (Helmholtz).

The physiological mixing of colors cannot be accomplished by the mixture of pigments or by allowing sunlight to pass successively through glasses of different colors, for in these cases rays corresponding to certain colors are absorbed by the medium through which the white light passes, and the phenomenon is the result of a process of subtraction and not addition. Light reaching the eye through red glass, for instance, looks red because all the rays except the red rays are absorbed, and light coming through green glass appears green for a similar reason. Now, when light is allowed to pass successively through red and green glass the only rays which pass through the red glass will be absorbed by the green. Hence no light will pass through the combination of red and green glass, and darkness results. But when red and green rays are mixed by any of the three methods above described the result of this process of addition is not darkness, but a yellow color, as will be understood by reference to the color diagram on p. 334. In the case of colored pigments similar phenomena occur, for here too light reaches the eye after rays of certain wave-lengths have been absorbed by the medium. This subject will be further considered in connection with color-theories.[1]

Color-theories.—From what has been said of color-mixtures it is evident that every color sensation *may* be produced by the mixture of a number of other color sensations, and that *certain* color sensations—viz. the purples—can be produced *only* by the mixture of other sensations, since there is no single wave-length corresponding to them. Hence the hypothesis is a natural one that *all* colors are produced by the mixture in varying proportions of a certain number of fundamental colors, each of which depends for its production upon the presence in the retina of a certain substance capable of being affected (probably through some sort of a photo-chemical process) by light of a certain definite wave-length. A hypothesis of this sort lies at the basis of both the Young-Helmholtz and the Hering theories of color sensation.

The former theory postulates the existence in the retina of three substances capable of being affected by red, green, and violet rays, respectively—*i. e.* by the three colors lying at the three angles of the color diagram given on p. 334

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[1] For an interesting discussion of modern theories of color-vision, see the address of Professor Frank P. Whitman on "Color-vision," *Science*, Sept. 9, 1898.

—and regards all other color sensations as produced by the simultaneous affection of two of these substances in varying proportions. Thus when a ray of blue light falls on the retina it stimulates the violet- and green-perceiving substances, and produces a sensation intermediate between the two, while simultaneous stimulation of the red- and green-perceiving substances produces the sensations corresponding to yellow and orange; and when the violet- and red-perceiving substances are affected at the same time, the various shades of purple are produced. Each of these three substances is, however, supposed to be affected to a slight extent by all the rays of the visible spectrum, a supposition which is rendered necessary by the fact that even the pure spectral colors do not appear to be perfectly saturated, as will be explained in connection with the subject of saturation. Furthermore, the disappearance of color when objects are very feebly or very brightly illuminated or when they are seen with the lateral portions of the retina (as described on p. 333) necessitates the additional hypotheses that these three substances are all equally affected by all kinds of rays when the light is of either very small or very great intensity or when it falls on the extreme lateral portions of the retina, and that they manifest their specific irritability for red, green, and violet rays respectively only in light of moderate intensity falling not too far from the fovea centralis of the retina.

The modifications of the Young-Hemholtz theory introduced by these subsidiary hypotheses greatly diminish the simplicity which was its chief claim to acceptance when originally proposed. Moreover, there will always remain a psychological difficulty in supposing that three sensations so different from each other as those of red, green, and violet can by their union produce a fourth sensation absolutely distinct from any of them—viz. white.

The fact that in the Hering theory this difficulty is obviated has contributed greatly to its acceptance by physiologists. In this theory the retina is supposed to contain three substances in which chemical changes may be produced by ether vibrations, but each of these substances is supposed to be affected in two opposite ways by rays of light which correspond to complementary color sensations. Thus in one substance—viz. the white-black visual substance—katabolic or destructive changes are supposed to be produced by all the rays of the visible spectrum, the maximum effect being caused by the yellow rays, while anabolic or constructive changes occur when no light at all falls upon the retina. The chemical changes of this substance correspond, therefore, to the sensation of luminosity as distinguished from color. In a second substance red rays are supposed to produce katabolic, and green rays anabolic changes, while a third substance is similarly affected by yellow and blue rays. These two substances are therefore spoken of as red-green and yellow-blue visual substances respectively.

It has been sometimes urged as an objection to this theory that the effect of a stimulus is usually katabolic and not anabolic. This is true with regard to muscular contraction, from the study of which phenomenon most of our knowledge of the effect of stimulation has been obtained, but it should be remembered that observations on the augmentor and inhibitory cardiac nerves have shown us that nerve-stimulation may produce very contrary effects. There seems to be, therefore, no serious theoretical difficulty in supposing that light rays of different wave-lengths may produce opposite metabolic effects upon the substances in which changes are associated with visual sensations.

A more serious objection lies in the difficulty of distinguishing between the sensation of blackness, which, on Hering's hypothesis, must correspond to active anabolism of the white-black substance, and the sensation of darkness (such as we experience when the eyes have been withdrawn for some time from the influence of light), which must correspond to a condition of equilibrium of the white-black substance in which neither anabolism nor katabolism is occurring.

Another objection to the Hering theory is to be found in the results of experiments in comparing grays or whites produced by mixing different colored rays under varying intensities of light. The explanation given by Hering of the production of white through the mixture of blue and yellow or of red and green is that when either of these pairs of complementary colors is mixed the anabolic and the katabolic processes balance each other, leaving the corresponding visual substance in a condition of equilibrium. Hence, the white-black substance being alone stimulated, the result will be a sensation of white corresponding to the intensity of the katabolic process caused by the mixed rays. Now, it is found that when blue and yellow are mixed in certain proportions on a revolving disk a white can be produced which will, with a certain intensity of illumination, be undistinguishable from a white produced by mixing red and green. If, however, the intensity of the illumination is changed, it will be found necessary to add a certain amount of white to one of the mixtures in order to bring them to equality. On the theory that complementary colors produce antagonistic processes in the retina it is difficult to understand why this should be the case.[1]

A color theory which is in some respects more in harmony with recent observations in the physiology of vision has been proposed by Mrs. C. L. Franklin. In this theory it is supposed that, in its earlier periods of development, the eye is sensitive only to luminosity and not to color—*i. e.* it possesses only a white-black or (to use a single word) a *gray*-perceiving substance which is affected by all visible light rays, but most powerfully by those lying near the middle of the spectrum. The sensation of gray is supposed to be dependent upon the chemical stimulation of the optic nerve-terminations by some product of decomposition of this substance.

In the course of development a portion of this gray visual substance becomes differentiated into three different substances, each of which is affected by rays of light corresponding to one of the three fundamental colors of the spectrum—viz. red, green, and blue. This differentiation may be supposed to occur in the cones rather than in the rods, which thus become organs specially adapted

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[1] The renewal of the rod pigment in a dim light may afford an explanation of this phenomenon (see C. Ladd Franklin: *Psychological Review*, v. 311).

for the perception of color (see p. 342). When a ray of light intermediate between two of the fundamental colors falls upon the retina, the visual substances corresponding to these two colors will be affected to a degree proportionate to the proximity of these two colors to that of the incident ray. Since this effect is exactly the same as that which is produced when the retina is acted upon simultaneously by light of two fundamental colors, we are incapable of distinguishing in sensation between an intermediate wave-length and a mixture in proper amounts of two fundamental wave-lengths.

When the retina is affected by two or more rays of such wave-lengths that all three of the color visual substances are equally affected, the resulting decomposition will be the same as that produced by the stimulation of the gray visual substance out of which the color visual substances were differentiated, and the corresponding sensation will therefore be that of gray or white.

It will be noticed that the important feature of this theory is that it provides for the independent existence of the gray visual substance, while at the same time the stimulation of this substance is made a necessary result of the mixture of certain color sensations.

Another color theory has recently been brought forward by Prof. G. E. Müller,[1] who substitutes for Hering's antagonistic processes of assimilation and dissimilation the conception of "reversible chemical actions"—*i. e.* actions in which the products of a chemical change can be used for the reconstruction of the original substance.

Color-blindness.—The fact that many individuals are incapable of distinguishing between certain colors—*i. e.* are more or less "color-blind"—is one of fundamental importance in the discussion of theories of color vision. By far the most common kind of color-blindness is that in which certain shades of red and green are not recognized as different colors. The advocates of the Young-Helmholtz theory explain such cases by supposing that either the red or the green perceiving elements of the retina are deficient, or, if present, are irritable, not by rays of a particular wave-length, but by all the rays of the visible spectrum. In accordance with this view these cases of color-blindness are divided into two classes—viz. the red-blind and the green-blind—the basis for the classification being furnished by more or less characteristic curves representing the variations in the luminosity of the visible spectrum as it appears to the different eyes. There are, however, cases which cannot easily be brought under either of these two classes. Moreover, it has been proved in cases of monocular color-blindness, and is admitted even by the defenders of the Helmholtz theory, that such persons see really only two colors—viz. blue and yellow. To such persons the red end of the spectrum appears a dark yellow, and the green portion of the spectrum has luminosity without color.

A better explanation of this sort of color-blindness is given in the Hering theory by simply supposing that in such eyes the red-green visual substance is deficient or wholly wanting, but the theory of Mrs. Franklin accounts for the phenomena in a still more satisfactory way; for, by supposing that the differ-

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[1] *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, 1875 and 1897.

entiation of the primary gray visual substance has first led to the formation of a blue and a yellow visual substance, and that the latter has subsequently been differentiated into a red and a green visual substance, color-blindness is readily explained by supposing that this second differentiation has either not occurred at all or has taken place in an imperfect manner. It is, in other words, an arrest of development.

Cases of *absolute* color-blindness occasionally occur. To such persons nature appears colorless, all objects presenting simply differences of light and shade.

In whatever way color-blindness is to be explained, the defect is one of considerable practical importance, since it renders those affected by it incapable of distinguishing the red and green lights ordinarily used for signals. Such persons are, therefore, unsuitable for employment as pilots, railway engineers, etc., and it is now customary to test the vision of all candidates for employment in such situations. It has been found that no satisfactory results can be reached by requiring persons to name colors which are shown them, and the chromatic sense is now commonly tested by what is known as the "Holmgren method," which consists in requiring the individual examined to select from a pile of worsteds of various colors those shades which seem to him to resemble standard skeins of green and pink. When examined in this way about 4 per cent. of the male and one-quarter of 1 per cent. of the female sex are found to be more or less color-blind. The defect may be inherited, and the relatives of a color-blind person are therefore to be tested with special care. Since females are less liable to be affected than males, it often happens that the daughters of a color-blind person, themselves with normal vision, have sons who inherit their grandfather's infirmity.

Although in all theories of color vision the different sensations are supposed to depend upon changes produced by the ether vibrations of varying rates acting upon different substances in the retina, yet it should be borne in mind that we have at present no proof of the existence of any such substances. The visual purple—or, to adopt Mrs. Franklin's more appropriate term, "the rod pigment"—was at one time thought to be such a substance, but for the reasons above given cannot be regarded as essential to vision.[1]

That a centre for color vision, distinct from the visual centre, exists in the cerebral cortex is rendered probable by the occurrence of cases of hemianopsia for colors, and also by the experiments of Heidenhain and Cohn on the influence of the hypnotic trance upon color-blindness.

Intensity.—The second of the above-mentioned qualitative modifications of light is its intensity, which is dependent upon the energy of vibrations of the molecules of the luminiferous ether. The sensation of luminosity is not, however, proportionate to the intensity of the stimulus, but varies in such a way that a given *increment* of intensity causes a greater difference in sensation with

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[1] In a recently developed theory by Ebbinghaus (*Zeitschrift für Psychologie und Physiologie der Sinnesorgane,* v. 145) a physiological importance in relation to vision is attached to this substance in connection with other substances of a hypothetical character.

feeble than with strong illuminations. This phenomenon is illustrated by the disappearance of a shadow thrown by a candle in a darkened room on a sheet of white paper when sunlight is allowed to fall on the paper from the opposite direction. In this case the absolute difference in luminosity between the shadowed and unshadowed portions of the paper remains the same, but it becomes imperceptible in consequence of the increased total illumination.

Although our power of distinguishing *absolute* differences in luminosity diminishes as the intensity of the illumination increases, yet with regard to *relative* differences no such dependence exists. On the contrary, it is found within pretty wide limits that, whatever be the intensity of the illumination, it must be increased by a certain constant fraction of its total amount in order to produce a perceptible difference in sensation. This is only a special case of a general law of sensation known as Weber's law, which has been formulated by Foster as follows: "The smallest change in the magnitude of a stimulus which we can appreciate through a change in our sensation always bears the same proportion to the whole magnitude of the stimulus."

Luminosity of Different Colors.—When two sources of light having the same color are compared, it is possible to estimate their relative luminosity with considerable accuracy, a difference of about 1 per cent. of the total luminosity being appreciated by the eye. When the sources of light have different colors, much less accuracy is attainable, but there is still a great difference in the intensity with which rays of light of different wave-lengths affect the retina. We do not hesitate to say, for instance, that the maximum intensity of the solar spectrum is found in the yellow portion, but it is important to observe that the position of this maximum varies with the illumination. In a very brilliant spectrum the maximum shifts toward the orange, and in a feeble spectrum (such as may be obtained by narrowing the slit of the spectroscope) it moves toward the green. Hence changes of intensity are associated with changes of color, and, as Haycraft[1] has observed, "we cannot abstract 'brightness' from our sensations of light as we can abstract 'loudness' from our sensations of sound." The curves in Figure 152 illustrate this shifting of the maximum of luminosity of the spectrum with varying intensities of illumination. The abscissas represent wave-lengths in millionths of a millimeter, and the ordinates the luminosity of the different colors as expressed by the reciprocal values of the width of the slit necessary to give to the color under observation a luminosity equal to that of an arbitrarily chosen standard. The curves from *A* to *H* represent the distribution of the intensity of light in the spectrum with eight different grades of illumination. This shifting of the maximum of luminosity in the spectrum explains the so-called "Purkinje's phenomenon"—viz. the changing relative values of colors in varying illumination. This can be best observed at nightfall, the attention being directed to a carpet or a wall-paper the pattern of which is made up of a number of different colors. As the daylight fades away the red colors, which in full illumination are

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[1] "Luminosity and Photometry," by John Berry Haycraft: *Journal of Physiology*, xxi. 126.

the most intense, becomes gradually darker, and are scarcely to be distinguished from black at a time when the blue colors are still very readily distinguished.

Function of Rods and Cones.—There is, as mentioned on p. 337, some reason to suppose that the rods and cones have different functions. That color sensation and accuracy of definition are most perfect in the central portion of the retina is shown by the fact that when we desire to obtain the best possible idea of the form and color of an object we direct our eyes in such a way that the image falls upon the fovea centralis of the retina. The luminosity of a faint object, however, seems greatest when we look not directly at it, but a little to one side of it. This can be readily observed when we look at a group of stars, as, for example, the Pleiades. When the eyes are accurately directed to the stars so as to enable us to count them, the total luminosity of the constellation appears much less than when the eyes are directed to a point a few degrees to one side of the object. Now, an examination of the retina shows only cones in the fovea centralis. In the immediately adjacent parts a small number of rods are found mingled with the cones. In the lateral portions of the retina the rods are relatively more numerous than the cones, and in the extreme peripheral portions the rods alone exist. Hence this phenomenon is readily explained on the supposition, which is supported by Ramón y Cajal's[1] recent observations, that the rods are a comparatively rudimentary form of visual apparatus, taking cognizance

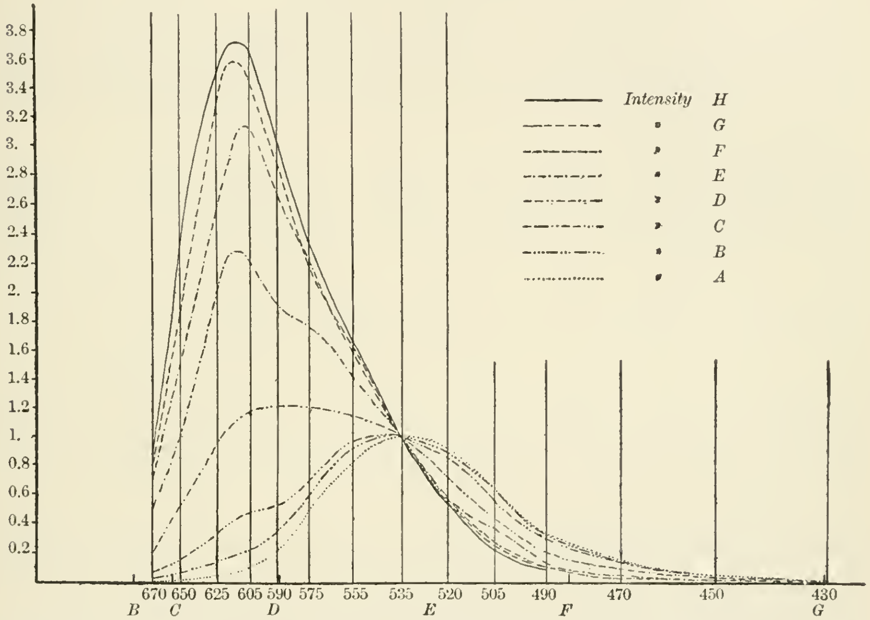

FIG. 152.—Diagram showing the distribution of the intensity of the spectrum as dependent upon the degree of illumination (König).

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[1] *Zeitschrift für Psychologie und Physiologie der Sinnesorgane,* xvi. S. 161.

of the existence of light with special reference to its varying intensity, and that the cones are organs specially modified for the localization of stimuli and for the perception of differences of wave-lengths. The view that the rods are specially adapted for the perception of luminosity and the cones for that of color derives support from the fact that in the retina of certain nocturnal animals—*e. g.* bats and owls—rods alone are present. This theory has been further developed by Von Kries,[1] who in a recent article describes the rods as differing from the cones in the following respects: (1) They are color-blind—*i. e.* they produce a sensation of simple luminosity whatever be the wave-length of the light-ray falling on them; (2) they are more easily stimulated than the cones, and are particularly responsive to light-waves of short wave-lengths; (3) they have the power of adapting themselves to light of varying intensity.

On this theory it is evident that we must get the sensation of white or colorless light in two different ways: (1) In consequence of the stimulation of the rods by any sort of light-rays, and (2) in consequence of the stimulation of the cones by certain combinations of light-rays—*i. e.* complementary colors. In this double mode of white perception lies perhaps the explanation of the effect of varying intensity of illumination upon the results of color-mixtures which has been above alluded to (see p. 337) as an objection to the Hering theory. The so-called "Purkinje's phenomenon," described on p. 340, is readily explained in accordance with this theory, for, owing to the greater irritability of the rods, the importance of these organs, as compared with the cones, in the production of the total visual sensation is greater with feeble than with strong illumination of the field of vision. At the same time, the power of the rods to respond particularly to light-rays of short wave-length will cause a greater apparent intensity of the colors at the blue than at the red end of the spectrum. In this connection it is interesting to note that the phenomenon is said not to occur when the observation is limited to the fovea centralis, where cones alone are found.[2]

Saturation.—The degree of saturation of light of a given color depends, as above stated, upon the amount of white light mixed with it. The quality of light thus designated is best studied and appreciated by means of experiments with rotating disks. If, for instance, a disk consisting of a large white and a small red sector be rapidly rotated, the effect produced is that of a pale pink color. By gradually increasing the relative size of the red sector the pink color becomes more and more saturated, and finally when the white sector is reduced to zero the maximum of saturation is produced. It must be borne in mind, however, that no pigments represent completely saturated colors. Even the colors of the spectrum do not produce a sensation of absolute saturation, for, whatever theory of color vision be adopted, it is evident that all the color-perceiving elements of the retina are affected *more or less* by all the rays of light. Thus when rays of red light fall upon the retina they will

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[1] *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, ix. 81.

[2] von Kries: *Centralblatt für Physiologie*, 1896, i.

stimulate not only the red-perceiving elements, but to a slight extent also (to use the language of the Helmholtz theory) the green- and violet-perceiving elements of the retina. The effect of this will be that of mixing a small amount of white with a large amount of red light—*i. e.* it will produce the sensation of incompletely saturated red light. This dilution of the sensation can be avoided only by previously exhausting the blue- and green-perceiving elements of the retina in a manner which will be explained in connection with the phenomena of after-images.

Retinal Stimulation.—Whenever by a stimulus applied to an irritable substance the potential energy there stored up is liberated the following phenomena may be observed: 1. A so-called latent period of variable duration during which no effects of stimulation are manifest; 2. A very brief period during which the effect of the stimulation reaches a maximum; 3. A period of continued stimulation during which the effect diminishes in consequence of the using up of the substance containing the potential energy—*i. e.* a period of fatigue; 4. A period after the stimulation has ceased in which the effect slowly passes away.

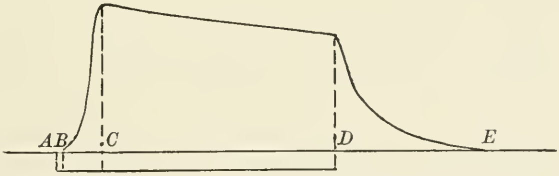

FIG. 153.—Diagram showing the effect of stimulation of an irritable substance.

The curve drawn by a muscle in tetanic contraction, as shown in Figure 153, illustrates this phenomenon. Thus, if $A\ D$ represents the duration of the stimulation, $A\ B$ indicates the latent period, $B\ C$ the period of contraction, $C\ D$ the period of fatigue under stimulation, and $D\ E$ the after-effect of stimulation showing itself as a slow relaxation. When light falls upon the retina corresponding phenomena are to be observed.

Latent Period.—That there is a period of latent sensation in the retina (*i. e.* an interval between the falling of light on the retina and the beginning of the sensation) is, judging from the analogy of other parts of the nervous system, quite probable, though its existence has not been demonstrated.

Rise to Maximum of Sensation.—The rapidity with which the sensation of light reaches its maximum increases with the intensity of the light and varies with its color, red light producing its maximum sensation sooner than green and blue. Consequently, when the image of a white object is moved across the retina it will appear bordered by colored fringes, since the various constituents of white light do not produce their maximum effects at the same time. This phenomena can be readily observed when a disk on which a black and a white spiral band alternate with each other (as shown in Figure 154, *A*) is rotated before the eyes. The white band as its image moves outward or inward over the retinal surface appears bordered with colors which vary with the rate of rotation of the disk and with the amount of exhaustion of the retina. Chromatic effects due to a similar cause are also to be seen when a disk, such as is shown in Figure 154, *B* (known as Benham's spectrum top), is rotated with moderate rapidity. The concentric bands of color appear in reverse order when the direction of rotation is reversed. The apparent movement of colored figures on a background of a different color when the eye moves rapidly over the object or the object is moved rapidly before the eye seems to depend upon this same retinal peculiarity. The phenomenon may be best observed when small pieces of bright-red paper are fastened upon a bright-blue sheet and the sheet gently shaken before the eyes. The red figures will appear to move upon the blue background. The effect may be best observed in a dimly-lighted room.

FIG. 154.—Disks to illustrate the varying rate at which colors rise to their maximum of sensation.

In this connection should be mentioned the phenomenon of "recurrent images" or "oscillatory activity of the retina."[1] This may be best observed when a black disk containing a white sector is rotated at a rate of about one revolution in two seconds. If the disk is brightly illuminated, as by sunlight, and the eye fixed steadily upon the axis of rotation, the moving white sector seems to have a shadow upon it a short distance behind its advancing border, and this shadow may be followed by a second fainter, and even by a third still fainter shadow, as shown in Figure 155. The distance of the shadows from each other and from the edge of the sector increases with the rate of rotation of the disk and corresponds to a time interval of about 0.015″. It thus appears that when light is suddenly thrown upon the retina the sensation does not at once rise to its maximum, but reaches this point by a sort of vibratory movement. The apparent duplication of a single very brief retinal stimulation, as that caused by a flash of lightning, may perhaps be a phenomenon of the same sort.

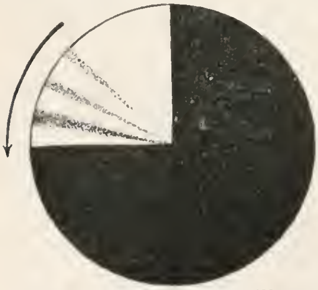

FIG. 155.—To illustrate the oscillatory activity of the retina (Charpentier).

Fatigue of Retina.—When the eye rests steadily upon a uniformly illu-

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[1] Charpentier: *Archives de Physiologie*, 1892, pp. 541, 629; and 1886, p. 677.

minated white surface (*e. g.* a sheet of white paper), we are usually unconscious of any diminution in the intensity of the sensation, but it can be shown that the longer we look at the paper the less brilliant it appears, or, in other words, that the retina really becomes fatigued. To do this it is only necessary to place a disk of black paper on the white surface and to keep the eyes steadily fixed for about half a minute upon the centre of the disk. Upon removing the disk without changing the direction of the eyes a round spot will be seen on the white paper in the place previously occupied by the disk. On this spot the whiteness of the paper will appear much more intense than on the neighboring portion of the sheet, because we are able in this experiment to bring into direct contrast the sensations produced by a given amount of light upon a fresh and a fatigued portion of the retina.[1]

The rapidity with which the retina becomes fatigued varies with the color of the light. Hence when intense white light falls upon the retina, as when we look at the setting sun, its disk seems to undergo changes of color as one or another of the constituents of its light becomes, through fatigue, less and less conspicuous in the combination of rays which produces the sensation of white.

The After-effect of Stimulation.—The persistence of the sensation after the stimulus has ceased causes very brief illuminations (*e. g.* by an electric spark) to produce distinct effects. On this phenomenon depends also the above-described method of mixing colors on a revolving disk, since a second color is thrown upon the retina before the impression produced by the first color has had time enough to become sensibly diminished. The interval at which successive stimulations must follow each other in order to produce a uniform sensation (a process analogous to the tetanic stimulation of a muscle) may be determined by rotating a disk, such as represented in Figure 156, and ascertaining at what speed the various rings produce a uniform sensation of gray. The interval varies with the intensity of the illumination from 0.1″ to 0.033″, and may, therefore, be used as a measure of the intensity, as in the method of "flicker photometry."[2] The special advantage of this method is that it affords a means of determining the relative intensity of lights of different colors. The duration of the after-effect depends also upon the length of the stimulation and upon the color of the light producing it, the most persistent effect being produced by the red rays. In this connection it is interesting to note that while with the rapidly vibrating blue rays a less

FIG. 156.—Disk to illustrate the persistence of retinal sensation (Helmholtz).

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[1] Although the retina is here spoken of as the portion of the visual apparatus subject to fatigue, it should be borne in mind that we cannot, in the present state of our knowledge, discriminate between retinal fatigue and exhaustion of the visual nerve-centres.

[2] Rood: *American Journal of Science,* Sept., 1893.

intense illumination suffices to stimulate the eye, the slowly vibrating red rays produce the more permanent impression.

After-images.—When the object looked at is very brightly illuminated the impression upon the retina may be so persistent that the form and color of the object are distinctly visible for a considerable time after the stimulus has ceased to act. This appearance is known as a "positive after-image," and can be best observed when we close the eyes after looking at the sun or other bright source of light. Under these circumstances we perceive a brilliant spot of light which, owing to the above-mentioned difference in the persistence of the impressions produced by the various colored rays, rapidly changes its color, passing generally through bluish green, blue, violet, purple, and red, and then disappearing. This phenomenon is apt to be associated with or followed by another effect known as a "negative after-image." This form of after-image is much more readily observed than the positive variety, and seems to depend upon the fatigue of the retina. It is distinguished from the positive after-image by the fact that its color is always complementary to that of the object causing it. In the experiment to demonstrate the fatigue of the retina, described on p. 345, the white spot which appears after the black disk is withdrawn is the "negative after-image" of the disk, white being complementary to black. If a colored disk be placed upon a sheet of white paper, looked at attentively for a few seconds, and then withdrawn, the eye will perceive in its place a spot of light of a color complementary to that of the disk. If, for example, the disk be yellow, the yellow-perceiving elements of the retina become fatigued in looking at it. Therefore when the mixed rays constituting white light are thrown upon the portion of the retina which is thus fatigued, those rays which produce the sensation of yellow will produce less effect than the other rays for which the eye has not been fatigued. Hence white light to an eye fatigued for yellow will appear blue.

If the experiment be made with a yellow disk resting on a sheet of blue paper, the negative after-image will be a spot on which the blue color will appear (1) more *intense* than on the neighboring portions of the sheet, owing to the blue-perceiving elements of that portion of the retina not being fatigued; (2) more *saturated*, owing to the yellow-perceiving elements being so far exhausted that they no longer respond to the slight stimulation which is produced when light of a complementary color is thrown upon them, as has been explained in connection with the subject of saturation.

Contrast.—As the eye wanders from one part of the field of vision to another it is evident that the sensation produced by a given portion of the field will be modified by the amount of fatigue produced by that portion on which the eye has last rested, or, in other words, the sensation will be the result of the stimulation by the object looked at combined with the negative after-image of the object previously observed. The effect of this combination is to produce the phenomenon of successive *contrast*, the principle of which may be thus stated: Every part of the field of vision appears lighter near a darker part and darker near a lighter part, and its color seen near another color approaches the complementary color of the latter. A contrast phenomenon similar in its effects to that above described may be produced under conditions in which negative after-images can play no part. This kind of contrast is known as *simultaneous contrast*, and may perhaps be explained on the theory that a stimulation of a given portion of the retina produces in the neighboring portions an effect to some extent antagonistic to that caused by direct stimulation.

A good illustration of the phenomenon of contrast is given in Figure 157, in which black squares are separated by white bands which at their points of intersection appear darker than where they are bordered on either side by the black squares.

A black disk on a yellow background seen through white tissue-paper appears blue, since the white paper makes the black disk look gray and the yellow background pale yellow. The gray disk in contrast to the pale yellow around it appears blue.

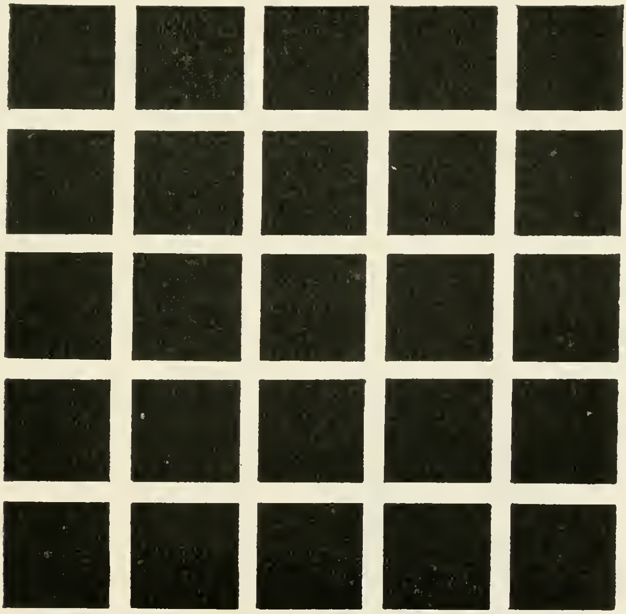

FIG. 157.—To illustrate the phenomenon of contrast.

The phenomenon of *colored shadows* also illustrates the principle of contrast. These may be observed whenever an object of suitable size and shape is placed upon a sheet of white paper and illuminated from one direction by daylight and from another by gaslight. Two shadows will be produced, one of which will appear yellow, since it is illuminated only by the yellowish gaslight, while the other, though illuminated by the white light of day, will appear blue in contrast to the yellowish light around it.

Space-perception.—Rays of light proceeding from every point in the field of vision are refracted to and stimulate a definite point on the surface of the retina, thus furnishing us with a local sign by which we can recognize the position of the point from which the light proceeds. Hence the size and shape of an optical image upon the retina enable us to judge of the size of the corresponding object in the same way that the cutaneous terminations of the nerves of touch enable us to judge of the size and shape of an object brought in contact with the skin. This spatial perception is materially aided by the muscular sense of the muscles moving the eyeball, for we can obtain a much more accurate idea of the size of an object if we let the eye rest in succession upon its different parts than if we gaze fixedly at a given point upon its surface. The conscious effort associated with a given amount of muscular motion gives, in the case of the eye, a measure of distance similar to that secured by the hand when we move the fingers over the surface of an object to obtain an idea of its size and shape.

The perception of space by the retina is limited to space in two dimensions —*i. e.* in a plane perpendicular to the axis of vision. Of the third dimension in space—*i. e.* of distance from the eye—the retinal image gives us no knowledge, as may be proved by the study of after-images. If an after-image of any bright object—*e. g.* a window—be produced upon the retina in the manner above described and the eye be then directed to a sheet of paper held in the hand, the object will appear outlined in miniature upon the surface of the paper. If, however, the eye be directed to the ceiling of the room, the object will appear enlarged and at a distance corresponding to that of the surface looked at.[1] Hence one and the same retinal image may, under different circumstances, give rise to the impression of objects at different distances. We must therefore regard the perception of distance not as a direct datum of vision, but, as will be later explained, a matter of visual judgment.

When objects are of such a shape that their images may be thrown successively upon the same part of the retina, it is possible to judge of their relative size with considerable accuracy, the retinal surface serving as a scale to which the images are successively applied. When this is not the case, the error of judgment is much greater. We can compare, for instance, the relative length of two vertical or of two horizontal lines with a good deal of precision, but in comparing a vertical with a horizontal line we are liable to make a considerable error. Thus it is difficult to realize that the vertical and the horizontal lines in Figure 158 are of the same length. The error consists in an over-estimation of the length of the vertical lines relatively to horizontal ones, and appears to depend, in part at any rate, upon the small size of the superior rectus muscle relatively to the other muscles of the eye. The difference amounts to 30–45 per cent. in weight and 40–53 per cent. in area of cross section. It is evident, therefore, that a given motion of the eye in the upward direction will require a more powerful contraction of the weaker muscle concerned in the movement than will be demanded of the stronger muscles moving the eye laterally to an equal amount.

FIG. 158.—To illustrate the over-estimation of vertical lines.

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[1] This power of the surface of projection to determine the apparent size and distance of the after-image may be to some extent influenced by the will.—Jeffries: *Journal of Boston Society of Medical Sciences*, vol. i. No. 9.

Hence we judge the upward motion of the eye to be greater because to accomplish it we make a greater effort than is required for a horizontal movement of equal extent.

The position of the vertical line bisecting the horizontal one (in Fig. 158) aids the illusion, as may be seen by turning the page through 90°, so as to bring the bisected line into a vertical position, or by looking at the lines in Figure 159, in which the illusion is much less marked than in Figure 158.

The tendency to over-estimate the length of vertical lines is also illustrated by the error commonly made in supposing the height of the crown of an ordinary silk hat to be greater than its breadth.

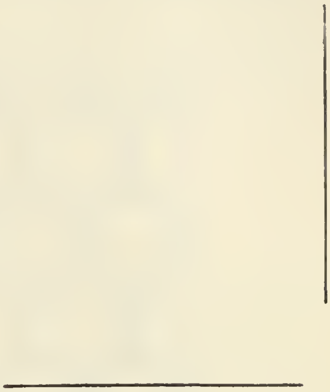

FIG. 159.—To illustrate the over-estimation of vertical lines.

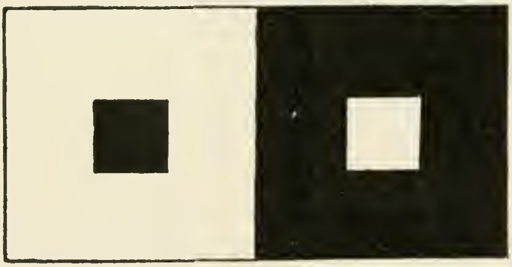

FIG. 160.—To illustrate the phenomenon of irradiation.

Irradiation. — Many other circumstances affect the accuracy of the spatial perception of the retina. One of the most important of these is the intensity of the illumination. All brilliantly illuminated objects appear larger than feebly illuminated ones of the same size, as is well shown by the ordinary incandescent electric lamp, the delicate filament of which is scarcely visible when cold, but when intensely heated by the electric current glows as a broad band of light. The phenomenon is known as "irradiation," and seems to depend chiefly upon the above-described imperfections in the dioptric apparatus of the eye, in consequence of which points of light produce small circles of dispersion on the retina and bright objects produce images with imperfectly defined outlines. The white square surrounded by black and the black square surrounded by white (Figure 160), being of the same size, would in an ideally perfect eye produce images of the same size on the retina, but owing to the imperfections of the eye the images are not sharply defined, and the white surfaces consequently appear to encroach upon the darker portions of the field of vision. Hence the white square looks larger than the black one, the difference in the apparent size depending upon the intensity of the illumination and upon the accuracy with which the eye can be accommodated for the distance at which the objects are viewed. The effect of irradiation is most manifest when the dark portion of the field of vision over which the irradiation takes place has a considerable breadth. Thus the circular white spots in Figure 161, when viewed from a distance of three or four meters, appear hexagonal, since the irradiation is most marked in the triangular dark space between three adjacent circles. A familiar example of the effect of irradiation is afforded by the appearance of the new moon, whose sun-illuminated crescent seems to be part of a much larger circle than the remainder of the disk, which shines only by the light reflected upon it from the surface of the earth.

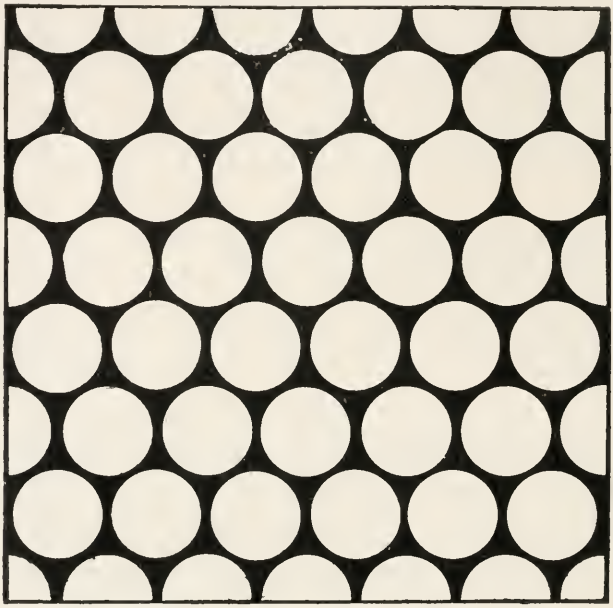

FIG. 161.—To illustrate the phenomenon of irradiation.

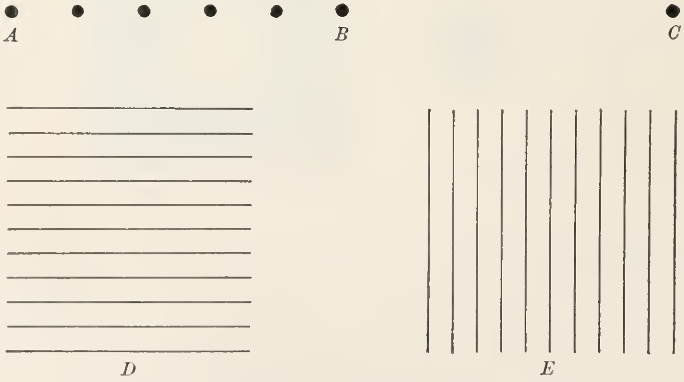

FIG. 162.—To illustrate the illusion of subdivided space.

Subdivided Space.—A space subdivided into smaller portions by intermediate objects seems more extensive than a space of the same size not so subdivided. Thus the distance from *A* to *B* (Fig. 162) seems longer than that from *B* to *C*, though both are of the same length, and for the same reason the square

D seems higher than it is broad, and the square *E* broader than it is high, the illusion being more marked in the case of *D* than in the case of *E*, because, as above explained, vertical distances are, as a rule, over-estimated.

The explanation of this illusion seems to be that the eye in passing over a subdivided line or area recognizes the number and size of the subdivisions, and thus gets an impression of greater total size than when no subdivisions are present.

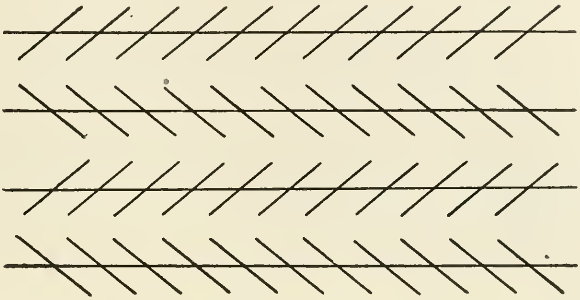

FIG. 163.—Zöllner's lines.

A good example of this phenomenon is afforded by the apparently increased extent of a meadow when the grass growing on it is cut and arranged in haycocks.[1]

The relations of lines to each other gives rise to numerous illusions of spatial perception, among the most striking of which are those afforded by the so-called "Zöllner's lines," an example of which is given in Figure 163. Here the horizontal lines, though strictly parallel to each other, seem to diverge and converge alternately, their apparent direction being changed toward greater perpendicularity to the short oblique lines crossing them. This illusion is to be explained in part by the tendency of the eye to over-estimate the size of acute and to under-estimate that of obtuse angles—a tendency which, according to Filehne,[2] is due to the fact that we are constantly surrounded by square-cornered objects (houses, furniture, etc.), the right angles of which, being seen obliquely, are projected onto our retinas as acute or obtuse angles. Knowing these angles to be right angles, we are constantly applying mental corrections to our visual data, and the habit thus acquired forces us to regard all acute and obtuse angles as nearer to right angles than they really are. The illusion in Zöllner's lines is more marked when the figure is so held that the long parallel lines make an angle of about

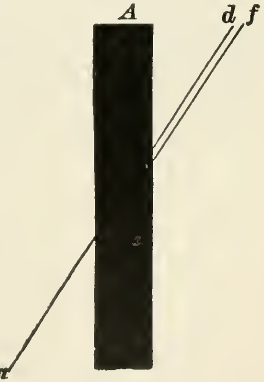

FIG. 164.—To illustrate illusion of space-perception.

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[1] It is interesting to note that a similar illusion has been observed when an interval of time subdivided by audible signals is compared with an equal interval not so subdivided (Hall and Jastrow: *Mind*, xi. 62).

[2] *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, xvii. S. 16.

45° with the horizon, since in this position the eye appreciates their real position less accurately than when they are vertical or horizontal. It is diminished, but does not disappear, when the eye, instead of being allowed to wander over the figure, is fixed upon any one point of the field of vision. Hence the motions of the eye must be regarded as a factor in, but not the sole cause of, the illusion.

FIG. 165.—To illustrate contrast in space-perception (Müller-Lyer).

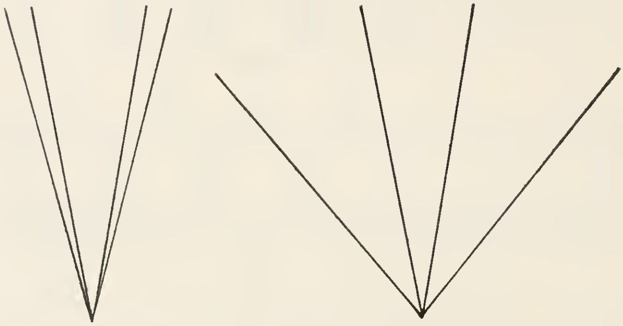

FIG. 166.—To illustrate contrast in space-perception (Müller-Lyer).

The illusion in Fig. 164, where the line *d* is the real and the line *f* the apparent continuation of the line *a*, is to be explained partly by the over-estimation of acute angles and partly, according to Helmholtz, by irradiation.

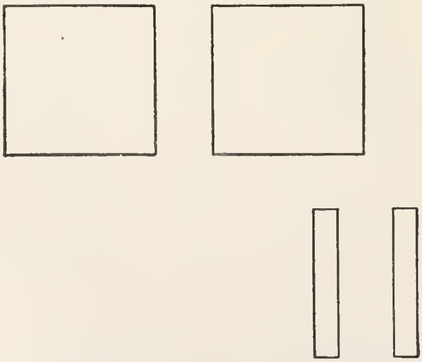

FIG. 167.—To illustrate contrast in space-perception (Müller-Lyer).

The fact that the illusion is greatly diminished by turning the figure on its side seems to show that the tendency to over-estimate vertical dimensions also plays a part in its production.

Our estimate of the size of given lines, angles, and areas is influenced by neighboring lines, angles, and areas with which they are compared. This influence is sometimes exerted in accordance with the principle of contrast, and tends to make a given extension appear larger in presence of a smaller, and smaller in presence of a larger extension. This effect is illustrated in Figure 165, in which the middle portion of the shorter line appears larger than the corresponding portion of the longer line, in Figure 166, in which a similar effect is observed in the case of angles, and in Figure 167, in which the space between the two squares seems smaller than that between the two oblong figures.

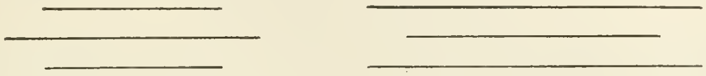

FIG. 168.—To illustrate so-called "confluxion" in space-perception (Müller-Lyer).

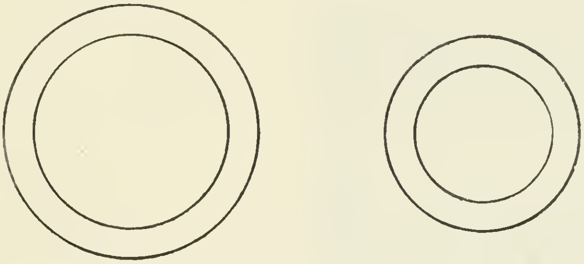

FIG. 169.—To illustrate so-called "confluxion" in space-perception (Müller-Lyer).

In some cases, however, an influence of the opposite sort[1] seems to be exerted, as is shown in Figure 168, in which the middle one of three parallel lines seems longer when the outside lines are longer, and shorter when they are shorter than it is itself, and in Figure 169, in which a circle appears larger if surrounded by a circle larger than itself, and smaller if a smaller circle is shown concentrically within it.

FIG. 170.—To illustrate the influence of angles upon the apparent length of lines (Müller-Lyer).

Lines meeting at an angle appear longer when the included angle is large than when it is small, as is shown in Figure 170. This influence of the included angle affords a partial explanation of the illusion shown in Figure 171, in which the horizontal line at *B* seems longer than at *A* ; but the distance

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[1] For this influence the name "confluxion" has been proposed by Müller-Lyer, from whose article in the *Archiv für Physiologie*, 1889, Sup. Bd., the above examples are taken.

between the extremities of the oblique lines seems also to affect our estimate of the horizontal line in the same way as the outside lines in Figure 168 influence our judgment of the length of the line between them.

FIG. 171.—Illusion of space-perception.

Einthoven[1] has recently explained this phenomenon as dependent upon indistinct vision in the lateral portions of the retina which causes the blurred images of the ends of the line *a* to appear nearer together than those of the line *b*. This effect of indistinctness of outline can be illustrated by photographing the lines more or less out of focus as shown in Figure 172 *a*. A similar explanation is given by Einthoven for the illusion of subdivided space described on p. 351.

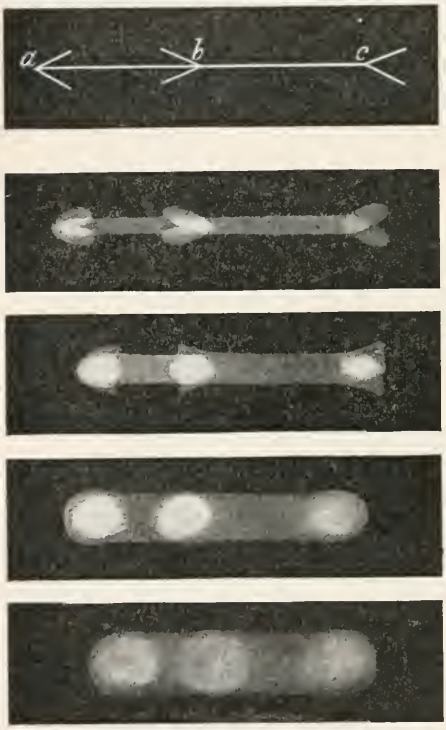

FIG. 172.—Illustrating Einthoven's explanation of space illusions through indistinct vision.

Perception of Distance.—The retinal image gives us, as we have seen, no *direct* information as to the distance of the object from the eye. This knowledge is, however, quite as important as that of position in a plane perpendicular to the line of vision, and we must now consider in what way it is obtained. The first fact to be noticed is that there is a close connection between the judgments of distance and of actual size. A retinal image of a given size may be produced by a small object near the eye or by a large one at a distance from it. Hence when we know the actual size of any object (as, for example, a human figure) we judge of its distance by the size of its image on the retina. Conversely, our estimate of the actual size of an object will depend upon our judgment of its distance. The fact that children constantly misjudge both the size and distance of objects shows that the knowledge of this relation is acquired only by experience. If circumstances mislead us with regard to the distance of an object, we necessarily make a corresponding error with regard to its size. Thus, objects seen indistinctly, as through a fog, are judged to be larger, because we suppose them to be farther off than they really are. The familiar fact that the moon seems to be larger when near the horizon than when near the zenith is also an illustration of this form of illu-

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[1] *Pflüger's Archiv*, lxxi. S. 1.

sion. When the moon is high above our heads we have no means of estimating its distance from us, since there are no intervening objects with which we can compare it. Hence we judge it to be nearer than when, seen on the horizon, it is obviously farther off than all terrestrial objects. Since the size of the retinal image of the moon is the same in the two cases, we reconcile the sensation with its apparent greater distance when seen on the horizon by attributing to the moon in this position a greater actual size.

If the retinal image have the form of a familiar object of regular shape—*e. g.* a house or a table—we interpret its outlines in the light of experience and distinguish without difficulty between the nearer and more remote parts of the object. Even the projection of the outlines of such an object on to a plane surface (*i. e.* a perspective drawing) suggests the real relations of the different parts of the picture so strongly that we recognize at once the relative distances of the various portions of the object represented. How powerfully a familiar outline can suggest the form and relief usually associated with it is well illustrated by the experiment of looking into a mask painted on its *interior* to resemble a human face. In this case the familiar outlines of a human face are brought into unfamiliar association with a receding instead of a projecting form, but the ordinary association of these outlines is strong enough to force the eye to see the hollow mask as a projecting face.[1] The fact that the projecting portions of an object are usually more brightly illuminated than the receding or depressed portions is of great assistance in determining their relative distance. This use of shadows as an aid to the perception of relief presupposes a knowledge of the direction from which the light falls on an object, and if we are deceived on the latter we draw erroneous conclusions with regard to the former point. Thus, if we look at an embossed letter or figure through a lens which makes it appear inverted the accompanying reversal of the shadows will cause the letter to appear depressed. The influence of shadows on our judgment of relief is, however, not so strong as that of the outline of a familiar object. In a case of conflicting testimony the latter usually prevails, as, for example, in the above-mentioned experiment with the mask.

Aided by these peculiarities of the retinal picture, the mind interprets it as corresponding in its different parts to points at different distances from the eye, and it is interesting to notice that painters, whose work, being on a plane surface, is necessarily in all its parts at the same distance from the eye, use similar devices in order to give depth to their pictures. Distant hills are painted with indistinct outlines to secure what is called "aërial perspective." Figures of men and animals are introduced in appropriate dimensions to suggest the distance between the foreground and the background of the picture. Landscapes are painted preferably by morning and evening light, since at these hours the marked shadows aid materially in the suggestion of distance.

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[1] In the experiment the mask should be placed at a distance of about two meters and one eye closed. Even with both eyes open the illusion often persists if the distance is increased to five or six meters.

The eye, however, can aid itself in the perception of depth in ways which the painter has not at his disposal. By the sense of effort associated with the act of accommodation we are able to estimate roughly the relative distance of objects before us. This aid to our judgment can, of course, be employed only in the case of objects comparatively near the eye. Its effectiveness is greater for objects not far from the near-point of vision, and diminishes rapidly as the distance is increased, and disappears for distances more than two or three meters from the eye.

When the head is moved from side to side an apparent change in the relative position of objects at different distances is produced, and, as the extent of this change is inversely proportional to the distance of the objects, it serves as a measure of distance. This method of obtaining the "parallax" of objects by a motion of the head is often noticeable in persons whose vision in one eye is absent or defective.

Binocular Vision.—The same result which is secured by the comparison of retinal images seen successively from slightly different points of view is obtained by the comparison of the images formed simultaneously by any object in the *two eyes*. In binocular vision we obtain a much more accurate idea of the shape and distance of objects around us than is possible with monocular vision, as may be proved by trying to touch objects in our neighborhood with a crooked stick, first with both eyes open and then with one eye shut. Whenever we look at a near solid object with two eyes, the right eye sees farther round the object on the right side and the left eye farther round on the left. The mental comparison of these two slightly different images produces the perception of solidity or depth, since experience has taught us that those objects only which have depth or solidity can affect the eyes in this way. Conversely, if two drawings or photographs differing from each other in the same way that the two retinal images of a solid object differ from each other are presented, one to the right and the other to the left eye, the two images will become blended in the mind and the perception of solidity will result. Upon this fact depends the effect of the instrument known as the stereoscope, the slides of which are generally pairs of photographs of natural objects taken simultaneously with a double camera, of which the lenses are at a distance from each other equal to or slightly exceeding that between the two axes of vision. The principle of the stereoscope can be illustrated in a very simple manner by drawing circles such as are represented in Figure 173 on thin paper, and fastening each

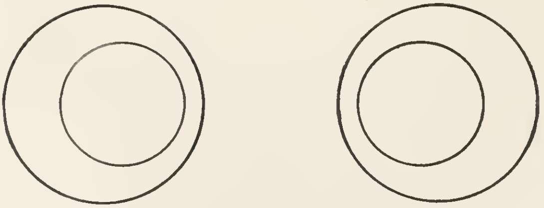

FIG. 173.—To illustrate stereoscopic vision.

pair across the end of a piece of brass tube about one inch or more in diameter and ten inches long. Let the tubes be held one in front of each eye with the distant ends nearly in contact with each other, as shown in Figure 174. If the tubes are in such a position that the small circles are brought as near to each other as possible, as shown in Figure 173, the retinal images will blend, the smaller circle will seem to be much nearer than the larger one, and the eyes will appear to be looking down upon a truncated cone, such as is shown in Figure 175, since a solid body of this form is the only one bounded by circles related to each other as those shown in this experiment.

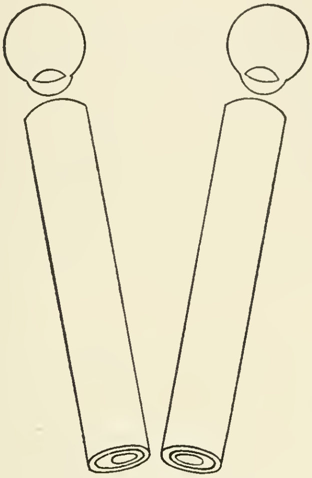

FIG. 174.—To illustrate stereoscopic vision.

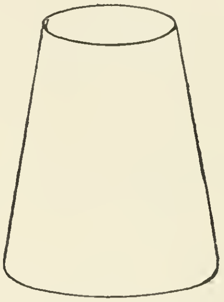

FIG. 175.—To illustrate stereoscopic vision.

Stereoscopic slides often serve well to illustrate the superiority of binocular over monocular vision. If the slide represents an irregular mass of rocks or ice, it is often very difficult by looking at either of the pictures by itself to determine the relative distance of the various objects represented, but if the slide is placed in the stereoscope the true relation of the different parts of the picture becomes at once apparent.

Since the comparison of two slightly dissimilar images received on the two retinas is the essential condition of stereoscopic vision, it is evident that if the two pictures are identical no sensation of relief can be produced. Thus, when two pages printed from the same type or two engravings printed from the same plate are united in a stereoscope, the combined picture appears as flat as either of its components. If, however, one of the pictures is copied from the other, even if the copy be carefully executed, there will be slight differences in the distances between the lines or in the spacing of the letters which will cause apparent irregularities of level in the different portions of the combined picture. Thus, a suspected banknote may be proved to be a counterfeit if, when placed in a stereoscope by the side of a genuine note, the resulting combined picture shows certain letters lying apparently on different planes from the rest.

Pseudoscopic Vision.—If the pictures of an ordinary stereoscopic slide be reversed, so that the picture belonging in front of the right eye is presented to the left eye, and *vice versâ*, the stereoscopic gives place to what is called a pseudoscopic effect—*i. e.* we perceive not a solid but a hollow body. The effect is best obtained with the outlines of geometrical solids, photographs of coins or medals or of objects which may readily exist in an inverted form. Where the photographs represent objects which cannot be thus inverted, such as buildings and landscapes, the pseudoscopic effect is not readily produced—another example of the power (see p. 355) of the outline of a familiar object to outweigh other sorts of testimony.

A pseudoscopic effect may be readily obtained without the use of a stereoscope by simply converging the visual axes so that the right eye looks at the left and the left eye at the right picture of a stereoscopic slide. The eyes may be aided in assuming the right degree of convergence by looking at a small object like the head of a pin held between the eyes and the slide in the manner described on p. 312. Figure 173, viewed in this way, will present the appearance of a hollow truncated cone with the base turned toward the observer. A stereoscopic slide with its pictures reversed will, of course, when viewed in this way, present not a pseudoscopic, but a true stereoscopic, appearance, as shown by Figures 138 and 139.

Binocular Combination of Colors.—The effect of binocularly combining two different colors varies with the difference in wave-length of the colors. Colors lying near each other in the spectrum will generally blend together and produce the sensation of a mixed color, such as would result from the union of colors by means of the revolving disk or by the method of reflected and transmitted light, as above described. Thus a red and a yellow disk placed in a stereoscope may be generally combined to produce the sensation of orange. If, however, the colors are complementary to each other, as blue and yellow, no such mixing occurs, but the field of vision seems to be occupied alternately by a blue and by a yellow color. This so-called "rivalry of the fields of vision" seems to depend, to a certain extent, upon the fact that in order to see the different colors with equal distinctness the eyes must be differently accommodated, for it is found that if the colors are placed at different distances from the eyes (the colors with the less refrangible rays being at the greater distance), the rivalry tends to disappear and the mixed color is more easily produced.

An interesting effect of the stereoscopic combination of a black and a white object is the production of the appearance of a metallic lustre or polish. If, for instance, the two pictures of a stereoscopic slide represent the slightly different outlines of a geometrical solid, one in black upon white ground and the other in white upon black ground, their combination in the stereoscope will produce the effect of a solid body having a smooth lustrous surface. The explanation of this effect is to be found in the fact that a polished surface reflects the light differently to the two eyes, a given point appearing brilliantly illuminated to one eye and dark to the other. Hence the stereoscopic combination of black and white is interpreted as indicating a polished surface, since it is by means of a polished surface that this effect is usually produced.

Corresponding Points.—When the visual axes of both eyes are directed to the same object two distinct images of that object are formed upon widely separated parts of the nervous system. Yet but a single object is perceived. The phenomenon is the same as that which occurs when a grain of sand is held between the thumb and finger. In both cases we have learned (chiefly through the agency of muscular movements and the nerves of muscular sense) to interpret the double sensation as produced by a single object.

Any two points, lying one in each retina, the stimulation of which by rays of light gives rise to the sensation of light proceeding from a single object are said to be "corresponding points." Now, it is evident that the *foveæ centrales* of the two eyes must be corresponding points, for an object always appears single when both eyes are fixed upon it. That double vision results when the images are formed on points which are not corresponding may be best illustrated by looking at three pins stuck in a straight rod at distances of 35, 45, and 55 centimeters from the end. If the end of the rod is held against the nose and the eyes directed to each of the three pins in succession, it will be found that, while the pin looked at appears single, each of the others appears double, and that the three pins therefore look like five.

The two *foveæ centrales* are not, of course, the only corresponding points. In fact, it may be said that the two retinas correspond to each other, point for point, almost as if they were superposed one upon the other with the foveæ together. The exact position of the points in space which are projected on to corresponding points of the two retinas varies with the position of the eyes. The line or surface in which such points lie is known as the "horopter." A full discussion of the horopter would be out of place in this connection, but one interesting result of its study may be pointed out—viz. the demonstration that when, standing upright, we direct our eyes to the horizon the horopter is approximately a plane coinciding with the ground on which we stand. It is of course important for security in walking that all objects on the ground should appear single, and, as they are known by experience to be single, the eye has apparently learned to see them so.

Since the vertical meridians of the two eyes represent approximately rows of corresponding points, it is evident that when two lines are so situated that their images are formed each upon a vertical meridian of one of the eyes, the impression of a single vertical line will be produced, for such a line seen binocularly is the most frequent cause of this sort of retinal stimulation. This is the explanation commonly given of the singular optical illusion which is produced when lines drawn as in Figure 176 are looked at with both eyes fixed upon the point of intersection of the lines and with the plane in which the visual axes lie forming an angle of about 20° with that of the paper, the distance of the lines from the eyes being such that each line will lie approximately in the same vertical plane with one of the visual axes. Under these circumstances each line will form its image on a vertical meridian of one of the eyes, and the combination of these images results in the perception of a third line, not lying in the plane of the paper, but apparently passing through it more or less vertically, and swinging round its middle point with every movement of the head or the paper. In this experiment it will be found that the illusion of a line placed vertically to the plane of the paper does not entirely disappear when one eye is closed. Hence it is evident that there is, as Mrs. C. L. Franklin has pointed out,[1] a strong tendency to regard lines which form their images approximately on the vertical meridian of the eye as themselves vertical. This tendency is well shown when a number of short lines converging toward a point outside of the paper on which they are drawn, as in Figure 177, are looked at with one eye held a short distance above the point of convergence. Even when the lines are not convergent, but parallel, so that their images cannot fall upon the vertical meridian of the eye, the illusion is not entirely lost. It will be found, for instance, that when the Zöllner lines, as given in Figure 163, are looked at obliquely with one eye from one corner of the figure, the short lines which lie nearly in a plane with the visual axis appear to stand vertically to the plane of the paper.

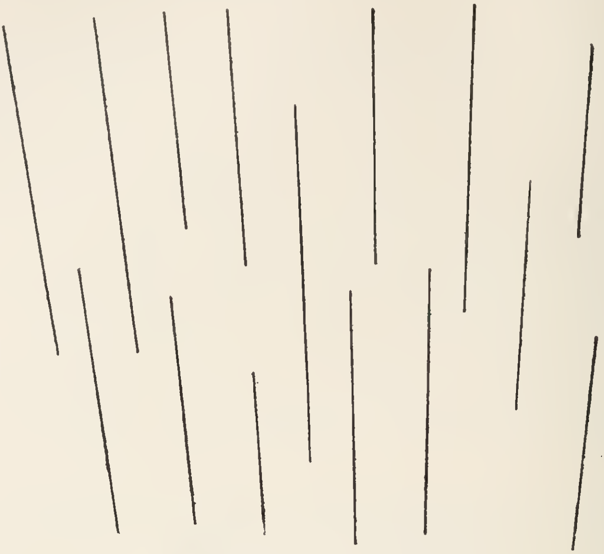

Fig. 177.—Monocular illusion of vertical lines.

Fig. 176.—Binocular illusion of a vertical line.

In this connection it may be well to allude to the optical illusion in consequence of which certain portraits seem to follow the beholder with the eyes. This depends upon the fact that the face is painted looking straight out from the canvas —*i. e.* with the pupil in the middle of the eye. The painting being upon a flat surface, it is evident that, from whatever direction the picture is viewed, the pupil will always seem to be in the middle of the eye, and the eye will consequently appear to be directed upon the observer. The phenomenon is still more striking in the case of pictures of which the one represented in Figure 178 may be taken as an example. Here the soldier's rifle

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[1] *Am. Journal of Psychology*, vol. i. p. 99.

is drawn as it appears to an eye looking straight down the barrel, and, as this foreshortening is the same in all positions of the observer, it is evident that when such a picture is hung upon the wall of a room the soldier will appear to be aiming directly at the head of every person present.

Fig. 178.—Illusion of lines always pointing toward observer.

In concluding this brief survey of some of the most important subjects connected with the physiology of vision it is well to utter a word of caution with regard to a danger connected with the study of the subject. This danger arises in part from the fact that in the scientific study of vision it is often necessary to use the eyes in a way quite different from that in which they are habitually employed, and more likely, therefore, to cause nervous and muscular fatigue. We have seen that in any given position of the eye distinct definition is limited to an area which bears a very small proportion to the whole field of vision. Hence in order to obtain an accurate idea of the appearance of any large object our eyes must wander rapidly over its whole surface, and we use our eyes so instinctively and unconsciously in this way that, unless our attention is specially directed to the subject, we find it difficult to believe that the power of distinct vision is limited to such a small portion of the retina. In most of the experiments in physiological optics, however, this rapid change of direction of the axis of vision must be carefully avoided, and the eye-muscles held immovable in tonic contraction.

Our eyes, moreover, like most of our organs, serve us best when we do not pay too much attention to the mechanism by which their results are brought about. In the ordinary use of the eyes we are accustomed to neglect after-images, intraocular images, and all the other imperfections of our visual apparatus, and the usefulness of our eyes depends very much upon our ability thus to neglect their defects. Now, the habit of observing and examining these defects that is involved in the scientific study of the eye is found to interfere with our ability to disregard them. A student of the physiology of vision who devotes too much attention to the study of after-images, for instance, may render his eyes so sensitive to these phenomena that they become a decided obstacle to ordinary vision.

B. THE EAR AND HEARING.

Anatomy and Histology of the Ear.—The organ of hearing may conveniently be divided into three parts: (1) The external ear, including the *pinna* or *auricle* and the *external auditory meatus;* (2) the middle ear, called the "tympanic cavity" or *tympanum;* and (3) the internal ear, or *labyrinth.* The labyrinth is situated in the dense petrous bone, and it contains a membranous sac of complex form which receives the peripheral terminations of the auditory nerve. This sac, therefore, is to the ear what the retina is to the eye; as the lens, cornea, etc. of the eye are simply physical media for the production of sharp images on the retina, so all parts of the organ of hearing are devoted solely to the accurate transmission of the energy of air-waves to the internal ear.

The External Ear.—*The pinna* or *auricle*, commonly known simply as the "ear" (Fig. 179), is a peculiarly wrinkled sheet of tissue, consisting essentially of yellow elastic cartilage covered with skin, and forming at the entrance of the auditory meatus a cup-shaped depression called the "concha."

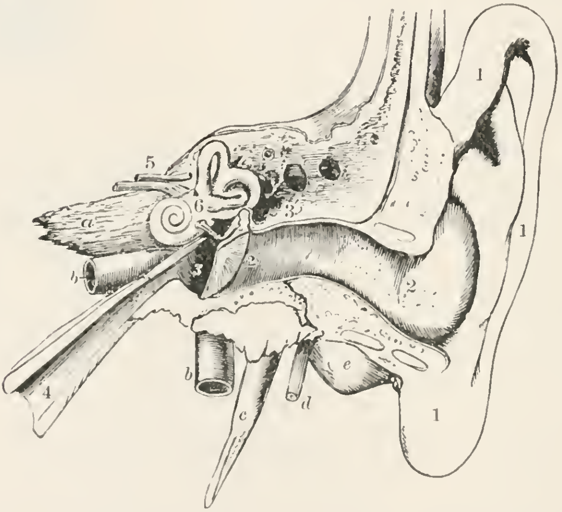

FIG. 179.—Diagram of organ of hearing of left side (Quain, after Arnold): 1, the pinna; 2, bottom of concha; 2-2', meatus externus; 3, tympanum; above 3, the chain of ossicles; 3', opening into the mastoid cells; 4, Eustachian tube; 5, meatus internus, containing the facial (uppermost) and auditory nerves; 6, placed on the vestibule of the labyrinth above the fenestra ovalis; *a*, apex of the petrous bone; *b*, internal carotid artery; *c*, styloid process; *d*, facial nerve, issuing from the stylo-mastoid foramen; *e*, mastoid process; *f*, squamous part of the bone.

The concha, and to some extent the whole auricle, serves a useful purpose in collecting, like the mouth of a speaking-trumpet, the waves of sound falling upon it; but in many of the lower animals the concha is relatively larger than in man, and, their ears being freely movable, the auricle becomes of greater physiological importance.

External Auditory Meatus.—In man the *external auditory meatus* or auditory canal is about one and a quarter inches in length, and it extends from the bottom and anterior edge of the concha to the *membrana tympani*, or tympanic membrane. Starting from the bottom of the concha, the general direction of the auditory canal is first obliquely upward and backward for about half an inch, and then inward and forward. Therefore, to look into the ear or to introduce the aural speculum the canal must be straightened by pulling the pinna upward and backward. The canal-wall is cartilaginous and movable for about half an inch from the exterior, but is osseous for the rest of its extent; it is lined by a reflexion of thin skin, on whose surface, in the cartilaginous part of the canal, open the ducts of numerous sebaceous and ceruminous glands.

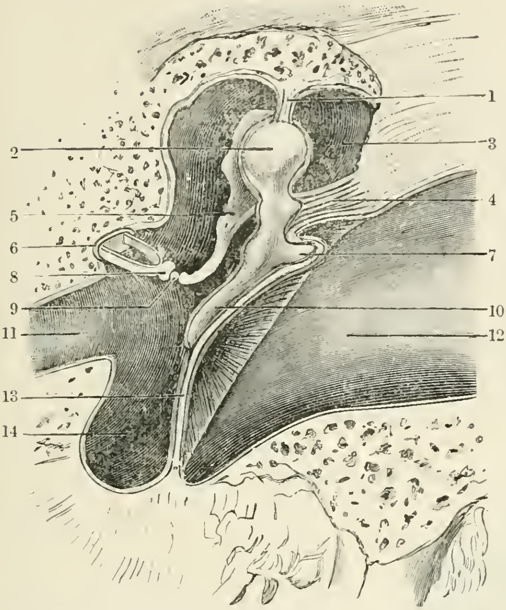

FIG. 180.—Tympanum of left ear, with ossicles *in situ* (after Morris): 1, suspensory ligament of malleus; 2, head of malleus; 3, epitympanic region; 4, external ligament of malleus; 5, processus longus of incus; 6, base of stapes; 7, processus brevis of malleus; 8, head of stapes; 9, *os orbiculare;* 10, manubrium; 11, Eustachian tube; 12, external auditory meatus; 13, *membrana tympani;* 14, lower part of tympanum.

Tympanum.—The middle ear, or *tympanum* (Figs. 179, 180), is shut off from the auditory canal by the tympanic membrane. It is an air-holding cavity of irregular shape in the petrous bone, and it is broader behind and above than it is below and in front. Posteriorly it is in open communication with the complex system of air-cavities in the mastoid bone known as the *mastoid antrum* and the *mastoid cells.* Anteriorly it is continuous with the pharynx through the Eustachian tube. The inner wall slants somewhat outward from top to bottom, and it is formed chiefly by part of the bony envelope of the internal ear. The surface of this wall is pierced by two apertures, the *fenestra ovalis*, or oval window, and the *fenestra rotunda*, or round window, leading into the cavity of the bony labyrinth; in life each fenestra is covered by a thin sheet of membrane, and the foot of the *stapes* is fastened by a ligamentous fringe in the oval window. The outer wall of the middle ear is made up of the tympanic

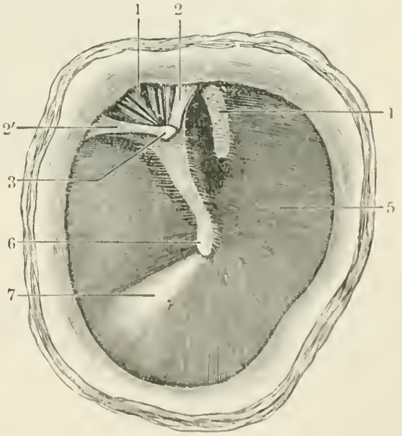

FIG. 181.—Otoscopic view of left *membrana tympani* (Morris): 1, *membrana flaccida;* 2, 2′, folds bounding the former; 3, reflection from processus brevis of malleus; 4, processus longus of incus (occasionally seen); 5, membrana tympani; 6, *umbo* and end of manubrium; 7, pyramid of light.

membrane and the ring of bone into which this membrane is inserted. The roof is formed by a thin plate of bone, the *tegmen*, which separates it from the cranial cavity, and the narrow floor, concave upward, is just above the jugular fossa. The cavity is lined by mucous membrane continuous with that of the Eustachian tube and the pharynx, and the membrane, like that of the Eustachian tube, is ciliated except over the surfaces of the ossicles and the tympanic membrane. Suppurative inflammation of the middle ear may not only involve the mastoid cells, but may also cause absorption of the thin plate of bone forming the roof of the tympanic cavity and the mastoid antrum. In this and in other ways inflammation may extend from the tympanic to the cranial cavity, making *otitis media*, or inflammation of the middle ear, the commonest source of pyogenic affections of the brain.[1]

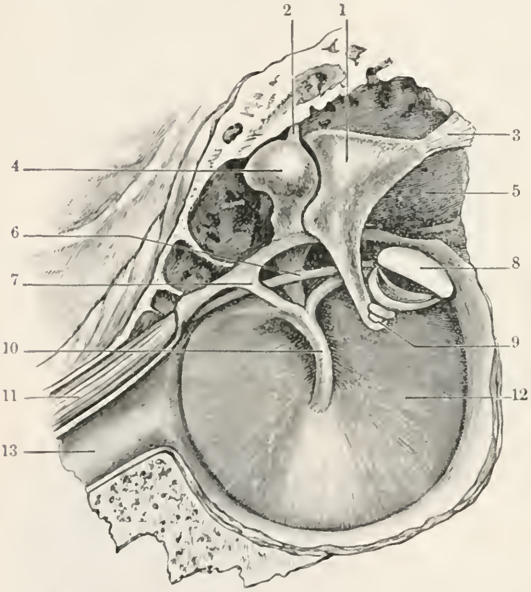

Fig. 182.[2]—Tympanum of right side with ossicles in place, viewed from within (after Morris): 1, body of incus; 2, suspensory ligament of malleus; 3, ligament of incus; 4, head of malleus; 5, epitympanic cavity; 6, *chorda tympani* nerve; 7, tendon of *tensor tympani* muscle; 8, foot-piece of stirrup; 9, *os orbiculare;* 10, manubrium; 11, tensor tympani muscle; 12, membrana tympani; 13, Eustachian tube.

Fig. 183.—The chain of auditory ossicles, anterior view (after Testut): 1, head of malleus; 2, long process of incus; 3, stapes.

Tympanic Membrane, or Drum-skin.—The membrana tympani (Figs. 181, 182) is a somewhat oval disk whose longer axis is directed from behind and above downward and forward, and whose length is about nine millimeters. The membrane is inserted obliquely to the axis of the auditory canal, so that the floor of the canal is longer than its roof. The membrana tympani, though so thin as to be semi-transparent, is composed of three layers of tissue. Externally it is covered by a thin plate of skin; internally, by mucous membrane; and between these lies the proper substance (*membrana propria*) of the membrane, made up chiefly of fibrous tissue. The greater number of the fibres of the membrana propria radiate from near the centre to the periphery of the membrane; but there are also circular fibres of elastic tissue which are most numerous in a ring near the attached margin of the membrane. The surface of the tympanic membrane is not flat, but is funnel-shaped, with the apex of the funnel pointing inward. Moreover, lines

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[1] Macewen: *Pyogenic Diseases of the Brain and Spinal Cord*, 1893.

[2] Figs. 180, 181, and 182 are taken by permission from Morris's *Text-Book of Anatomy*, Phila., 1893.

drawn from the centre to the margin of the membrane would not be straight, but would be curved slightly, with the convexity outward, this shape being due to the tension of the elastic circular fibres of the membrane. The membrane, throughout the greater part of its circumference, is inserted in a groove in a bony ring set in the wall of the auditory canal, but a small arc at its superior portion is attached directly to the wall of the canal. The segment of membrane corresponding to this arc, known as the *membrana flaccida*, lacks the tenseness of the rest of the drum-skin.

Viewed through the aural speculum, the normal tympanic membrane has a pearly lustre (Fig. 181). The handle of the malleus, or *manubrium*, inserted within its fibrous layer, can be seen as an opaque ridge running from near the upper anterior margin downward and backward and ending in the *umbo*, or central depression, where the membrane is drawn considerably inward by the tip of the manubrium. It is from this point that the radial fibres of the *membrana propria* diverge.

At the top of the manubrium is a shining spot which is the reflection from the short process of the malleus where it presses against the membrane. From this point two delicate folds of the membrane run to the periphery—one forward and the other backward. They form the lower border of the *membrana flaccida*, or *Shrapnell's membrane*, in which there is less fibrous tissue than in the remaining part of the membrane, and the cutaneous and mucous layers are also less tense than elsewhere. A bright reflection of triangular shape, known as the "pyramid of light," is seen in the lower quadrant of the tympanic membrane. The apex of this bright triangle is at the tip of the manubrium, and its base is on or near the periphery of the membrane.

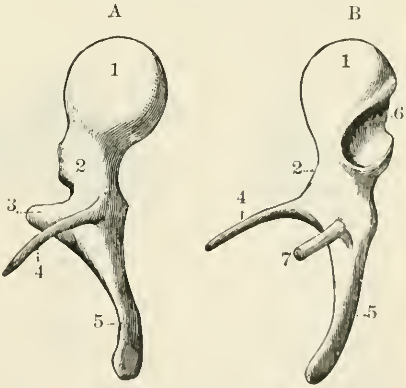

FIG. 184.—Malleus of the right side: A, anterior face; B, internal face (after Testut): 1, capitulum or head of malleus; 2, cervix or neck; 3, processus brevis; 4, processus gracilis; 5, manubrium; 6, grooved articular surface for incus; 7, tendon of m. tensor tympani.

Auditory Ossicles.—The tympanic membrane is put into relation with the internal ear by a chain of bone, the *auditory ossicles*, known as the *malleus*, the *incus*, and the *stapes*, so called from their fancied resemblance to a hammer, an anvil, and a stirrup (Figs. 180, 182, 183). The malleus (Fig. 184) is 18 to 19 millimeters long; it presents a rounded head, grooved on one side for articulation with the incus, a short neck, and a long handle or *manubrium*, which is inserted in the tissue of the tympanic membrane from a point on its upper periphery to a little below its centre. The *processus brevis* of the malleus is a low conical projection which springs from the top of the manubrium and presses directly against that segment of the tympanic membrane known as the *membrana flaccida*, through which it can be seen shining on inspection with the ear-speculum. The *processus gracilis*, or *pro-*

cessus Folianus, long and slender, arises from an eminence just below the neck of the malleus, and, passing forward and outward, is inserted in the Glaserian fissure in the wall of the tympanum. The malleus is held in position partly by ligaments; the *suspensory* or *superior ligament* passes downward and outward from the roof of the tympanum to be inserted into the head of the malleus. The main portion of the *anterior ligament* is attached to the neck of the malleus just above the *processus gracilis;* it embraces the latter, and, passing forward, finds its origin in the anterior wall of the tympanum and in the Glaserian fissure. Another division of this ligament, the *external ligament*, arises and is attached more externally than that just described. The ligaments of the malleus serve to keep its head in position. The external ligament, being attached above the axis of rotation of the hammer, prevents the head of this bone from moving too far inward, and the manubrium from being pushed too far outward. The superior ligament, owing to its oblique course, restrains the head of the hammer from moving too far outward.

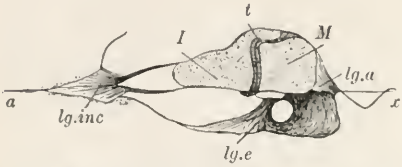

FIG. 185.—Ligaments of the ossicles and their axis of rotation (from Foster, after Hensen). The figure represents a nearly horizontal section of the tympanum, carried through the heads of the malleus and incus: *M*, malleus; *I*, incus; *t*, articular tooth of incus; *lg.a* and *lg.e*, external ligament of malleus; *lg.inc*, ligament of the incus; the line *a–x* represents the axis of rotation of the two ossicles.

The *incus*, *ambos*, or anvil-bone (Fig. 186) is shaped somewhat like a bicuspid tooth. Its thicker portion is hollowed on the surface and is covered with cartilage for articulation with the head of the malleus. It has two processes, a long and a short, which project at right angles to each other; the former has a length of 4½ millimeters, and the latter a length of 3 to 3½ millimeters. When in position the long process descends nearly parallel with the manubrium, but it has less than three-fourths the length of the latter. The free end of the long process is turned sharply inward at right angles, and terminates in a round projection, the *os orbiculare*, which is provided with cartilage for articulation with the head of the *stapes*. The short process is

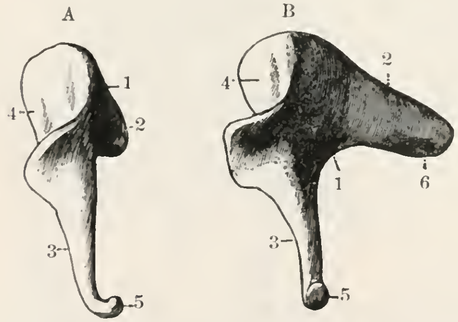

FIG. 186.—The incus of the right side: A, anterior face; B, internal face (after Testut): 1, body of incus; 2, processus brevis; 3, processus longus; 4, articular surface for the malleus; 5, a convex tubercle, processus lenticularis, for articulation with stapes; 6, rough surface for attachment of the ligament of the incus.

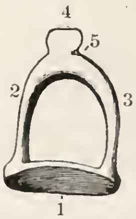

FIG. 187.—The stapes (after Testut): 1, base; 2, anterior crus; 3, posterior crus; 4, articulating surface of head of the bone; 5, cervix or neck.

conical in shape and is thicker than the long process. It has a horizontal position, and is attached by a thick ligament to the posterior wall of the tympanum.

The *stapes* (Fig. 187) articulates with the end of the long process of the incus; its plane is horizontal and about at right angles to that process. It measures 3 to 4 millimeters in length and about 2½ millimeters in breadth. The base of the stapes is somewhat oval in shape, the superior margin being convex and the inferior being slightly concave. It is set in the fenestra ovalis, an aperture measuring about 3 millimeters by 1½ millimeters, and is held in place by a narrow membrane made up of radial fibres of connective tissue. When in position, the inner face of the base of the stirrup is covered with lymphatic endothelium and is washed by the perilymph of the internal ear; the outer face, like the other tympanic bones and the wall of the cavity, is covered by thin mucous membrane.

Movement of the Ossicles.—The malleus-incus articulation is so arranged that with outward movements of the manubrium the head of the malleus glides freely in the joint; but the lower margins of the articulating surfaces project in such a way that the prominences lock together when the manubrium moves inward. Thus, in inward movements of the tympanic membrane and its attached manubrium, the malleus and the incus move together like one rigid piece of bone, the motions of the manubrium and the long process of the incus being parallel. Of the malleus-incus articulation Helmholtz[1] says: "In its action it may be compared with the joints of the well-known Breguet watch-keys, which have rows of interlocking teeth, offering scarcely any resistance to revolution in one direction, but allowing no revolution whatever in the other." In the outward movements the locking teeth or projections are probably still kept in apposition, under ordinary circumstances, through the elastic reaction of the ligament and the stapedial attachment of the incus. Should, however, the tympanic membrane be forced unduly outward, as by increase of pressure within the tympanum or by rarefaction of air in the auditory meatus, the incus only follows the malleus for a certain distance, the latter completing its motion by gliding in the joint. There is thus no danger of the stapes being torn out of the oval window. The hammer and the anvil, suspended by their ligaments, move freely about an axis one end of which is found at the origin of the anterior part of the anterior ligament of the malleus, and the other end in the origin of the ligament which is continuous with the short process of the incus (Fig. 185). In inward motions of the tympanic membrane the ossicles move like a single bone around the axis of suspension; and as the distance measured from the axis of rotation to the tip of the manubrium, where the power is applied, is about one and one-half times the distance to the end of the long process of the incus, where the effect is produced, the motions transmitted to the stapes can have but two-thirds the amplitude of the movements of the tip of the manubrium, but have one and one-half times their force. It will be noticed that a large proportion of the mass of both anvil and hammer is found above their axis of rotation; this upper portion acts as a counterpoise to the parts below which are directly

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[1] *Sensations of Tone*, trans. by Ellis, 1885, p. 133.

concerned in the lever action. The bony lever being thus balanced, it is less difficult to understand its known sensitiveness to impulses that are inconceivably weak. The tense tympanic membrane, by reason of its funnel shape, resists strong inward compression; hence the stapes is prevented from being pressed too far inward. The maximum amplitude of motion of the stapes in the fenestra is very small, being only about $\frac{1}{18}$ millimeter to $\frac{1}{14}$ millimeter, while that of the centre of the tympanic membrane is about $\frac{1}{12}$ millimeter to $\frac{1}{9}$ millimeter.

The functional movements of the auditory ossicles are not molecular but are molar vibrations, the chain of bones moving in a body. The sole purpose of this apparatus of the middle ear is to transmit exactly the variations of pressure in the air of the external auditory meatus to the perilymph which bathes the foot of the stapes—in other words, to convert air-waves into a similar series of water-waves. In the words of Helmholtz,[1] "The mechanical problem which the apparatus within the drum of the ear had to solve was to transform a motion of great amplitude and little force, such as impinges on the drum-skin, into a motion of small amplitude and great force, such as had to be communicated to the fluid in the labyrinth."

The adaptation of the apparatus of the middle ear to this end is worthy of careful consideration. In the first place, it will be noticed that the area of the fenestra ovalis which receives the impulses of the stapes is but a small fraction of the surface of the tympanic membrane on which the air-waves impinge, the latter area being some fifteen to twenty times greater than the former, so that the energy of air-motion is, in a fashion, concentrated. In the second place, as previously observed, the lever mechanism of the auditory ossicles is such that the movements of the end of the long process of the incus have two-thirds the amplitude of those of the tip of the manubrium, but about one and one-half times their force. It should also be noticed that the membrane fastening the foot of the stapes in the fenestra is somewhat less tense on the upper side, so that the top of the oval foot-piece has a freer motion than the bottom, and the head of the stirrup rises slightly with inward motions. In the third place, it has been demonstrated by Helmholtz[2] that the shape of the tympanic membrane peculiarly adapts it for transforming weak movements of wide amplitude into strong ones of small compass. For this membrane is not a simple funnel depressed inwardly, but the radii are slightly curved with the convexity outward, a shape chiefly due to the tension of the elastic circular fibres of the membrane on its inner face, these being most numerous toward the circumference. Air-waves beating upon this convexity flatten the curve somewhat, and their whole energy must be concentrated, with increased intensity but loss of motion, at the central point of the membrane. This effect may be illustrated by holding a slightly-curved brass wire, several inches in length, with its plane perpendicular to the surface of a table and supported on its ends. When one end of the wire is held immovable, up-and-down motions of the arch are transferred to the free end with diminished

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[1] *Op. cit.*, p. 134.

[2] *Op. cit.*

amplitude. The wire represents a single radial fibre of the tympanic membrane, and the funnel shape of this membrane is adapted to concentrating this motion of the radial fibres upon the manubrium. The same effect is illustrated by the fact that when a string or a rope is stretched between two points, no matter how tightly, it always sags at its middle; the weight of the cord, however slight, is sufficient to give it a curved course, and produces a corresponding traction on the points of support.

Eustachian Tube.—That the tympanic membrane may maintain its freedom of motion, it is obviously necessary that the *average* atmospheric pressure on each side of it should remain the same. This equality of pressure is maintained through the medium of the *Eustachian tube*, a somewhat trumpet-shaped canal which, beginning in the lower anterior walls of the tympanum, runs downward, forward, and inward, and terminates in a slit in the side of the upper part of the pharynx. The Eustachian tube is lined, like the walls of the tympanum, with ciliated epithelium, the cilia working in such a way as to carry into the pharynx such secretions as may arise from the mucous membrane of the middle ear. The pharyngeal opening of the Eustachian tube is probably normally closed, but it may easily be made to open by increase or decrease of air-pressure within the pharynx, as may be produced by closing the nose and mouth and either forcing air into the pharynx by strong expiration or rarefying it by suction. In the former case the air-pressure within the tympanum is increased, and in the latter it is diminished. When air is thus made to enter or to leave the tympanum, a sensation of a sudden snap and a dull crackling noise in the ear is experienced. The lower end of the tube is normally opened during the act of swallowing, and it is at this moment that the intra- and extra-tympanic air-pressures are equalized.

Muscles of the Middle Ear.—Two muscles are devoted to adjusting the tension of the auditory mechanism of the middle ear. The *tensor tympani* is lodged within a groove which is just above and about parallel with the Eustachian tube. It terminates externally in a long tendon which bends nearly at right angles round the outer edge of the groove and is inserted into the handle of the malleus near the neck. Contraction of the tensor tympani thus pulls inward the tympanic membrane, increases its tension, and somewhat dampens its vibrations. At the same time a strain is put upon the chain of ossicles, the toothed processes of the malleus and incus are brought more closely together, and the foot of the stapes is pressed into the oval window, increasing the pressure upon the fluids of the internal ear. It is said that the relaxed tympanic membrane, particularly after section of the tensor tympani muscle, is thrown into sympathetic vibration with comparative ease, and is in this condition best adapted to respond to weak aërial impulses and to the periodic waves of musical notes. When the membrane is tense its vibrations are damped, and it is particularly fitted to transmit noises and consonantal sounds, and thus the muscle involved would seem important to the clear transmission of ordinary speech, though its effect would be to decrease the acuteness of hearing. According to Hensen,[1] the tensor tympani muscle

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[1] *Hermann's Handbuch der Physiologie*, 1880.

is excited to reflex contraction by the initial waves of a sound, resulting in a closer union of the toothed processes of the malleus and incus, so that there is less loss of motion in the subsequent vibrations. But Ostermann[1] believes the muscle to be chiefly a protective mechanism which by its contraction prevents oscillation of so wide an amplitude as to be hurtful, and that its reflex action is called forth chiefly by very loud noises (Pl. 1, Fig. 1). The *stapedius* is a small muscle imbedded in the inner wall of the tympanum, near the fenestra ovalis. Its tendon, passing forward, is inserted into the neck of the stapes. Contraction of the muscle would cause a slight rotation of the stapes round a vertical axis, so that the hinder part of the foot of the ossicle would be pressed more deeply into the fenestra, while the remaining portion would be drawn out of it. Its action probably reduces the pressure in the cavity of the perilymph, and thus is antagonistic to that of the tensor tympani (Pl. 1, Fig. 2, A, B).

Vibrations of the Tympanic Membrane.—It is a general physical law that every elastic body can be made to vibrate more easily at one definite rate than at any other. The musical tone represented by this rate of vibration is known as the *prime* or fundamental tone of the body. Membranes have fundamental tones (see p. 383), whose pitch is determined by their area, thickness, and tension, but they differ from rods and strings in being less strictly confined to a single fundamental tone in their vibration. The tympanic membrane is quite peculiar in that it can hardly be said to have a definite fundamental tone. It would obviously be a great imperfection in an organ of hearing were certain sounds intensified by it out of proportion to others, as would be the case if the tympanic membrane had a marked fundamental tone of its own. This is prevented in the case of the membrana tympani probably both by reason of the peculiar form of its surface and its structure, and also because its oscillations are damped by the pressure of the malleus held in position by the other mechanisms of the tympanum. When the tympanic membrane is perforated or is wholly removed, without destructive inflammatory changes in the middle ear, sounds are still heard, though usually with diminished loudness. A musician who had suffered this accident was no longer able to play his violin, probably because sounds of different pitch ceased to be perceived in their true relations of loudness. We may thus conclude that the function of the tympanic membrane is not only to guard against injury to the delicate membranes of the fenestræ and the internal ear, but also to transmit to the ossicles sonorous vibrations with their true proportion of intensity. The membranes covering the round and oval windows of the internal ear have no means of damping sympathetic vibrations (see p. 385), and, should complex air-waves strike directly upon them, they would, probably, by sympathetic resonance, respond more powerfully to tones of certain pitch than to any others.

The sensation of sound may be excited by conduction through the bones of the skull as well as in the ordinary way. Thus, a tuning-fork set vibrating and held between the teeth or on the forehead is heard perfectly, and more

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[1] *Archiv für Anatomie und Physiologie*, 1898, S. 75.

loudly when the ears are closed than when open. The vibrations thus conducted probably partly affect the internal ear directly, and partly indirectly by setting in oscillation the tympanic membrane. It is said that when the sound of a tuning-fork held close to the ear dies away, it may again be heard if the handle of the fork be pressed against the teeth. When the tone now fails, it once more becomes audible if one of the ear-passages is lightly closed, and the sound seems to be on the side which is closed. The sensation failing, it may again be aroused if the appropriately formed handle of the fork be inserted in the auditory meatus.[1]

Normal individuals differ greatly in their keenness of hearing, and tests show frequently disparity in the sensibility of the two ears. The hearing ability of children is said to improve up to the age of twelve years. There is no functional relation between keen hearing and sensibility to pitch.[2]

The Internal Ear, or Labyrinth.—The internal ear is the site of the true organ of hearing. The *membranous labyrinth* (Pl. 1, Fig. 4; Fig. 191) is a complicated system of membranous tubes and sacs, in which terminate at particular points the filaments of the auditory nerve; it is contained within a chamber, the bony labyrinth, hollowed out in the petrous bone. The cavity of the bony labyrinth (Figs. 188, 189) consists of a median part, the *vestibule*, which is prolonged posteriorly in the system of *semicircular canals* and anteriorly in the *cochlea.* The vestibule is a space which measures about one-fifth of an inch in diameter, and it is perforated in its outer wall by an oval opening known as the *fenestra ovalis.* The *semicircular canals* are three tubes of circular section, known respectively as the anterior or superior, the posterior, and the

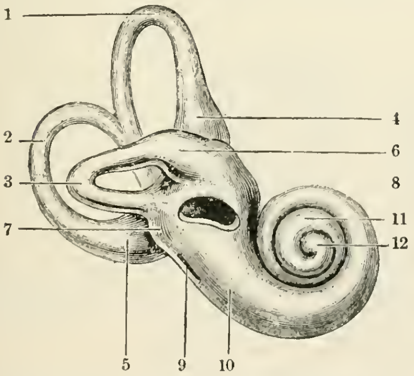

FIG. 188.—Right bony labyrinth, viewed from outer side: the figure represents the appearance produced by removing the petrous bone down to the denser layer immediately surrounding the labyrinth (from Quain, after Sömmering): 1, 2, 3, the superior, posterior, and horizontal semicircular canals; 4, 5, 6, the ampullæ of the same; 7, the vestibule; 8, the fenestra ovalis; 9, fenestra rotunda; 10, first turn of the cochlea; 11, second turn; 12, apex.

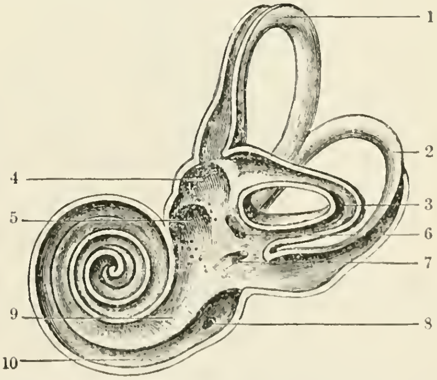

FIG. 189.—Interior view of left bony labyrinth after removal of the superior and external walls (from Quain, after Sömmering): 1, 2, 3, the superior, posterior, and horizontal semicircular canals; 4, fovea hemi-elliptica; 5, fovea hemispherica; 6, common opening of the superior and posterior semicircular canals; 7, opening of the aqueduct of the vestibule; 8, opening of the aqueduct of the cochlea; 9, the scala vestibuli; 10, scala tympani; the lamina spiralis separating 9 and 10.

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[1] Rinne, quoted by Hensen: *Hermann's Handbuch der Physiologie*, 1880, Bd. iii. Th. 2, S. 26.

[2] Seashore: "Studies in Psychology," *Bulletin University of Iowa*, 1899.

external or horizontal semicircular canal. Their planes are at right angles to one another, so that they occupy the three possible dimensions of space. The external canal lies in a nearly horizontal plane, while the other two approach the vertical. Each canal is dilated at one extremity into a globular cavity which is more than twice the diameter of the canal itself, and which is known as the *ampulla*. The anterior and posterior canals unite near the ends not provided with ampullæ, and they enter the vestibule as a common tube. Anteriorly the cavity of the vestibule is continued as a tube of complex internal structure which is coiled upon itself two and one-half times, and which, from its resemblance to the shell of a snail, is known as the *cochlea* (Pl. 1, Fig. 3). The osseous cochlea may be conceived as formed by a bony tube turned about a bony central pillar, the *modiolus*, which diminishes in diameter from the base to the apex of the cochlea. From the modiolus a bony shelf stretches into the cavity of the tube, incompletely dividing it into two tubular chambers, winding round the modiolus like a circular staircase, the upper of which chambers we shall soon learn to know as the *scala vestibuli*, and the lower chamber as the *scala tympani* (Fig. 190; Pl. 1, Fig. 3). The bony shelf mentioned above as partly bisecting the cochlear tube has, of course, like the latter, a spiral course, and is known as the *lamina spiralis;* its importance as a supporter of the auditory-nerve filaments will soon be seen.

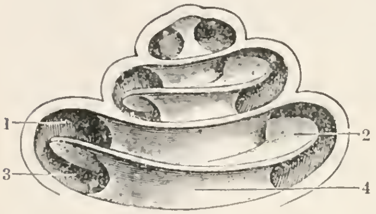


FIG. 190.—Diagram of the osseous cochlea laid open (after Quain): 1, scala vestibuli; 2, lamina spiralis; 3, scala tympani; 4, central pillar or modiolus.

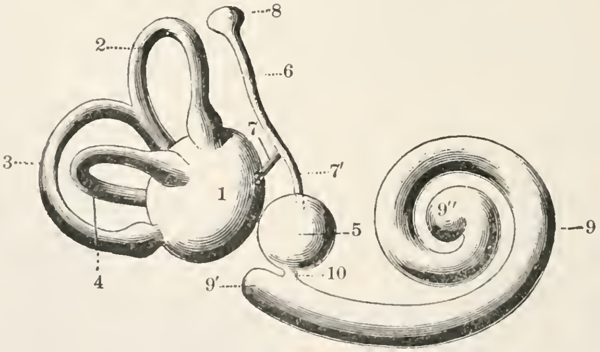


FIG. 191.—Diagram of right membranous labyrinth seen from the external side (after Testut): 1, utricle; 2, 3, 4, superior, posterior, and horizontal semicircular canals; 5, saccule; 6, ductus endolymphaticus, with 7, 7′, its twigs of origin; 8, saccus endolymphaticus; 9, canalis cochlearis, with 9′, its vestibular cul-de-sac, and 9″, its blind extremity; 10, canalis reuniens.

Contained within the cavity of the bony labyrinth, and parallel with its walls, is the *membranous labyrinth*, in which are found the essential structures of the organ of hearing (Pl. 1, Fig. 4; Fig. 191). The membranous labyrinth is filled with a somewhat watery, mucin-holding fluid, the *endolymph*, while a similar fluid, the *perilymph*, is found outside it and within the osseous labyrinth. The

Explanation of Plate 1.

Fig. 1.—Schematic representation of displacement of the auditory ossicles due to contraction of the tensor tympani muscle (Testut): *a*, external auditory meatus; *b*, tympanic cavity; *c*, vestibule of the bony labyrinth; *d*, fenestra ovalis; 1, membrana tympani; 2, handle of malleus; 3, head of malleus; 4, insertion of tendon of tensor tympani; 5, long or vertical process of incus; 6, head of incus; 7, stapes. (The arrow indicates the direction of traction of the tensor tympani muscle; and the lines in red indicate the change in the position of the parts produced by it.)

Fig. 2.—Schematic representation of the displacement of the stapes due to contraction of the stapedius muscle (Testut): *A*, the stapes in repose; *B*, stapes during contraction of stapedius muscle; 1, base of stapes; 2, anterior border of fenestra ovalis; 3, the pyramid; 4, tendon of stapedius muscle; *a*, anterior portion of annular ligament of stapes, longer than *b*, posterior portion of same ligament; *x*, *x*, anteroposterior diameter of fenestra ovalis, passing through the base of the resting stapes; *y*, point of passage of the vertical line which represents the axis of rotation of the stapes.

Fig. 3.—The three parts making up the bony cochlea (schematic, from Testut): *A*, the columella; *B*, spiral tube containing the scalæ; *C*, lamina spiralis; *D*, the three parts in their normal relations.

Fig. 4.—Schematic representation of the perilymphatic and endolymphatic spaces. The former appear in black, and the latter are colored blue (Testut): 1, utricle; 2, saccule; 3, semicircular canal; 4, canalis cochlearis; 5, ductus endolymphaticus with its two branches of origin; 6, saccus endolymphaticus; 7, canalis reuniens, or canal of Hensen; 8, scala tympani; 9, scala vestibuli; 10, their communication at the helicotrema; 11, aquæductus vestibuli; 12, aquæductus cochlearis; 13, periosteum; 14, dura mater; 15, stapes in the fenestra ovalis; 16, fenestra rotunda with its membrane.

FIG. 1.

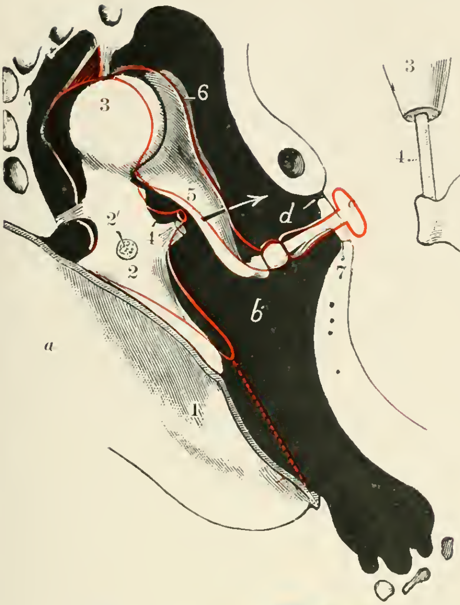


FIG. 2.

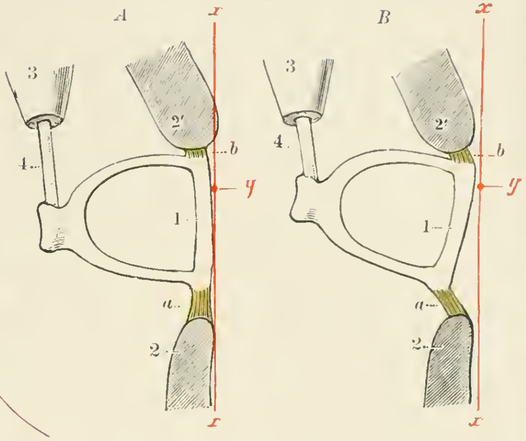


FIG. 3.

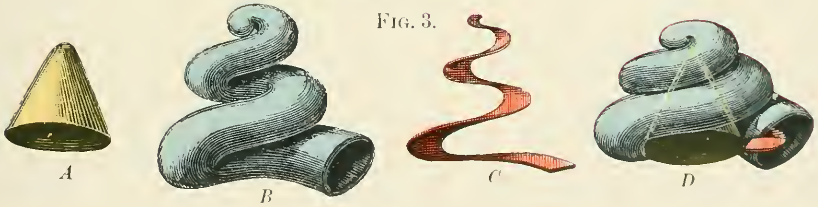
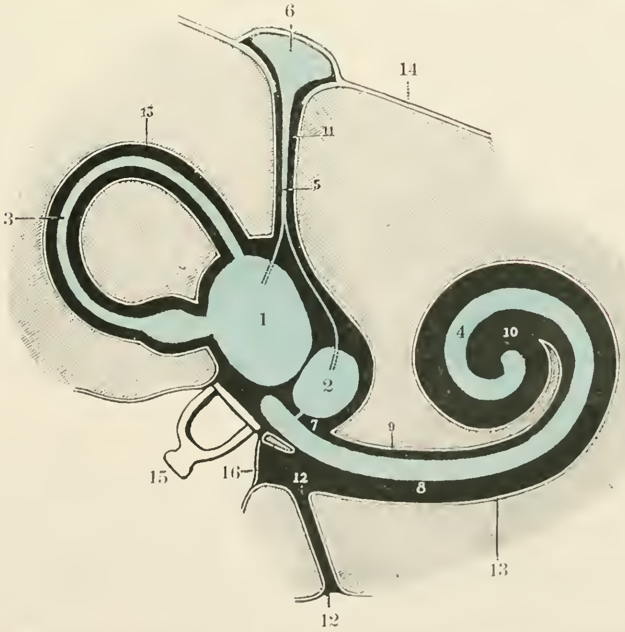

A *B* *C* *D*

FIG. 4.



perilymph space, which is lined by lymphatic epithelium, is in communication, along the sheath of the auditory nerve, with the subdural and subarachnoid lymph-areas of the brain. Numerous sheets and bars of connective tissue cross from the wall of the bony to that of the membranous labyrinth and help support the latter. That part of the membranous labyrinth lying within the vestibule is composed of two separate sacs—a larger posterior, known as the *utricle* or *utriculus,* and a smaller, more anterior, known as the *saccule* or *sacculus.* The plane of division between the two sacs ends opposite the fenestra ovalis (Pl. 1, Fig. 4). Though the sacs are quite separate, their cavities are indirectly continuous, through the union of two small tubes arising from either sac, which tubes unite to form the *ductus endolymphaticus,* a tube running inward through a canal in the petrosal bone and ending blindly in a dilated flattened extremity, the *saccus endolymphaticus,* this being supported between the layers of the *dura mater* within the cavity of the skull (Pl. 1, Fig. 4). Bundles of auditory-nerve fibres penetrate the wall of each sac. The utricle gives rise to the membranous semicircular canals, which communicate with it at five points, it being remembered that the anterior and posterior canals fuse into a single tube at the ends not provided with ampullæ, and that they have a common entrance into the utricle. The saccule is continuous by a narrow tube, the *canalis reuniens,* with that division of the membranous labyrinth contained within the cochlea and known as the *canalis cochlearis.* The auditory nerve really consists of two distinct divisions having separate origins and different distributions. One of these branches passes finally to the cochlea, and the other to the vestibule and the semicircular canals. The nerve approaches the labyrinth by way of a canal known as the *meatus auditorius internus,* and on reaching the angle between the vestibule and the base of the cochlea the cochlear division passes to the cochlea. The remainder of the nerve consists of two divisions, the superior of which is distributed to the utricle and to the ampullæ of the anterior and horizontal semicircular canals; the inferior branch supplies the saccule and the posterior semicircular canal. The inner wall of both utricle and saccule is developed at a particular spot into a low mound, the *macula acustica,* made up of an accumulation of the connective-tissue elements of the membranous wall and covered by a peculiarly modified epithelium, the *auditory epithelium* (Fig. 192). All the auditory-nerve filaments that enter the saccule and utricle respectively pass to these mounds and there enter into relation with the auditory epithelium.

As the auditory-nerve endings are confined to a particular area in the utricle and the saccule, so the nerve-fibres supplying the semicircular canals are limited to a certain part of the ampulla of each canal. The tissue of the wall of the ampulla is developed into a ridge projecting into the cavity in a direction across its long axis. This ridge, present in each ampulla, is called the *crista acustica;* it is capped by a thick layer of columnar epithelial cells, the auditory epithelium, which thins away at the border of the crista into the sheet of flattened cells by which the rest of the ampulla is lined. The auditory cells (Fig. 192) are said to be of two kinds—one, cylindrical in shape and reaching only part way to the basement membrane, the *hair-cells;* the other, narrow and elongated, the supporting or *sustentacular cells.* The former are peculiar in the fact that from their free ends there project long, stiff, hair-like processes. The filaments of the ampullary-nerve branches pass through the cristæ and encircle the bodies of the hair-cells. The cells covering the *maculæ acusticæ* have essentially the same structure as those just described, though in the maculæ the auditory hairs are shorter than in the cristæ. Seated on the free surface of the macular epithelium is a fibrous mass which is said to be a normal structure, and not, like a somewhat similar mass found covering the cristæ in post-mortem section, a coagulum due to the method of preparation. Imbedded in the membrane over the maculæ of both saccule and utricle are small crystals, *otoliths* or *otoconia,* composed chiefly of carbonate of lime. Otoconia are also found less constantly in the ampullæ and even in the perilymph space of the cochlea. In fishes there are large masses of calcareous matter, otoliths, attached to the wall of the auditory sac.

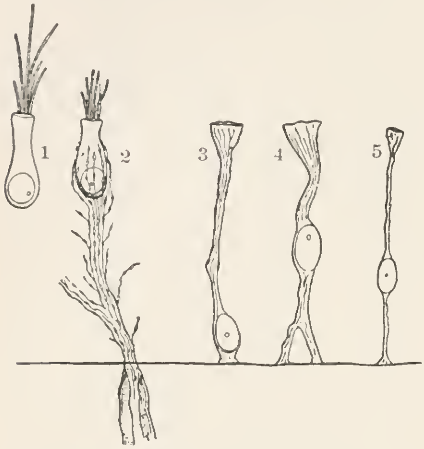


FIG. 192.—Diagram showing the epithelial cells of a macula or a crista (after Foster): 1, cylinder or hair-cell; 2, the same, enveloped in a nest of nerve-fibrils; 3, 4, 5, forms of rod- or spindle-cells.

General Anatomy of the Cochlea.—By far the most complex structure of the ear is found in the cochlea (Pl. 1. Figs. 1, 3, 4; Figs. 188–191). The bony cochlea continues from the anterior wall of the vestibule, and in the upright position of the head the axis of the modiolus is nearly horizontal, pointing, from base to apex, outward and slightly down and forward, the base of the cochlea being formed by the inner surface of the petrous bone. The membranous cochlea, *canalis* or *ductus cochlearis,* is a tube of nearly triangular cross-section which winds round the modiolus from base to apex (Fig. 193). The base or outer side of this triangle is attached closely to the bony wall of the cochlea; the upper side, supposing the modiolus to be vertical with its apex above, is made of a thin sheet of cells known as the *membrane of Reissner;* the lower side is made up partly of the bony margin of the *lamina spiralis* and partly of a membrane, radially striated, stretched across from the edge of the spiral lamina to the side wall of the cochlea; this is called the basilar membrane, *membrana basilaris.* The coiled tube forming the bony cochlea is thus divided by the *lamina spiralis* and the *canalis cochlearis* into three tubes which wind spirally and parallel round the modiolus. The *canalis cochlearis* contains endolymph, and its cavity ends blindly above and below, but is continuous by way of the narrow *canalis reuniens* with that of the saccule. The tubes above and below the *canalis cochlearis* are perilymph-spaces; it will be noticed that there is no such space on the outer side of the membranous cochlea.

The upper tube, when followed down to the base of the cochlea, is found to open freely into the vestibule of the labyrinth; it is therefore known as the *scala vestibuli.* The lower tube ends blindly at the base of the cochlea, but, where this part bulges into the tympanum as the "promontory" of its inner wall, it is perforated by the aperture known as the *fenestra rotunda,* whose proper membrane alone prevents the perilymph from escaping into the middle ear. This tube is therefore known as the *scala tympani.* From its central position the membranous cochlear canal is frequently known as the *scala media.* The scala vestibuli and the scala tympani both decrease in size as they wind from the base to the apex or *cupola* of the cochlea; the membranous cochlear canal, on the contrary, increases in section from base to apex until near the top; hence the width of the basilar membrane and the

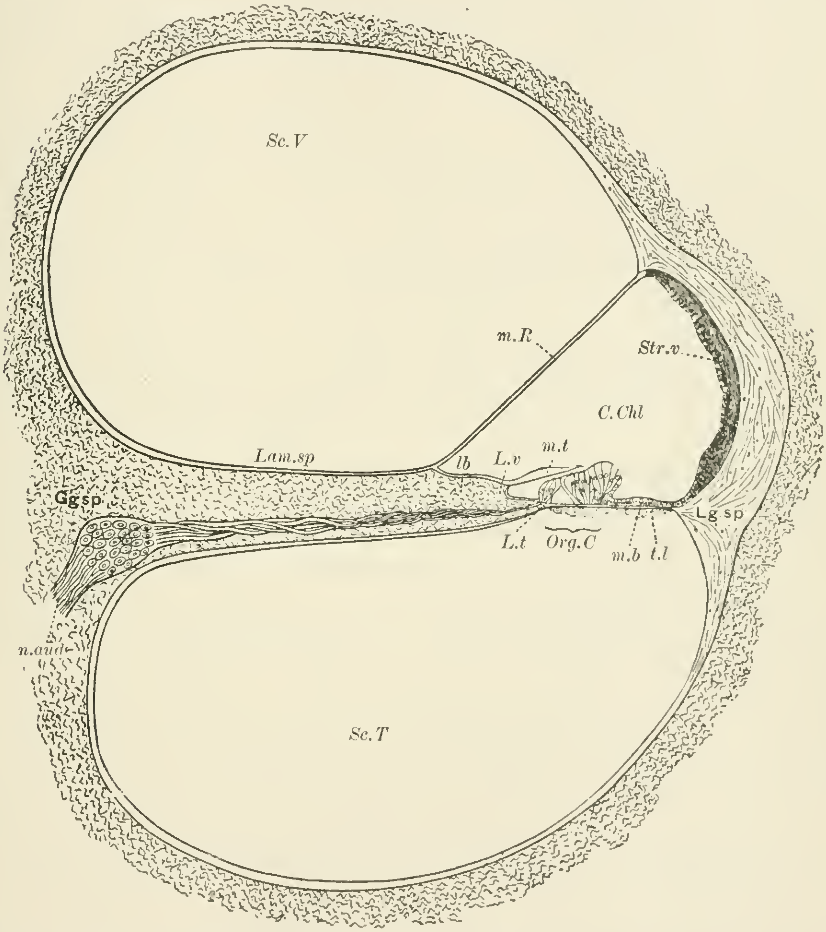


FIG. 193.—Diagram of a transverse section of a whorl of the cochlea (after Foster): *Sc.V*, scala vestibuli; *Sc.T*, scala tympani; *C.Chl*, canalis cochlearis; *Lam.sp*, lamina spiralis; *Gg.sp*, ganglion spirale; *n.aud*, auditory nerve; *m.R*, membrane of Reissner; *Str.v*, stria vascularis; *Lg.sp*, ligamentum spirale; *t.l*, lymphatic epithelioid lining of basilar membrane on the tympanic side; *m.b*, basilar membrane; *Org.C*, organ of Corti; *L.t*, labium tympanicum; *lb*, limbus; *L.v*, labium vestibulare; *m.t*, tectorial membrane.

length of its radial fibres increase from below upward. The scala vestibuli and the scala tympani have no communication except through a small aperture under the cupola of the cochlea, known as the *helicotrema;* this is bounded by the hook-like termination, the *hamulus*, of the bony lamina spiralis, which forms the greater part of a ring completed by the pointed blind extremity of the canalis cochlearis fastened above it to the cupola.

The Transmission of Vibrations through the Labyrinth.—Vibrations of the tympanic membrane are transmitted as pulses of very small amplitude to the membrane covering the fenestra ovalis. The relatively considerable body of perilymph bathing the inner face of this membrane must be thus set in motion, and there starts a fluid-wave which is free to make its way throughout the perilymph-spaces of the vestibule and the semicircular canals. It may pass from the vestibule along the scala vestibuli to its top, through the helicotrema, and back by way of the scala tympani, at whose bottom it finally surges against the membrane covering the fenestra rotunda; or the wave may be transmitted directly across the membranous cochlea. The fluids of the labyrinth being physically incompressible, the function of the fenestra rotunda as a sort of safety-valve seems evident. Politzer inserted a glass tube in the round window, and found that fluid in the tube rose when strong air-pressure was brought to bear on the outer side of the tympanic membrane. The cavity of the membranous labyrinth (Pl. 1, Fig. 4) is nowhere in communication with the perilymph-space about it, and we must therefore assume that the irritation of the auditory cells seated in its wall must depend on vibrations transmitted from the perilymph directly through the membranous sacs and tubes.

Like the perilymph-space, the cavity of the membranous labyrinth is in communication throughout, though in certain situations the connection of adjacent parts is very indirect. Thus, though the semicircular canals open freely at both ends into the utricle, the utricle and saccule are only brought into union by the two narrow tubes that unite to form the ductus endolymphaticus. It will be noted that by means of this duct the membranous labyrinth is really continued into the cranial cavity. The saccule in turn is continuous with the scala media of the cochlea by way of the canalis reuniens.

The Membranous Cochlea and the Organ of Corti (Figs. 193–195).—The cochlear division of the auditory nerve, together with the nutrient blood-vessels, penetrates the modiolus at its base and runs up through the spongy interior of the bony pillar. As the nerve ascends through the modiolus its fibres are gradually all diverted to run in a radial direction between the bony plates of the lamina spiralis, to terminate in the *organ of Corti* of the canalis cochlearis. A collection of nerve-cells is interposed in the course of the auditory fibres at the base of the *lamina spiralis.*

A complete view of the nerves of the cochlea would show a central pillar of nerve-fibres diminishing in thickness from below upward, and winding round this pillar a spiral sheet of radially-disposed nerve-fibres containing, near their point of departure from the central pillar, a spiral line of ganglion-cells; this collection of cells is therefore known as the *ganglion spirale.* The thin, free edge of the bony *lamina spiralis* is, in the recent state, thickened by a development of connective tissue forming a promontory known as the *limbus.* The free edge of the *limbus* is in turn shaped in such a way as to make a short, sharp projection in the plane of the upper surface of the lamina and a longer projection in the plane of its lower surface, leaving the free margin between them hollowed out. The upper projection, which is known as the vestibular lip, *labium vestibulare,* serves for the attachment of the tectorial membrane, *membrana tectoria,* presently to be described. The lower projection is called the tympanic lip (*labium tympanicum*); to it is attached the inner margin of the basilar membrane, on whose inner half is seated the very complex structure known as the organ of Corti.

The *basilar membrane* is a thin sheet of fibrillated connective tissue stretched tightly between the tympanic lip of the limbus on the inside and the spiral ligament (see p. 379) on the outside. The more median part of the membrane, which supports the organ of Corti, is thin and rigid and is fibrillated in a radial direction. The outer part, which is first thicker and then thinner again near its point of attachment, is distinctly composed of radial fibres cemented together; the isolated fibres are characterized by being stiff and brittle.

The *organ of Corti* (Figs. 193, 194) has as its supporting basis a series of peculiarly modified epithelial cells, known as the *rods of Corti* (Fig. 195, B, B′), which are disposed along the edge of the spiral lamina in two rows, an inner and an outer. The inner rods have their feet on the basilar membrane near its median attachment; they lean outward and upward, and at their upper extremity join or articulate with the heads of the outer rods, whose feet are fastened to the basilar membrane more externally. The two rows of rods are thus joined together like the rafters of a house, and enclose beneath them a canal known as the *tunnel* of the organ of Corti. The inner rods are more numerous than the outer, so that the latter are fastened rather between than to the ends of the former. Leaning against the inner or median side of the inner row of rods is a single row of hair-cells (Fig. 194), much like those described as seated on the maculæ and cristæ of the labyrinth, to which hair-cells filaments of the auditory nerve are distributed. Closely applied to the single row of hair-cells, on the inner side, are several rows of columnar cells gradually decreasing in size toward the median line, and beneath the whole is a group of nuclei. External to the outer row of rods, and separated from it by a space, are four parallel rows of hair-cells known as the *cells of Corti;* their bodies do not reach downward as far as the basilar membrane, and just below each row is a bundle of nerve-fibres which have traversed the tunnel of Corti and then have changed their direction from a radial to a longitudinal or spiral one. These fibres, and others having a more direct course, one by one end in clusters encircling the individual hair-cells.

Four rows of peculiarly-modified columnar cells, the *cells of Deiters,* are inserted closely between the cells of Corti, the outermost row being external to the fourth row of Corti. These cells rest below on the basilar membrane. Still external to these groups of cells is a series of rows of tall columnar cells of simple character supported upon the basilar membrane, and rapidly decreasing in height externally into a layer of cuboidal epithelium covering the outer part of the basilar membrane. The rods of Corti are peculiarly shaped at the top, the upper extremity of each being bent at an angle so as to project externally and parallel with the basilar membrane; these projections are the *phalangar processes* of the rods, the *phalanges* of the inner row overlapping those of the outer row. These phalangar processes of the rods form the points of attachment—in fact, the beginning—of the *reticulate membrane* (*membrana reticulata*), a peculiar cuticular, network-like structure formed of rings and cross-bars, having the appearance of certain vegetable tissues seen under the microscope. The reticulate membrane stretches across the outer rows of hair-cells, the body of each of which is enclosed and is held at its top within a ring of the network (Fig. 195, D).

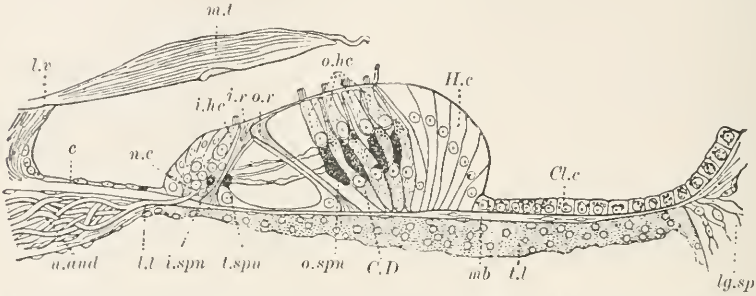


FIG. 194.—Diagram of the organ of Corti (from Foster, after Retzius): *i.r*, inner rod of Corti; *o.r*, outer rod of Corti; *i.hc*, inner hair-cell; *n.c*, the group of nuclei beneath it; *o.hc*, outer hair-cells, or cells of Corti; *C.D*, the twin cells of Deiters (four rows); *n.aud*, the auditory nerve perforating the tympanic lip, *l.t*, and lost to view among the nuclei beneath the inner hair-cells; *i.spn*, the inner spiral strand of nerve-fibrils; *t.spn*, the spiral strand of the tunnel; *o.spn*, the outer spiral strand belonging to the first row of outer hair-cells; the three succeeding spiral strands belonging to the three other rows are also shown; nerve-fibrils are shown stretching radially across the tunnel; *H.c*, Hensen's cells; *Cl.c*, Claudius' cells; *t.l*, lymphatic epithelioid lining on the side toward the scala tympani; *lg.sp*, ligamentum spirale; *c*, cells lining the spiral groove, overhung by the vestibular lip, *l.v*; *m.t*, tectorial membrane; a fragment, torn from it, remains attached to the organ of Corti just outside the outermost row of hair-cells.

Each of the cells of Deiters, described above, is continued upward in a process which is attached to a cross-bar or a ring of the reticulate membrane next outside its companion-cell of Corti. The inner or median line of the Deiters cell is also modified into a cuticular thread fused below to the basilar membrane and above to a ring of the reticulate membrane. Thus the auditory hair-cells of Corti may be regarded as suspended from the reticulate membrane, which in turn is supported by the cuticular processes of the cells of Deiters, which rest upon the basilar membrane, and by the phalangar processes of the rods of Corti. The physical contact of the cells of Corti with those of Deiters is so intimate—if, indeed, their substance is not continuous—that impulses generated in the one can probably easily be communicated to the other.

The upper wall of the canalis cochlearis is made of a sheet of homogenous, fibrillated connective tissue covered with flat cells, and stretches from the limbus of the spiral lamina outward and upward to the side wall of the cochlea. It is known as the *membrane of Reissner.* The periosteal connective tissue of the bony wall of the cochlea is generally well developed within the area enclosed between the membrane of Reissner and the membrana basilaris; it is particularly thick at the line of division between the scala media and the scala tympani, where it forms a projecting ridge at the outer attachment of the basilar membrane. This ridge is the *spiral ligament;* an extension from it, gradually decreasing in thickness, reaches into both the vestibular and the tympanic scala.

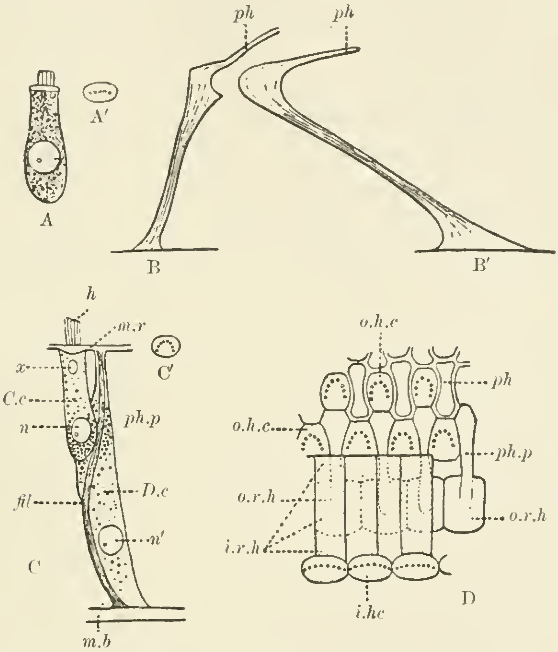


Fig. 195.—Diagram of the constituents of the organ of Corti (from Foster, after Retzius): A, inner hair cell; A′, the head, seen from above; B, inner, B′, outer, rod of Corti; *ph*, in each, is the phalangar process; C, the twin outer hair-cell; *C.c*, the cell of Corti; *h*, its auditory hairs; *n*, its nucleus; *x*, Hensen's body; *D.c*, cell of Deiters; *n′*, its nucleus; *ph.p*, its phalangar process; *fil*, the cuticular filament; *m.b*, basilar membrane; *m.r*, reticulate membrane; c′, the head of a cell of Corti, seen from above; D, the organ of Corti, seen from above; *i.hc*, the heads of the inner hair-cells; *i.r.h*, the head and phalangar process of the inner rod; *o.r.h*, the head of the outer rod, with *ph.p*, its phalangar process, covered to the left hand by the inner rods, but uncovered to the right; *o.h.c*, the heads of the cells of Corti, supported by the rings of the reticulate membrane; *ph*, one of the phalangæ of the reticulate membrane.

A thick layer of both columnar and cuboidal epithelium lines the connective tissue forming the outer wall of the canalis cochlearis. This epithelium is peculiar in that the blood-vessels of the underlying connective tissue penetrate between the epithelial cells themselves. The *tectorial membrane* (*membrana tectoria*) is a sheet of radially-fibrillated tissue, thin at its point of attachment to the vestibular lip of the limbus, and becoming thicker and then thinner again as it stretches out over the organ of Corti, reaching as far as the most external row of hair-cells. It is said to lie in actual contact with the rods of Corti and the free ends of the hair-cells, and it has been presumed to serve as a damper for the vibrations imparted to the organ of Corti.

The researches of Howard Ayers[1] have led him to conclusions concerning the minute anatomy of the ear materially different from those just presented. Thus, Ayers asserts that the so-called *membrana tectoria* is nothing more than the matted mass of hairs "which spring from the tops of the hair-cells and form a waving plume on the crest of the ridge of the organ of Corti." He also holds the *membrana reticulata* and several other structures described by different authors to be nothing more than artefacts produced by the methods of preserving and manipulating the specimens. According to Ayers, the cochlear nerves end *in* the hair-cells and *not* freely between them, and they are probably continuous with the auditory hairs.

Theory of Auditory Sensation.—It can hardly be doubted that the nervous structures of the cochlea form an organ of special sense for the perception of musical tones and probably of noises as well. But no trustworthy conclusion can be maintained as to the precise mode of action of the auditory apparatus. The fact that the rods of Corti are absent from the cochleæ of birds, which evidently are capable of appreciating musical tones, shows that these structures may be accessory, but are not essential parts of the sensory apparatus. Starting from the fact that the basilar membrane splits readily in a radial direction, in which, moreover, it is tightly stretched between its attachments, Helmholtz[2] long ago proposed the theory that the basilar membrane behaves toward vibrations reaching it like a series of stretched strings. As the wires of a piano have different rates of vibration according to their length, and respond sympathetically to correspondingly different notes sounded in their neighborhood, so it has been supposed that different radial fibres of the basilar membrane are set into sympathetic vibration by different rates of vibration in the fluids bathing them. These vibrations must be imparted to the structures in the organ of Corti, and the irritation of the nerves connected with the cells of Corti is a natural sequel. It may be repeated that, though the canal of the bony cochlea as a whole diminishes in diameter from base to cupola, the canal of the membranous cochlea, the scala media with its lower wall or basilar membrane, increases in diameter. Thus the radial fibres of the basilar membrane are longest near the apex of the cochela. The radial width of the basilar membrane, measured near the bottom, middle, and top, respectively, is given as 0.21 millimeter, 0.34 millimeter, and 0.36 millimeter. The waves of physical sound are thus supposed to be analyzed in the peripheral sense-organ, each auditory nerve-fibre exciting in consciousness a tone of a particular pitch, and the mind perceiving the simultaneous effects of different pendular vibrations as notes of different quality.

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[1] Ayers: *Journal of Morphology*, May, 1892.

[2] Helmholtz: *Tonempfindungen*, 1877, S. 240.

C. THE RELATION BETWEEN PHYSICAL AND PHYSIOLOGICAL SOUND.

Production of Sound-waves.—Sound, in its physiological meaning, is a sensation which is the conscious appreciation of internal changes occurring in certain cells of the cerebral cortex. Fibres of the auditory nerve come into close relation with these cells, and in whatever way those fibres are excited the result is one and the same, a sensation of sound.

The elaborate apparatus of the middle and internal ear is so constructed that the energy of mechanical oscillations in the external air is transmitted to the terminations of the auditory nerves in a manner to excite them.

Sound, in a physical sense, consists in waves of alternate condensation and rarefaction travelling in the air from the point of origin of the sound, much as waves radiate over the surface of water from the point where a stone is dropped. Any sudden impulse, such as a puff of air, or the vibration of a solid body, as a stretched string or a tuning-fork, pushes the adjacent molecules of air against those further removed, and this impulse produces an area, or aërial shell, of increased density or condensation. The air being perfectly elastic, the molecules, relieved from pressure, spring back even beyond the position of equilibrium, and leave an area of decreased density or rarefaction. Thus a wave, consisting of a shell of condensation succeeded by a shell of corresponding rarefaction, moves through the air. This single air-wave is the simplest element of physical sound. When a number, no matter how great, of sound-waves simultaneously excite the same particle of air, the resultant motion of that particle is the algebraic sum of all the motions imparted to it by the single sound-waves considered separately. As any elastic body, when set vibrating, continues its oscillations for a time, so is it probable that strictly isolated air-waves do not occur. Any elastic body, such as a stretched string, or a tuning-fork, when set in vibration, sends out from itself a series of air-waves which succeed one another at a rate identical with the rate of vibration of the elastic body. Such a regular succession of air-waves striking upon the tympanic membrane sets the latter into correspondingly regular oscillations and produces in the auditory apparatus the sensation of *musical tone*.

Loudness and Musical Pitch.—The more vigorous the vibrations of the oscillating body, the more forcibly are the air-molecules which are struck by it driven forward; and the greater their excursion or *amplitude* of movement, the greater is the force with which the tympanic membrane is driven inward when the moving air-wave strikes it. The *loudness* of the tone manifestly depends upon the extent of motion of the tympanic membrane, as does this on the *amplitude* of air-motion. Different elastic bodies have different natural rates of oscillation. The more rapid the rate, the more frequent is the succession of air-waves that strike upon the ear. It is said that the apparent pitch of a tone is raised when its intensity is lowered, and that such an elevation of pitch may equal one-fifth of a tone.[1] Musical *pitch* is determined by the number of air-waves which pass a given point in a unit of time, or, in other words, by the rate of vibration of the sound-producing body. When

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[1] Broca: *Jahresbericht der Physiologie*, 1897, S. 111.

the vibration-rate increases the pitch is elevated, and *vice versâ*. If some body capable of producing sound should have its rate of vibration changed gradually from 5 or 10 vibrations per second to 50,000 per second, no sensation of sound would be aroused until the vibrations reached the rate of about from 16 to 24 per second. The droning note of the 16-foot organ-pipe and the lowest bass of the piano represent a vibration-rate of 33 per second. In most persons sounds cease to be audible when the air-waves have a frequency of 16,000 per second, though to some the note produced by 40,000 vibrations is perceptible. It seems clear that some animals hear tones whose pitch is so elevated as to make them inaudible to human ears. When a moving bell or whistle, as of a locomotive, rapidly approaches, its pitch seems to rise, and then to fall as it recedes. The reason for this variation is that the motion of the locomotive adds to or subtracts from the number of sound-waves reaching the ear in a given time. In musical execution and in the ordinary uses of life the limits in the pitch of sounds are much narrower. Thus, as just stated, the lowest bass of the piano (C_1) represents a vibration-rate of 33 in a second, while the highest treble (c''''') has that of 4224. As to the absolute number of vibrations necessary to produce the sensation of sound, it has been found that 2 or 3 vibrations excite the sensation of a mere stroke; 4 or 5 vibrations are necessary to give a tone; and some 20 or 40 are required to develop the full musical qualities of a tone.[1] That is to say, when a musical tone falls upon the ear its characteristics cannot be appreciated until 20 to 40 vibrations have been completed.

Thus, from a physical scale representing aërial vibrations of indefinitely various rapidity the mind selects and appreciates as *sound* a very small fraction.

Tympanic Membrane as an Organ of Pressure-sense.—There is good reason to suppose that variations in air-pressure succeeding one another too slowly or too irregularly to produce sound-sensation are still of great importance in the extensive realm of sensations which but obscurely excite our consciousness. Slow inward movements of the tympanic membrane may still give rise to a perception of external changes. Thus, a blind man has been able to say correctly that he has passed by a fence, and whether it be of solid board or of open picket. If any one with closed eyes holds a book at half-arm's length in front of the ear, a different sensation will be experienced according as the book is turned flat or edgewise to the face; the feeling is one of "shut-in-ness" or "open-ness," respectively. The air is in ceaseless agitation, and its waves, striking against various objects, must be reflected to the ear with an intensity dependent on the position and the physical character of the reflecting media. We may assert that the tympanic membrane is the peripheral organ of a *pressure-sense* by which we become more or less accurately aware of the nature and position of surrounding objects, irrespective of the sensations of sight and hearing. Whether that group of sensations depends on the excite-

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[1] Mach: *Physikalischen Notizen Lotos*, Aug., 1873; V. Kries und Auerbach: *Du Bois-Reymond's Archiv für Physiologie*, 1877, S. 297; Helmholtz: *Sensations of Tone*, translated by Ellis.

ment of tactile nerves in the tympanic membrane or of the auditory filaments in the internal ear is yet uncertain.[1] Such sensations probably form an important quota of that complex system of sensations which do not obtrude themselves on consciousness, but which, nevertheless, bring information from the outer world, and have an intimate association with the more or less reflex movements that preserve the equilibrium of the body.

Overtones and Quality of Sound.—We have thus far considered only simple tones produced by simple vibrations of elastic bodies. Thus, a stretched string plucked at its middle vibrates throughout its whole length, the greatest amplitude of movement being at the middle point, which moves to and fro like a pendulum. It is very rare that a body set vibrating confines itself to a single pendular movement. Thus, a stretched string when struck not only moves as a single cord, but the string may break up, as it were, into two halves, each vibrating independently, but with twice the rate of movement of the whole length of string. Not only is this the case, but the string in its vibration also breaks up into chords of one-third, one-fourth, one-fifth, etc. of its original length, giving rise to vibrations three, four, and five times as rapid as those produced by the whole string. In musical phrase, the middle *c* of the piano, when this key is struck, gives not only a note *c* representing 132 vibrations, but also its octave *c′* of 264 vibrations, the fifth above this of 396 vibrations, the second octave, 528, the third above this, 660, and so on. The vibration of a string, then, sends to the ear a complex series of tones each of which represents a simple pendular motion of the air. The lowest tone, that produced by the slowest rate of vibration of the string as a whole, is known as the *fundamental tone.*

The pitch of the fundamental tone determines our estimate of the pitch of the whole complex note. The other tones produced by segmental vibration of the string are known as *partial tones, upper partials*, or *overtones* The fundamental tone is usually stronger than its accompanying overtones, the successively higher upper partials diminishing rapidly in intensity. Some musical instruments produce notes with a longer series of overtones than do others; the human voice is particularly rich in overtones. Instruments differ also in the greater or lesser strength and in the relative prominence of the individual overtones accompanying the fundamental. *It is the number and the relative prominence of the overtones in a musical note that determine its quality.* Thus, a violin, a cornet, and a piano, though sounding a note of the same pitch, would never be mistaken the one for the other; our discrimination of their notes depends simply upon the difference in the relative strength and the number of their overtones, the fundamental tone being the same throughout. The brilliancy and richness of musical notes is dependent on their wealth of upper partials. It is believed that a sound-producing body, like a stretched string, does not send to the ear a separate set of waves representing each of its segmental vibrations, but that all the waves aroused by it fuse together into a single series of waves of peculiar form. Such a composite wave may be

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[1] W. James: *Psychology*, 1890, vol ii. p. 140.

represented graphically by depicting under one another a series of waves having two, three, four, etc. times the rate of succession of the curve indicating the fundamental tone. If a vertical line be drawn across the series representing the vibration-rates of the various tones, and an algebraic addition be made of the distance of each point of intersection above or below the line of rest, the result will determine the position of the composite curve on the same vertical (Fig. 196). It is evident that the form of the composite wave must change with every change in the number and relative prominence of musical overtones, and the movement imparted by it to the tympanic membrane and the wave generated in the perilymph must have corresponding differences. Notes of different quality are produced by composite air-waves of different forms. But waves differing in form may still produce notes of the same quality; for if, in the graphical figure, one or more of the curves representing simple tones be slid to the right or the left, the form of the composite wave will thereby be changed, but not the quality of the sound produced by it. In other words, change of phase of the partial tones does not alter the quality of the note.[1] The quality of any complex note may be reproduced by sounding together a series of tuning-forks which have, respectively, the vibration-rate of the fundamental tone and that of one of the overtones of the complex note.

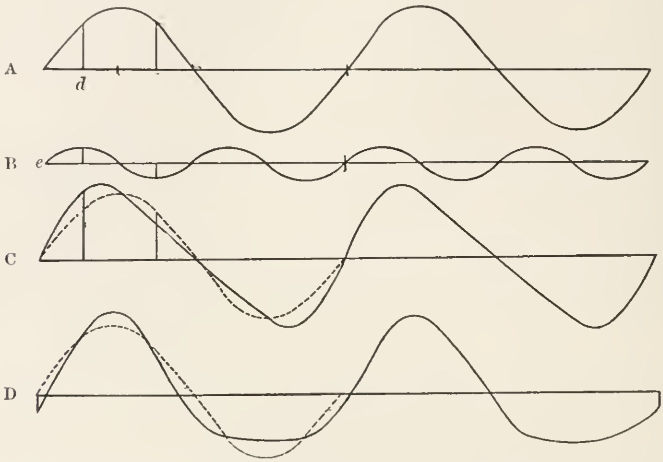

FIG. 196.—The curve B represents twice the vibration-rate of A. When the two curves are combined by the algebraic addition of their ordinates, the result is the periodic curve C (solid line), having a different form; the dotted line of C is a reproduction of A. If B is displaced to the right until *e* falls under *d* in A (change of phase), the combination of A and B will give the curve D, the dotted line in D representing A as before. (After Helmholtz.)

Analysis of Composite Tones by the Ear.—According to the theory outlined on page 380, the composite wave, beating against the sensitive organ of the cochlea, is again analyzed into the elements composing it, one part of the basilar membrane vibrating sympathetically with one partial tone, another with another. The isolated irritation of each nerve-element arouses in the mind the idea of a tone of a certain pitch and loudness; but when a number

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[1] Helmholtz, *op. cit.*, pp. 30-34.

of such elements are simultaneously stimulated, the mind takes note, not of the individual sensations thereby aroused, but of a resultant sensation formed by the fusion of these.

That apparently simple tones are actually made up of a number of partials, having rates of vibration which form simple multiples of the fundamental tone, may easily be demonstrated at the open piano. If any note, as C in the bass clef, be struck while the key of its octave *c* is depressed, and then the struck string be damped, it will be found that the octave *c* rings out with its proper note. So in turn the *g* above that, the second octave and the *e* above that, may be made to sound when the lower C is struck, because each of these strings is so tuned that its fundamental note has the same vibration-rate as one of the overtones of the lower C. A note sung near the piano may in the same way be analyzed more or less completely into its component tones. The organ of hearing certainly has some such power of musical analysis, for some cultivated ears can not only follow any special instrument in a playing orchestra, but can even distinguish the overtones in a single musical note.

The ear has little or no power of distinguishing difference of pitch in tones of less than 40 or more than 4000 vibrations per second; but in the upper median parts of the musical scale the sensitiveness to change of pitch is very acute. Thus, according to Preyer,[1] in the double-accented octave a difference of pitch of one-half vibration in a second can be detected; that is, in the octave included between 500 and 1000 vibrations per second, 1000 degrees of pitch can be perceived.

Every elastic body is capable of *sympathetic vibration;* that is, air-waves beating upon it at its own natural rate of vibration set it into corresponding motion. In the same manner a heavy pendulum may be forced into violent movement by exceedingly light taps with the finger, the only necessary condition being that the impulses imparted by the finger be exactly timed to the periodic motion of the pendulum or to some multiple of it. A body capable of sympathetic vibration with some particular tone is set into vibration by that tone, and reinforces or magnifies it, whether the tone exists alone or as the fundamental of a complex note, or is contained in the latter simply as an upper partial.

The analysis of musical sounds is usually carried out by the use of resonators, which are hollow cylinders or spheres of glass or of metal, rather widely open at one pole, and narrow-pointed at the opposite end for insertion into the ear. The mass of enclosed air vibrates, according to its size and shape, at some particular rate, and it is very readily set into sympathetic vibration whenever its fundamental tone is contained in any sound reaching it. By this means it is possible strongly to magnify, and thus select, the individual overtones contained in a note. The vowel sounds of human speech owe their difference of quality to the adjustment in size and shape of the resonant air-chambers above the vocal cords.

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[1] *Ueber die Grenzen der Tonwahrnehmung*, June, 1876.

Inharmonic Overtones.—It will be remembered that all the overtones contained in a musical note are produced by vibrations which are simple multiples of the rate of the fundamental tone. These overtones are properly called *harmonic* upper partials; they are, according to Helmholtz, particularly characteristic of stretched strings and narrow organ-pipes. But most elastic bodies have proper tones which are not exact multiples of the fundamental, and which may be termed *inharmonic* upper partials. The high-pitched jingle heard when a tuning-fork is first struck represents the inharmonic upper partials of the fork. Stretched membranes have a great number of such inharmonic overtones. Inharmonic upper partials, as might be expected, rapidly die out in a note of which they form a part. It is evident that inharmonic proper tones, when nearly of the same pitch, must interfere with one another and repress the development of a well-marked fundamental tone.

Production of Beats.—When two tones of slightly different pitch are sounded together, the more rapid vibrations overtake the slower, so that at certain periods the crests, or phases of condensation, of two waves fall together, and the result is a phase of increased condensation and louder sound. The waves immediately cease to correspond, and diverge more and more until the crest of one falls upon the trough of another, the result being silence, or at least great diminution in the intensity of the sound. Such alternate augmentation and diminution of the waves give rise to pulses in the sound, known technically as *beats*. This is one of the most familiar and important phenomena of musical art. If two tuning-forks on resonance-boxes vibrate in unison, a piece of wax stuck to the prong of one fork will lower its tone and give rise to beats. The undulating sound caused by striking a bell or the rim of a thin glass tumbler is due to beats. When two notes not included in a perfect chord are sounded on the piano, beats are heard not only from the interference of the fundamental tones, but of the upper partials as well. It is the absence of beats in notes which should be in harmony, as those of the major chord, that determines the instrument to be in tune. When two tones produce beats, the number of beats in a given time is equal to the difference between the number of vibrations involved in the two tones in the same time. For example, a tone produced by 256 vibrations in a second sounded with one of 228 vibrations would give 28 beats in a second. It is evident that the frequency of beats may be increased either by increasing the interval between the tones or by striking tones of the same interval in a higher part of the scale. Beats which are not too frequent—from four to six in a second—have important musical value, but when they number thirty or forty in a second they become exceedingly disagreeable, irritating the ear in a manner analogous to the effect of a flickering light on the eye. When sufficiently near together the beats no longer produce an intermittent sensation. The number of beats in a second required to result in this fusion increases as we ascend the musical scale, varying from 16 beats at C of 64 vibrations per second to 136 beats at c''' of 1024 vibrations.[1] The reason for this variation lies in the progressive shortening of the waves as the

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[1] Mayer: *Sound*, 1891.

sound becomes higher in pitch; for it is obvious that as we ascend the scale, and the waves of sound become progressively shorter, spaces would be left between the individual waves unless their number were proportionately increased.

Harmony and Discord.—Tones are *concordant*, or *harmonize*, when they produce no beats on being sounded together; they are *discordant* when beats are produced, and the painful sense of dissonance increases in intensity up to about 33 beats per second. Perfect concord is obtained by blending notes whose vibrations are to each other as small whole numbers.

Thus, in the major cord	C	E	G	c
the vibration-numbers are	132	165	198	264
their ratios are	4	5	6	8

If notes the ratios of whose vibration-rates can be represented only by large whole numbers are combined, a discord is formed, for the reason that their upper partials interfere with one another and cause beats; there is no especial virtue in the small integer.[1]

Thus, in the discord	C	D	E
the vibration-numbers are	132	148.5	165

which are not reducible to small whole numbers.[2]

Combinational Tones.—When two tones are sounded together, there is produced a new, usually weaker, tone, whose vibration-number is the numerical difference between the vibration-rates of the original tones. It is therefore known as a *differential tone.* Such tones may arise from upper partials as well as from the fundamentals; they do not appear to be formed, as might be supposed, by the fusion of beats. Other "combinational" tones of more intricate relations, as well as beats, arise from the interaction of vibrations when many different notes, as those of an orchestra, are sounded together. To calculate the physical result of the combination of these impulses, which it is the duty of the tympanic membrane to transmit, is a problem of exceeding complexity.

Résumé.—To sum up the subject, musical sounds are distinguished in sensation by the three factors, *loudness*, *pitch*, and *quality*, sometimes called *color* or *timbre.* These sensations depend in turn on definite physical characters of air-waves: their *amplitude*, or the extent of motion of the air-molecules; their *frequency*, or rate of succession of the waves; their *form*, which is determined by the pitch and relative predominance of the upper partials combined with the fundamental tone.

Fatigue.—That the ear is subject to fatigue toward a note that has been sounded is easily demonstrated in the following way: Strike a single note of, say, a major chord on the piano, and immediately afterward sound the full chord; the quality of the latter will be altered from its normal character, owing to the lessened prominence of the note which had been struck.[3] We may therefore not improperly speak of a successive contrast in auditory sensa-

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[1] Tyndall: *Sound.*

[2] Waller: *Human Physiology*, 1891.

[3] Foster: *Text-book of Physiology*, 5th ed., 1891.

tions, analogous to visual successive contrast, by which our perception of every sound is colored by the sounds which have preceded it.

Imperfections of the Ear.—Notwithstanding the mechanical provisions for making the external and middle ear a perfect transmitting apparatus, sound-perception is more or less modified by the action of the mechanism under certain conditions. Thus, Helmholtz believed that various combinational tones owe their origin chiefly to a periodic clicking in the joint between the malleus and incus bones. The resonance of the ear is a familiar fact, and through it high-pitched tones between e'''' and g'''' are reinforced and heard with undue loudness. Certain hissing sounds, the chirp of a cricket or the note of a locust, thus gain their intensity. This resonance probably is a feature of the external auditory meatus, since it is at once destroyed by applying a small resonator to the ear (Helmholtz).

Perception of Time Intervals.—The ear is eminently the sense apparatus for determining small intervals of time. Flashes of light succeeding each other at the rate of twenty-four in a second are fused in a continuous luminous impression by the eye, but by the ear at least one hundred and thirty-two auditory impulses as beats may be heard separately in a second. The power which the ear possesses of resolving complex air-waves into the host of pendular vibrations which may enter into their formation finds no analogy in the eye (Helmholtz).

Musical Tones and Noises.—The important feature of the physical processes which give rise to musical tones is their *periodicity*. Every musical tone is produced by a regular succession of alternate rarefactions and condensations in the air. The remaining class of sounds, known as *noises*, differs from musical sounds in the respect that such sounds are produced by an irregular succession of air-waves—one in which the interval between phases of condensation and rarefaction does not remain constant as in a musical note. Noises are for the most part made up of short musical notes so associated as not to "harmonize" with one another. As expressed by Helmholtz, the sensation of a *musical* tone is due to a rapid *periodic motion* of a sonorous body; the sensation of a *noise*, to *non-periodic* motions.

Functions of Different Parts of the Ear.—Concerning the functions of the different parts of the internal ear in their relation to sound-perception, it is generally believed, as previously stated, that the basilar membrane of the cochlea, with the nervous elements seated on it, is the organ concerned in the reception and transmission of musical sounds. There are a sufficient number of fibres in the basilar membrane to allow several to vibrate with every audible tone.

It cannot, however, too strongly be impressed that no theory of physiological action should be accepted definitively without rigid experimental proof, and such evidence concerning the definite functions of the cochlea is almost wholly wanting. The sensory hair-cells on the maculæ of the saccule and the utricle have been thought to have the duty of vibrating in response to any agitation imparted to the perilymph, without regard to its periodic character; they might thus be termed sense organs for the perception of noises. Evidence will be adduced later (p. 407) for the belief that they are peripheral organs for the preservation of static equilibrium.

The hair-cells on the cristæ of the ampullæ of the semicircular canals seem to have a special function in giving rise to sensations caused by changing the position of the head ; they thus are organs concerned with the preservation of the equilibrium of the body.

Judgment of Direction and Distance.—The distance and direction from which sounds come to the ear are not perceived directly, but our estimate of them is a judgment based on the loudness and quality of the sound sensation, combined with a power of reasoning from past experience. Thus, in seeking to discover the direction whence a sound comes, it is usual for an observer to turn the head to the position in which the sound is heard loudest, and thus to form an opinion as to the direction whence it comes. Errors of judgment as to the direction are frequent, owing to the sound reflected from some object appearing louder than that coming in a direct line from its source. It is said that when there is total deafness in one ear every sound seems to have its origin on the side of the healthy ear. When the eyes are closed, sounds originating in the median plane of the head are very imperfectly localized, but tend to be projected upward, and somewhat in front, since this is the space from which most sounds come to us.[1] The quality as well as the loudness of a sound varies according to the distance of its source. Thus the lower tones die away earliest as a sound recedes, bringing the overtones into undue prominence. The art of

FIG. 197.—End-bulbs from human conjunctiva (from Quain, after Longworth): A, ramification of nerve-fibres in the mucous membrane, and their termination in end-bulbs, as seen with a lens; B, end-bulb, highly magnified; *a*, nucleated capsule; *b*, core, the outlines of its component cells not seen; *c*, entering nerve-fibre branching, its two divisions to end in the bulb at *d*.

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[1] Seashore: *Loc. cit.*

the ventriloquist consists largely in altering the quality of the sounds he produces to imitate the quality they would naturally have if arising under the conditions which he would lead his hearers to believe to be their origin. A comparatively feeble sound near at hand may have the same quality as a loud one heard at a distance; thus, a frog croaking in an adjoining room was once mistaken by the writer for a large dog barking outside the building.

D. CUTANEOUS AND MUSCULAR SENSATIONS.

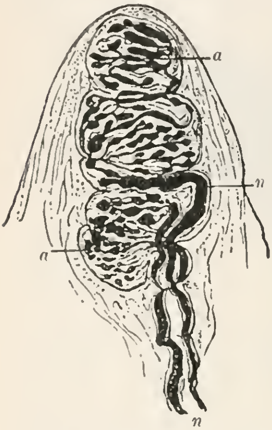

FIG. 198.—Tactile corpuscle within a papilla of the skin of the hand (from Quain, after Ranvier): *n*, *n*, two nerve-fibres passing to the corpuscle; *a*, *a*, terminal varicose ramifications of the axis-cylinder within the corpuscle.

General Importance of the Cutaneous and Muscular Sensations.—Cutaneous sensations are aroused by the operation of some form of energy on the skin, and they include the sensations of *touch*, of *temperature*, and of *pain*. By *muscular sensation* is meant the appreciation which we have of the intensity and direction of muscular effort. Closely allied to this sensation is a *general sensibility* through which we gain a knowledge of the relative position of the parts of our bodies, irrespective of movements. The direction, size, distance, and surface features of external objects are usually made known to us through the sense of sight or of hearing. Yet these fundamental facts regarding the things about us do not become a part of knowledge through direct visual and auditory perception. Such knowledge is based on complex judgments concerning the meaning of auditory and visual phenomena according as they have, in past experience, been interpreted by tactile and muscular perceptions. That is, when reduced to its simplest terms, our most practical and important knowledge of the world is the outgrowth of tactile and muscular perceptions; by and with them all other sense-perceptions of objects have been corrected and compared. Thus, so simple a feat as the estimate of the size of a distant object is the result of a complex judgment based on tactile and muscular experience. Through the sense of sight we perceive the ratio of the visual angle subtended by

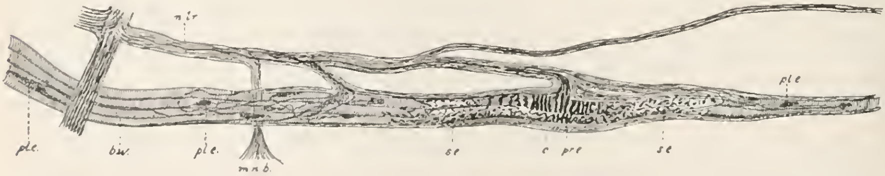

FIG. 199.—Semi-schematic figure of a neuromuscular spindle of the first type, namely, with complex nerve-ending; adult cat: *c.*, capsule; *m. n. b.*, motor nerve-bundle; *pl. e.*, plate-ending; *n. tr.*, nerve-trunk: *pr. e.*, primary ending; *s. e.*, secondary ending; *b. w.*, axial muscle-fibres. (From Ruffini. *Journal of Physiology*, vol. xxiii.)

the object to that of the whole field of vision; but as objects of different size may fill the same visual angle when at different distances from the eye, our estimate of their size depends upon the distance at which we suppose them to be situated. The distinctness of the surface features of the body afford the mind an important clue, since experience shows that details of surface in a body become more obscure as we recede from that body. But more important data concerning distance come from the sense of muscular innervation, or feeling of the intensity of muscular contraction, by which we estimate the degree of convergence of the optic axes when the object is focussed, and still more by the perception of the amount of muscular effort necessary to sweep the optic axes over the ground surface intervening between the observer and the object. When objects approach the near-point of vision the sense of innervation of the pupillary muscles affords important evidence of their distance.

That fundamental education concerning the outer world which engages the earliest years of every child consists in accumulating and systematizing with other sense-perceptions tactile and muscular impressions of objects. A sensation is no sooner felt than some muscular movement involving a definite muscular feeling is made by which the character of the sensation is changed and experimentally tested under different conditions. The physiological process involved in building up sense-knowledge, therefore, embraces in alternation sensation excited by external objects, motion accompanied by muscular sensation, and change in the original sensation. In other words, the motor and sensory impulses form a sort of balance, and both are necessary.

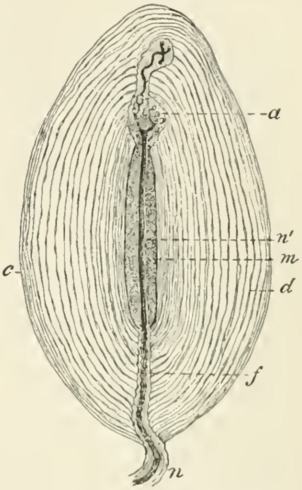

FIG. 200.—Magnified view of a Pacinian body from the cat's mesentery (from Quain, after Ranvier): *n*, stalk with nerve-fibre enclosed in sheath of Henle, passing to the corpuscle; *n′*, its continuation through the coil, *m*, as a pale fibre; *a*, termination of the nerve in the distal end of the core (the terminations are not always arborescent); *d*, lines separating the tunics of the corpuscles; *f*, channel through the tunics, traversed by the nerve-fibre; *c*, external tunics of the corpuscle.

Ending of Sensory Nerve-fibres in the Skin.—The afferent nerves supplied to the skin have several modes of termination. In the commonest form the plexus of medullated nerve-fibres found in the dermis close under the epidermis gives off twigs which, losing the medullary sheath, pierce the epidermis and here form a network among the cells of the Malpighian layer, the single fibres ending freely in this position (Fig. 207). So numerous are they that it would appear that every epithelial cell (of mucous membrane as well as skin) is in contact with one or more nerve-fibrils. These axis-cylinder threads are often varicose and usually end freely among the epithelial cells, but in some cases they are expanded at their terminations into well-defined sensory end-plates. In the corium and subcutaneous connective tissue (mesoblastic) sensory nerves may terminate in the manner just described. But they are frequently modified into or form a part of definite structures of various forms, which may be regarded as peripheral sense-organs of the skin.[1] Some of these terminal organs are known respectively as *end-bulbs, touch-corpuscles,* and *Pacinian bodies* (Figs. 197–200). Each organ consists of a more or less conical body in which a nerve-fibre terminates. The *end-bulbs* are found only on the dermis of the conjunctiva and the lips, and in modified form on the sensitive surfaces of the genital organs (Fig. 197). The *touch-corpuscles,* though apparently absent from the greater part of the body, occur in great numbers in the skin of the palmar surface of the hand and that of the fingers, especially at their tips; at the edge of the eyelids and the lips; on the soles of the feet and the toes; and on the surface of the genital organs. The touch-corpuscle often occupies a papilla of the dermis directly under the epidermis (Fig. 198). The *Pacinian bodies,* which are oval corpuscles, larger than the foregoing, and easily visible to the unaided eye, are found not in the skin proper, but in the subcutaneous connective tissue beneath it. They are found in abundance beneath the skin of the palm of the hand and the sole of the foot; they are also numerous along the nerves of the joints, and even among the sympathetic nerves supplying the abdominal organs (Fig. 200). "Ruffini's endings, found in the subcutaneous tissue of the finger, are formed by the branching and anastomosis of terminal axis-cylinders inclosed within a special connective-tissue envelope. Various other modifications of sensory nerve termination have been described.

1. Sense of Touch.—*The Relations between Sensation and Stimulus.*—Many so-called "tactile sensations," such as wetness, hardness, roughness, etc., are not simple sensations at all, but are complex judgments built up out of the association of certain tactile, temperature, and muscular sensations, and conveying to us a knowledge of the surface, substance, and form of bodies.

When analyzed, the sense of touch is nothing more than a sense of *pressure* applied to the skin. To test the *pressure sensibility* of the skin the object whose weight is to be estimated must not be lifted in the ordinary way, for that would bring into play the muscular sensations. If the skin of the hand is to be tested, the hand must be placed upon some firm support, such as a table, and the weights be laid upon the skin. The smallest perceptible weight that can thus be felt varies with the situation to which it is applied. Thus, the greatest sensitiveness to pressure is found on the forehead, the temples, the back of the hand, and the forearm, where a weight of .002 gram ($\frac{1}{30}$ grain) can be perceived. The weight must be increased to .005 to .015 gram to be felt by the fingers, and to 1.0 gram when laid on the finger-nail.[2]

The power of discriminating differences of pressure applied to the skin is tested by finding the smallest increase that must be added to a weight in order that it may be perceived as being heavier. This increment is not, as might be supposed, the same for weights of different value, but it bears a distinct proportion to them. Thus, a weight of 11 grains may just be perceptibly heavier than one of 10 grains; but if we start with a weight of 100 grains,

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[1] *Cf.* Barker: *The Nervous System,* 1899, pp. 361-421.

[2] Aubert und Kammler: *Moleschott's Untersuchungen,* 1859, Bd. v. S. 145.

a single grain added to it will arouse no difference of sensation, an increment of 10 grains being necessary in order that one weight may appear heavier than the other. This fact is the basis for Weber's law of the relation between stimulus and sensation; this law may be formulated as follows: *The amount of stimulus necessary to provoke a perceptible increase of sensation always bears the same ratio to the amount of stimulus already applied.* This law is found to be only approximately correct, especially when very small and very large weights are compared. Fechner attempted to express more exactly the relation between the intensity of stimulus and sensation in his "psycho-physical law," thus: *The intensity of sensation varies with the logarithm of the stimulus.* In other words, the sensation increases in arithmetical progression, while the stimulus increases in geometrical progression. With moderate weights a difference of pressure is perceptible when the ratio of increase is smaller than when either very small or very large weights are used; that is, sensitiveness to pressure-change is keenest under moderate stimulation.

It is said that the forehead, the lips, and the temples appreciate an increase of $\frac{1}{40}$ to $\frac{1}{30}$ of the weight estimated, while the skin of the head, the fingers, and the forearm requires an increase of $\frac{1}{20}$ to $\frac{1}{10}$ for its perception. In this as in other kinds of sensation it is the difference, or variation of intensity, of the sensation of which the mind takes particular cognizance. One touch-sensation is more acutely perceived when contrasted with another than when felt alone. Weber[1] found the discrimination of pressure-differences to be finer when two weights were laid in rapid succession on the same skin-area than when the weights were applied either simultaneously or successively to different parts. If a finger be dipped in a cup of mercury or of water having the same temperature as the skin, the pressure will be marked only at the margin between the air and the fluid, and if the finger be moved up and down it will seem as if a ring were being slid back and forth upon it. The constant pressure of the mercury upon the submerged finger is not felt. The fingers are particularly sensitive to intermittent variations of pressure—a facility the use of which is manifest when the function of these parts is considered.

Two weights, in being tested, should press upon equal areas of skin; according to Weber,[2] if two equal weights have different superficial expanse, that which touches the larger skin-surface, and thereby excites the greater number of touch-nerves, will appear to be the heavier. The important part played by judgment and mental inference in such experiments is shown by the facts that when it is sought to compare weights by lifting them and with the aid of sight, the smaller of two equal weights seems to be the heavier; and of two objects having the same size and weight, that which appears to be the smaller seems heavier.[3] The simultaneous excitement of other sensations may modify that of pressure; thus, when two coins of equal weight,

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[1] "Tastsinn und Gemeingefühl," *Wagner's Handwörterbuch der Physiologie*, 1846.

[2] Quoted in *Hermann's Handbuch der Physiologie*, Bd. iii. 2, S. 336.

[3] Dressler: *American Journal of Psychology*, 1894, vol. vi. No. 3.

but one warm and the other cold, are laid upon the hand or the forehead, the cold one appears to be much the heavier.

There is a sensation of *after-pressure* depending for its strength on the amount of the weight and the length of time this weight has been applied. In fact, this after-sensation may produce a striking effect on consciousness, a familiar example of which is the persistence of the sense of pressure of the hat-band after the head-covering is removed. Even light weights leave an after-sensation, and, in order to be perceived as separate, must be applied at intervals of not less than $\frac{1}{480}$ to $\frac{1}{610}$ of a second. It is said that when the finger is applied to the rim of a rotating wheel provided with blunt teeth, the separate teeth are no longer felt, and the margin seems smooth, when the contacts succeed each other at the rate of 500 to 600 in a second.[1] Vibrations of a string cease to be appreciated by the finger when they have a rate of between 1500 and 1600 per second.

The Localization of Touch-sensation.—When a touch-sensation is felt, the mind inevitably refers the irritation to some particular part of the surface of the body, and the sensation seems to be localized in this area. On the accurate localization of tactile sensations depends not only the safety of the individual, but also the performance of the ordinary acts of life.

We may suppose that to each area of peripheral distribution of tactile nerve-fibres in the skin there corresponds an area of tactile nerve-cells in the brain. It can hardly be doubted that the nerve-cells are divided into physiological groups characterized by inherent and inborn quality-differences in the sensations aroused by their respective excitements. The reference of the sensations aroused by the excitement of definite nerve-cells to definite parts of the periphery is a power acquired through the physiological experiences of the earliest months of life. Through the sense of sight the seat of irritation is recognized, and through muscular sensation its relation to surrounding parts is experimentally explored, so that cumulative harmonious experiences of tactile, visual, and muscular sensations finally bring into correspondence the various areas with definite varieties of touch-sensation, or, to use an expression of Lotze's,[2] every area of the skin acquires a "local sign" by which it is distinguished in consciousness.

This power of localization differs widely for different parts of the skin. The fineness of the localizing sense for any skin-area is easily estimated by determining how far apart the tips of a pair of compasses, applied to the skin, must be separated in order to be felt as two. For this experiment the compass-points must be smooth, and they should not be applied heavily. The general result of such an inquiry is that the compass-points may be nearer together, and still be distinguished as two, in proportion as the surfaces to which they are applied have greater mobility. Since it is just such parts of the body as the tips of the tongue and the fingers that are chiefly used in determining the position of objects, the advantage of such an arrangement is obvious. The

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[1] Landois and Stirling: *Human Physiology*, 1886.

[2] Funke, in *Hermann's Handbuch der Physiologie*, Bd. iii. 2, S. 404.

skin can thus be marked out in areas (*tactile areas*), within each of which the compass-points are felt as a single object, but if they are separated so as to fall beyond the borders of these areas, they are at once perceived to be two.

The following figures[1] represent the distances at which the compass-points can just be distinguished as double when applied to various parts of the body:

Tip of tongue	1.1 mm.
Palm of last phalanx of finger	2.2 "
Palm of second phalanx of finger	4.4 "
Tip of nose	6.6 "
Back of second phalanx of finger	11.1 "
Back of hand	29.8 "
Forearm	39.6 "
Sternum	44 "
Back	66 "

It will be observed that accuracy of localization and sensitiveness to pressure find their most perfect manifestations in widely separate regions of the skin.

Tactile areas are found to have a general oval form with the long axis parallel with the long axis of the member investigated. If the compass-points, separated, say, half an inch apart, be passed over the skin of the palm from the middle of the hand to the finger-tips, the sensation will be that of a single line gradually separating into two diverging lines. The result, of course, depends on the compass-points passing successively through areas of finer localization. If an area be marked out on a part of the skin where localization is poor, within which area two points simultaneously applied appear to be one, a single point moved within it is still perceived to change its place, and two points successively applied may be perceived to occupy different positions. The mental fusion or separation of the two compass-points cannot depend altogether on their being placed over the terminal twigs of the same or of two adjoining nerve-fibres, for, were this the case, the points could be discriminated when separated by a very small distance across the line drawn between the endings of adjoining nerve-fibres, while on either side the points would have to be much more widely separated in the area of distribution of a single fibre. The important factor in the mental separation of two stimulated points is, that between such points there shall be found a certain number of sensory elements which are unstimulated.[2] Practice in such experiments greatly increases the power to localize impressions. This improvement is evidently due not to the establishment of new nerves, but to a more perfect discrimination of sensations in the nerve-centres. Dressler[3] found that after practice for four weeks, the compass-points which at the beginning had to be separated 18 millimeters on the skin of the forearm to be distinguished, could, at the end of the period, be recognized as two when only about 4 millimeters apart. Almost as great an improvement of localizing power was gained by the unexercised

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[1] Foster's *Physiology*, 5th ed., 1891.

[2] Weber: "Tastsinn und Gemeingefühl." *Wagner's Handwörterbuch der Physiologie*, 1846.

[3] Dressler: *Loc. cit.*

corresponding area of the skin of the opposite arm, but not by adjacent areas; in other words, the localizing power is central, not peripheral. Practice aroused in both tactile areas a peculiar quality of sensation by which the area was recognized. The improvement in localizing power is gradually lost if unexercised.

Pressure-points.—It has been found that if a light object, such as a lead-pencil, be allowed to rest by a narrow extremity successively on different parts of the skin, its weight will appear very different according to the part which is touched. If the spots on which the weight appears greatest be marked with ink, they will be found to have a constant position, and the skin may therefore be mapped out in areas of *pressure-points,* which are believed to indicate the place of ending of pressure-nerve filaments. The pressure-points are relatively few in number and are principally collected about the hair-follicles.

The Importance of the End-organ.—The sense of touch or pressure is a special sense; that is, any irritation conveyed to the nerve-centres in which the nerves of pressure terminate gives rise to a feeling of touch, just as disturbance in the visual or the auditory centre is recognized in consciousness as a sensation of sight or of sound. The complex anatomical structures known as *sense-organs* may be considered as instruments each of which is differentiated in a manner to make it particularly irritable toward some special form of energy. Thus, the retina is most sensitive to the luminiferous ether; the organ of Corti, to waves of endolymph, etc. To this differentiation of structure the sensitiveness of the body to the forces of nature is chiefly due. The peripheral ending of the pressure nerve, whether a naked axis-cylinder or a touch-corpuscle, is no doubt modified to be particularly irritable toward that form of energy manifested in the molecular vibration of the tissue solids, brought about by contact with foreign objects. Hairs, particularly those in certain localities of some animals, as the whiskers of the cat, appear to have the function of transmitting mechanical vibrations to the nerve-endings in greater intensity than could be accomplished through the skin alone.

No true sense of touch is aroused by direct irritation of a nerve-trunk or exposed tissue, and touch-sensations do not arise from irritation of the internal surfaces of the body. A fluid of the temperature of the body gives, when swallowed, no sensation in the stomach; when cooler or warmer than the body, there is a sensation due, probably, to a transmission of temperature change to the skin of the abdomen.

Touch Illusions.—Certain peculiar errors in judgment may arise when tactile sensations are associated in a manner unusual in experience. Thus, in an experiment said to have been devised by Aristotle, if the forefinger and the middle finger be crossed, a marble rolled between their tips will appear to be two marbles; if the crossed finger-ends be applied to the tip of the nose, there seems to be two noses. The illusion is due to the fact that under ordinary circumstances simultaneous tactile sensations from the radial side of the forefinger and the ulnar side of the middle finger are always caused by two different objects. It is a not uncommon surgical operation to replace a loss of skin on the nose by cutting a flap in the skin of the forehead, without injury to the nerves, and sliding the flap round upon the nose. Touching the piece of transplanted skin gives the patient the sensation of being touched, not upon the nose, but upon the forehead; after a time, however, a new fund of experience is accumulated, and the sensation of contact with the transplanted flap is rightly referred to the nose. Persons who have suffered amputation of a lower limb often complain of cramps and other sensations in the lost toes. The illusion no doubt comes from irritation, in the nerve-stump, of fibres which previously bore irritations from the toes.

2. **Temperature Sense.**—The skin is also an organ for the detection of changes of temperature in the outer world. Such temperature differences probably make themselves manifest by raising or lowering the temperature of the skin itself, and thus in some way irritating the terminal parts of certain sensory nerves, the *temperature nerves.* The sensitiveness of the skin to temperature variations is not the same in all parts; thus, it is more acute in the skin of the face than in that of the hand; in the legs and the trunk the sensibility is least. We refer temperature sensations, somewhat like those of touch, to the periphery of the body, and localize them on the surface. The skin over various parts of the body may have different temperatures without exciting corresponding local differences of sensation. Thus, the forehead and the hand usually seem to be of the same temperature, but if the palm be laid upon the temples, there is commonly felt a decided sensation of temperature change in one or both surfaces. As in other sensations, fatigue and contrast play an important part in the sense perceptions of temperature, and stimuli of rapidly-changing intensity provoke the strongest sensations; thus, when two fingers are both dipped into hot or cold water, the fluid seems hotter or colder to that finger which is alternately raised and lowered.

In changing to a place of different temperature the skin for a time seems warmer or cooler, but soon the temperature sensation declines, and on returning to the original temperature the reverse feeling of cold or of warmth is experienced. For every part of the skin, then, there is a degree of temperature, elevation above or depression below which arouses respectively the feeling of warmth or of cold, and the temperature of the skin determining the physiological null-point may vary within wide limits.

The smallest differences of temperature that can be perceived fall, for most parts of the skin, within 1° C. The skin of the temples gives perception of differences of 0.4°–0.3° C. The surface of the arm discriminates 0.2°; the hollow of the hand, 0.5°–0.4°; the middle of the back, 1.2°.[1]

The size of the sensory surface affected modifies the intensity of temperature sensation: if the whole of one hand and a single finger of the other hand be dipped into warm or cold water, the temperature will seem higher or lower to the member having the greatest surface immersed.

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[1] Nothnagel: *Deutsches Archiv für klinische Medicin,* 1866, ii. S. 284.

Cold and Warm Points.—The skin is not uniformly sensitive to temperature changes, but its appreciation of them seems to be limited to certain points distributed more or less thickly over the surface. These spots appear to be the places of termination of the temperature nerves in the epidermis (Fig. 201). There is little doubt that there are two distinct varieties of temperature nerves, one of which appreciates elevation of temperature, or heat, and the other diminution of temperature, or cold. Thus, if a blunt-pointed metal rod be warmed and be touched in succession to various parts of the skin, at certain spots it will be felt as very warm, while at others it will not seem warm at all. If, on the contrary, the rod be cooled, a series of *cold points* may in the same way be made out. The point of an ordinary lead-pencil may be used with some success to pick out the cold spots. The "cold points" are more numerous than the "hot," and those of each variety are more or less distinctly grouped round centres, as would be expected from the manner of nerve-distribution, though the groups overlap to some extent (Fig. 201). Certain substances appear to act, probably by chemical means, as specific excitants of the two sets of nerves. Thus, menthol applied to the skin gives a sensation of cold, while an atmosphere of carbon dioxide surrounding an area of skin gives a sensation of warmth.[1]

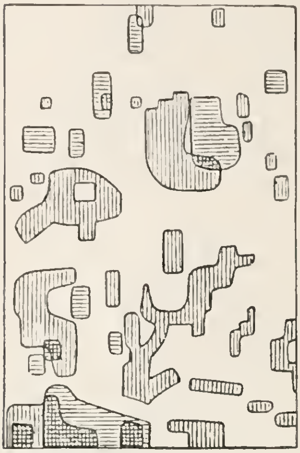

FIG. 201.—Cutaneous "cold" spots (vertical shading) and "hot" spots (horizontal shading), anterior surface of the thigh (from Waller, after Goldscheider).

The specific difference of the two sets of temperature nerves is indicated by the fact that when a warm and a cold body held close together are simultaneously brought near the skin, the sensation is either one of both warmth and cold, or now one and now the other sensation predominates.[2] Any stimulation, whether mechanical or electrical, applied to the sensitive points thus far described in the skin, for the appreciation of either pressure, heat, or cold, provokes, when effective, only the proper sensation of that point; any irritation of a cold, hot, or pressure point gives rise, respectively, to the sensation of cold, heat, or pressure alone.

As in other organs of special sense, the peripheral terminations of the temperature nerves seem modified to be especially irritable toward their appropriate form of physical stimulus. Cold or heat directly applied to the nerve-trunk excites no temperature sensation. Thus, if the elbow be dipped into a freezing mixture, as the lowered temperature penetrates to the ulnar nerve the sensation will be one, not of cold, but of dull pain, and it will be referred to

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[1] Goldscheider: *Du Bois-Reymond's Archiv für Physiologie*, 1886, 1887; Blix: *Zeitschrift für Biologie*, 1884; Donaldson: *Mind*, 1885, vol. xxxix.

[2] Czermak: *Sitzungsberichte d. Wiener Akad.*, 1855, S. 500; Klug: *Arb. d. physiol. Anstalt zu Leipzig*, 1876, S. 168.

the hand and the fingers. The internal mucous surfaces of the body, from the œsophagus to the rectum, inclusive, have no power of discriminating temperature sensations; a clyster of water cooled to from 7° to 16° C., if not held too long, is only perceived as cold when the water escapes through the skin of the anus.

The doctrine of *specific nerve energy*, enunciated by E. H. Weber, was intended to convey the idea elaborated above, that each nerve of special sense, however irritated, gives rise to its own peculiar quality of sensation. But it seems clear that the existence and quality of the sensation are, respectively, properties of the activity, not of the nerve-fibre, but of the peripheral end-organ and the nerve-centres.

3. **Common Sensation and Pain.**—The sensations thus far considered have been called *special sensations*, because each affects the consciousness in quite a different way, and any irritation which excites the sense apparatus provokes a sensation of definite quality and measurable intensity.

Pain is a sensation which, according to a common but unproved belief, is the result of sufficiently intensifying any of the simple sensations.

Pains have received various names to distinguish their quality, according to the mode in which experience shows they may have been produced, as cutting, tearing, burning, grinding, etc. One peculiar mark that distinguishes painful sensations is the lack of complete localization. While lesser pains are referred with fair exactness to different parts of the body, and even to those internal parts devoid of tactile sensibility, greater pains radiate and seem diffused over neighboring parts. Pain also differs from special sensation in the long latent period preceding its development. The evidence of physiological experiment is against the belief that any irritation of the nerves of so-called "special senses" can produce pains, but it teaches that this sensation is the result of the excessive or unnatural stimulation of a group of nerves whose function is to give rise to what is indefinitely called "common sensation." By this term is designated that consciousness which we more or less definitely have, at any moment, of the condition and position of the various parts of our bodies. When tactile, temperature, and visual sensations are eliminated, we are still able to designate with considerable accuracy the position of our limbs, and we become aware with extraordinary exactness of any change in that position, indicating the possession of a *posture sense*. The nerves of common sensation must, then, be continuously active in carrying to the sensorium impulses which, though they do not excite distinct consciousness, probably are of the utmost importance in keeping the nerve-centres informed of the relative positions and physiological condition of the various parts of the organism, and it is not improbable that they are the afferent channels for many reflex acts which tend to preserve the equilibrium of the body. The sudden failure of these sensations in a part of the body would probably be felt as acutely as the silence which succeeds a loud noise to which the ear has become accustomed. Pain is thought to be the result of excessive stimulation of the nerves of common sensation, though it must be admitted that we know next to nothing of the anatomical and physiological conditions on which this sensation is dependent. It is said not only that most internal organs possess no definite tactile or thermal sensibility, but that, when normal, such irritation as is caused by cutting, burning, and pinching seems to cause no pain;[1] let them, however, become inflamed, and their sensitiveness to pain is sufficiently acute. The facts of labor-pains, of colic, and other visceral disturbances which are attended by no inflammatory condition show, however, that the factors on which the existence of pain depends are not as yet fully understood.

The physiological facts on which is based the belief in "common sensation" are indisputable, but the evidence for a special nervous apparatus for such sensibility is based rather on exclusion of known nerve-organs than on positive demonstration. In the category of common sensations have been included also such feelings as "tickling," shivering, hunger, thirst, and sexual sensations. The feeling of fatigue which follows either muscular or mental exertion may be placed in the same group.

A general feature of common sensations is their subjective character; they are not definitely localized within the body, nor are they projected external to it, as in the case of the "special senses."

Between the common sensation and its existing cause there is no measurable proportion, as is found, for instance, in the study of the pressure sense. It may be stated that pressure and temperature sensations were within a recent period grouped among common sensations, and future investigations may possibly limit each of the feelings now classed together as "common sensations" to definite anatomical structures.

When the punctiform distribution of various sensations in the skin is investigated, some points are found in which no other sensation than that of pain can be excited, and it has been thought that such spots mark the place of ending of nerves of common sensibility.

According to v. Frey, the pain-points are much more numerous than the pressure points, more than 100 falling within a square centimeter of skin, and their nerves are probably more superficial. They require about 1000 times as great an intensity of stimulus for their excitement as do the pressure-nerves; they have a long, latent period of stimulation and are inert to rapid changes in the stimulus. This author believes that the free nerve-endings are sense-organs for pain, the end-bulbs for cold, the terminal coils, or networks, for heat, and the tactile corpuscles for pressure-sensations.[2]

Transferred or "Sympathetic" Pains; Allochiria.—It has long been a matter of clinical observation that disease seated in certain internal organs is often accompanied by superficial pain and tenderness in widely removed parts of the body; for example, a decayed tooth frequently causes intense pain in the ear; disease of heart or of aorta may cause pain between the shoulders,

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[1] Foster's *Physiology*, 1891, p. 1420.

[2] Hermann's *Jahresbericht ü. Physiologie*, 1897, Bd. v. S. 115; 1896, Bd. iv. S. 113; 1895, Bd. iii. S. 111.

etc. The subject has received most accurate investigation from Head,[1] who has shown that there is an intimate nervous connection between the internal organs and definite areas of the skin, manifested by pain and tenderness appearing in sharply-localized regions on the surface when definite organs become disordered. He has also demonstrated that disorders of the thoracic and abdominal viscera not only produce pain and tenderness on the surface of the body, but also cause pain and tenderness over certain areas of the scalp. Head is inclined to explain the topographical association of skin-tenderness with visceral disorders by the assumption that the nerve-supplies of the parts so related find their origin within the same segment of the spinal cord. The sensory result of visceral irritation may be summarized in the following way: "When a painful stimulus is applied to a part of low sensibility in *close central connection* with a part of much greater sensibility, the pain produced is felt in the part of higher sensibility rather than in the part of lower sensibility to which the stimulus was actually applied."

Certain transferred pains are explained by Meltzer[2] in the following manner: An inflamed or irritated organ originates a succession of sensory stimuli, which do not awake consciousness because they are continuous. There is, nevertheless, a summation of such irritations within the central organ which elevates its plane of irritability to such an extent that sensory impulses reaching the implicated nerve-centre from any part of the body arouse it above the threshold of consciousness and give rise to sensations which are referred to the seat of peripheral inflammation or constant irritation. For example, the subject of a mild alveolitis may feel in the teeth a stronger pain than is felt in the nose when a concentrated solution is thrown into the latter organ.

That this transferred localization may characterize other sensations than those of pain has been definitely observed by Obersteiner,[3] who found that in patients suffering from certain central nervous lesions tactile irritation of a certain point on the skin was referred by them to some other part of the body, usually the corresponding point on the other side. He designated this transference of sensation by the term *allochiria,* meaning a confusion of sides.

4. **Muscular Sensation.**—Closely allied to common sensation, if not a part of it, is *muscular sensation.* If two weights are to be compared, we naturally do not lay them on the skin to determine their pressure-difference, but we lift and weigh them in the hands, and experience shows that a much more accurate estimate may thus be made.

We undoubtedly have a keen perception of the tension of a muscle, and therefore of the amount of resistance against which it is contracting. This perception may be the outcome of a direct consciousness of the amount of motor energy sent out from the motor cells, or it may be due to the inflow of sensory impulses which show the tension to which the muscles have been subjected. The latter view has more to be said in its favor.

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[1] *Brain,* 1893–4.

[2] S. J. Meltzer: *Philadelphia Medical Journal,* August 5, 1899, p. 12.

[3] *Brain,* 1881.

Recent researches have demonstrated the existence of an abundant supply of sensory nerves, whose excitement must depend upon the exercise of skeletal muscles. Ciaccio[1] has described the termination of sensory nerves in tendons as a splitting up of the nerve-fibres whose axis-cylinders, in the form of varicose threads, end freely as spirals or rings around the tendon-bundles. The joints seem to be particularly rich in sensory nerve-supply. Golgi[2] first described certain special modes of ending of sensory nerves just at the junction of the voluntary muscle with its tendon. This terminal organ is a fusiform corpuscle consisting of several delicate connective-tissue envelopes with nuclei, and is situated on the surface of the tendon. One to several nerve-fibres enter each corpuscle, and, dividing and losing their medullary sheaths, break up into an arborization of naked axis-cylinders. The skeletal muscles themselves are extraordinarily rich in sensory nerve-supply. According to Sherrington,[3] "the proportion of afferent-fibres to total myelinate fibres ranges from a little more than one-third in some muscular nerves to a full half in others." These sensory fibres end, for the most part, in the so-called "muscle-spindles," which are fusiform bodies, usually just visible to the unaided eye (Fig. 199, p. 390). The spindles are for the most part scattered between the ordinary muscle-fibres, though many abut upon intramuscular septa or are in the immediate vicinity of aponeuroses. As many as thirteen spindles have been counted in one cross-section of the genio-glossus muscle. Sherrington[4] calculates that the number of spindle-organs is sufficient to account for nearly or quite two-thirds of all the afferent fibres demonstrated to exist in the nerve-trunks of the limb muscles. It is worth observing that the spindle-organs have not been demonstrated in the eye muscles nor in the intrinsic muscles of the tongue. The muscle-spindle consists of a central core of modified muscle-fibres inclosed in an outer capsule formed of several layers of concentrically disposed membranous lamellæ composed of connective tissue. Between the capsule and the central muscle-bundle is a wide lymph-space traversed by a network of delicate filaments. In forming the spindle two or three ordinary muscle-fibres of the red variety become invested at the proximal end of the organ by a definite sheath of connective tissue. As they penetrate further into this envelope the muscle-fibres tend to split lengthways, each fibre giving rise to perhaps three "daughter"-fibres, which are proportionally of less diameter. The striation and fibrillation are frequently confined to the outer portion of these daughter-fibres, some of which are devoid of sarcolemma. For the middle third of its course in the muscle-spindle each daughter-fibre becomes thickly crusted with a sheet of nuclei. Toward the distal end of the spindle the muscle-fibres often merge in tendon-bundles, which finally combine with the fibrous tissue forming the capsule of the spindle; so that of the two ends of the axial bundle within the spindle, one is muscular and the other is tendinous.

According to Ruffini,[5] sensory nerves may end upon the axial muscle-

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[1] Barker: *The Nervous System*, 1899, p. 405.

[2] *Ibid.*

[3] Sherrington: *Journal of Physiology*, 1895, vol. xvii. p. 229.

[4] *Ibid.*

[5] Ruffini: *Ibid.*, 1898, xxiii. 190.

fibres of the spindle in either or all of three different modes (Fig. 199): 1. The axis-cylinder may flatten out and twine in rings and spirals about the muscle-fibre. 2. The axis-cylinder may break up into a number of leaflets applied to the muscle-fibre (secondary mode). 3. The axis-cylinder may end in a plate of varicose fibrils resembling the motor end-plate.

When we consider that it is through muscular sensation that we derive our most accurate conceptions of the form, weight, and position of objects, and through which we explore our own body-surface and distinguish its areas of localization; that this is the fundamental sense by which the sensations arising in most other organs are tested and verified; and that it is from the sense of muscular movement that we can form ideas of time and space,—it may well be regarded as the mother of all sense-perceptions. Normal muscles, even when functionally inactive, are still in a state of tonic contraction; it is not improbable that this tone is a reflex action whose sensory element is formed by the impulses travelling along nerves of muscular sensation. Such impulses are probably indispensable to the preservation of the equilibrium of the body.

Sherrington found that if he separated the aponeurosis belonging to the distal portion of the vastus medialis muscle, under which the muscle-spindles are numerous, the knee-jerk could no longer be excited through the muscle.

Our appreciation of the weight of bodies is determined by lifting them. But even in so simple an exercise of the muscular sense as this the judgment is subject to extraordinary illusions depending on the preconception of the weight of a body, and consequent muscular effort put forth in lifting it. When bodies having the same weight and size, such as appropriately loaded pieces of iron, cork, and wood, are compared, the specifically lighter body will seem to be heavier. "Before lifting an object we normally estimate the approximate weight by sight, and the effort to be exerted in lifting is adjusted semi-automatically upon the basis of this preliminary estimate. If insufficient effort is put forth at the beginning of the lifting, the weight of the object will be overestimated. If too great effort is put forth, the weight of the object will be underestimated."[1] In comparing the weight of objects having different sizes the illusion takes another direction. Thus an inflated paper bag may be estimated to have the same weight as a piece of lead weighing sixty times as much.[2]

The clinical study of disease in the central nervous system affords strong evidence of the functional independence of the sense organs involved in the appreciation of touch, heat, cold, and pain. In certain diseases of the spinal cord, areas of skin may be mapped out in which sensations of pressure are lost, but those of temperature remain, and *vice versâ*. In other diseases the patient can appreciate warmth applied to the skin, but not cold.

The sensations of cold and pressure seem to be usually lost or retained together, while those of warmth and pain have a similar connection. It is a peculiar fact that sometimes in the early stages of ether and chloroform narcosis the sense of touch remains while that of pain is abolished. Funke[3] refers

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[1] Seashore: *Op. cit.*

[2] Wolfe: *Psychological Review*, 1898, p. 25.

[3] "Der Tastsinn," *Hermann's Handbuch der Physiologie*, Bd. iii. S. 2.

to two cases in which, while the tactile sense was preserved, muscular sensation was lost, and an object could be held in the grasp only while the eyes were turned upon it.

Hunger and Thirst.—Hunger and thirst are peculiar sensations which depend partly on local and partly on general causes. Diminution in the bulk of water and of circulating aliment in the body no doubt causes excitement of sensory nerves on which depend the feelings of thirst and hunger, but in ordinary life these feelings are dependent on the physical condition of certain mucous surfaces. Any circumstance which causes drying of the lining membrane of the mouth provokes thirst, and some condition of the empty stomach arouses hunger. Thirst may be assuaged by introducing water directly into the stomach through a gastric fistula, though to effect the purpose a larger quantity must be employed in this way than by the mouth. Hunger in a somewhat similar manner may be appeased by rectal alimentation. It seems probable, however, that these sensations as usually felt are the result of a sort of habit, depending on the physiological condition of the secreting and absorbing mechanisms of the alimentary canal.

Clinical observation has shown that "bulimia," or voracious appetite, is frequently a result of disease in certain parts of the central nervous system. We are therefore justified in speaking of a "hunger-centre."[1]

E. The Equilibrium of the Body; the Function of the Semicircular Canals.

The term *equilibrium*, as applied to the condition of the body, whether at rest or in motion, indicates a state in which all the skeletal muscles are under control of nerve-centres, so that they combine, when required, to resist the effect of gravity or to execute some co-ordinated motion. The preservation of equilibrium is manifestly of fundamental importance in animal life, and we find, accordingly, several mechanisms sharing in this function. That the motor co-ordinating centres may act properly, they must receive sensory impressions conveying information of the relative position of the body at any given moment. The sum-total of these sensations may be characterized as the *sense of equilibrium*, and it is probably not going too far to assume that every known sensation contributes to this fund of information. Thus, in ordinary life the position of objects is commonly determined by the sense of sight: when one tries to walk while looking through a prism, objects are not properly localized by vision, and improper co-ordination results. The contact of the soles of the feet with the ground, and that of the surface of the body with various objects, are common sources of information as to our relation with the environment. Standing upright, and still more when in motion, the muscular sense is active in appreciating the tension, active or passive, of the muscles. In the erect position, with eyes closed, a writing point attached to the head will show that the body sways in a peculiar manner indicating successive contraction of different groups of muscles; and a person with failure of muscular and tactile sen-

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[1] Ewald: *Diseases of the Stomach*, p. 397.

sibility, as in locomotor ataxy, cannot stand with eyes closed, and his movements, even when sight is employed, are exaggerated and unnatural. Attention has previously been called to the fact that air-waves, irrespective of those producing sound-sensations, exert an influence upon the tympanic membrane by which we are capable of appreciating the presence and, to some extent, the physical character of objects. Whether this sensation involves the nerves of touch, those of common sensibility, or those distributed to the internal ear, is uncertain.

In the absence of any of these sensations the loss may be made up by more perfect development of others. Ordinarily, the sensory information from all these sources, when compared in consciousness, harmonizes and gives rise to a concrete idea of position. Frequently, however, one of the sources of sense-impression suddenly fails us or its testimony conflicts with that of other sense organs; the result is disturbance of equilibrium. A very common outcome of this conflict of sensations is *dizziness* or *nausea*. The distress arising from wearing ill-fitting glasses and the sensations experienced when one looks down from a high eminence are examples in point. Internal disorders exciting nerves of common sensation have the same effect, though the relation borne by visceral sensations to equilibrium is very ill known. A false idea of position of the body, a sense of falling in one direction or another, may lead to sudden effort of recovery by which the person is precipitated to the opposite side. Thus, when looking at rapidly-moving water erroneous ideas of equilibrium are gained through the visual sense, and there is a strong tendency for the body to precipitate itself in one direction or another. When, in going up a staircase, one miscalculates the number of steps, a peculiar sensation of want of equilibrium is aroused through the muscular sense. It is clear, then, that the sense of equilibrium is served by various sense organs, and a complete discussion of this function would entail a consideration of the whole field of nerve-muscle physiology. There is, however, good reason for believing that there is a special sense organ for determining the position and direction of movement of the head and, by inference, of the whole body. The terminal organ of this sense apparatus of equilibrium is found in the system of semicircular canals of the internal ear.

Experiments on the lower animals, chiefly performed on birds, show a constant motor disturbance to follow division of any or all of the semicircular canals. These disturbances are of two kinds. When the animal is at rest it does not stand in a natural fashion, but *sprawls* in a more or less exaggerated degree. It holds its head in an unnatural position, as with the vertex touching the back, or with the beak turned down toward the legs or bent over to one side. Immediately after the operation, and whenever it is disturbed, the animal goes through peculiar *forced* movements, together with rolling or twitching of the eyes, of various kinds and degrees of violence, depending on the position and number of canals severed. The disturbance varies from simple unsteadiness in gait, with swaying motions of the head, to complete lack of co-ordination and a violence of movement almost comparable to that of a chicken whose head has been cut off. Essentially the same results have been determined to follow injury of the semicircular canals of widely different groups of animals.

These results have been explained by the assumption that the hair-cells on the *cristæ acusticæ* of the ampullæ of the semicircular canals are irritated by increase or decrease of pressure of the endolymph upon them, and thus give rise to sensory impressions from which ideas of change of position are derived. Section of the canal, by draining off the endolymph, would cause abnormal pressure-irritation. The anatomical relations of the semicircular canals afford an obvious basis for this view, for the canals of each ear are almost exactly at right angles to one another, occupying the three planes of space; considering the two ears, the horizontal canals are nearly in the same plane, and the anterior vertical canal of one side is nearly parallel with the posterior vertical canal of the other side. Any possible movement of the head would thus produce an increase of endolymph-pressure upon the hair-cells in one ampulla and a decrease of pressure in the ampulla of the parallel canal, and every change of position would be accompanied by the irritation of definite ampullæ with definite degrees of excitement (Fig. 202). Experiments on man afford considerable support to this theory of the function of the semicircular canals. A person with eyes closed and with muscular and tactile sensations eliminated, supported on a table which can be rotated in all directions, can determine with considerable accuracy not only that he is moved, but in what direction and, to some extent, through how great an angle. Further, when brought to rest after a series of rotations the person under observation feels a sensation of motion in the opposite direction. Each of these results should be expected to follow were the theory in question correct. The observations of James have shown that with deaf mutes in whom the internal ear was at fault rapid rotation in an ordinary "swing" failed to produce the dizziness which is the common effect in ordinary individuals. On the other hand, diseases which may be supposed to alter the intra-labyrinthine pressure are characterized by the symptoms of vertigo and inco-ordination of movement. The presumable effect of cutting the semicircular canals is that the escape of endolymph changes the pressure upon the sensory hair-cells and gives the animal the sensation of falling in one direction or another, so that he is impelled to make compensatory or *forced* movements to counteract this imaginary change of position. In birds and in fishes, whose life is passed more or less exclusively in a medium in which tactile and muscular sensation can contribute little to the sense of equilibrium, the semicircular canals are especially well developed.[1] In fishes, though section of the canals themselves produces no disturbance, division of

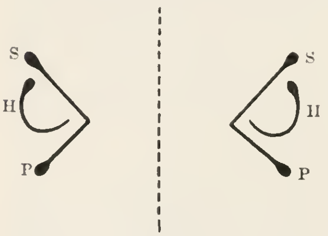

FIG. 202.—Diagrammatic horizontal section through the head to illustrate the planes occupied by the semicircular canals (after Waller): S, superior canal; P, posterior canal; H, horizontal canal.

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[1] Sewall: *Journal of Physiology*, 1884, iv. p. 339.

the nerves supplying the ampullæ usually gives rise to marked forced movements, as shown in somersaults, spiral swimming, etc., when set free in the water. When, however, the nerves are cut with great care, with sharp scissors, so as to avoid traction on or crushing of the nerves, such forced movements do not follow.

Lee[1] found that when a fish is turned in different positions there is a compensatory change in the direction of the fins and the optic axes determined by the semicircular canal in whose plane the movement is made. He concludes that "Each canal has a principal and a subordinate function. The former is the appreciation of rotational body movements in its own plane and toward its side of the body; the latter is the appreciation of similar movements, but in the opposite direction." Electric stimulation of the ampullary nerves or mechanical pressure upon the ampullæ excites equally definite movements of eyes and fins, and the ocular result of nerve-irritation is the exact opposite of that of nerve-section.

The difference in function between the divisions of the internal ear is indicated by investigations on albinos. White animals with blue eyes are deaf, but possess the normal power of equilibration. Rawitz[2] found the cochlea in such creatures to be much reduced and the organ of Corti atrophied, while the semicircular canals were normal.

According to Lee[3] and others, the equilibrium of rest and motion, or static and dynamic equilibrium, depends upon the irritation of different nerve-terminals. The manner of action of the latter has been considered. As to the nervous mechanism on which *static* equilibrium depends, Lee is of the opinion that the knowledge of the position of the head while at rest comes from the relation of the otoliths in the vestibular sacs to the nerve-endings on the *maculæ acusticæ.* These otoliths form considerable masses in the ears of fishes, and the intensity and direction of their pressure upon hair-cells must vary with the spatial relations of the head, and thus be comparable, in the sense of position which they arouse, to the tactile sensations derived from the soles of the feet in man.

The opinion may be ventured that in the semicircular canals we have a sense-organ of a peculiar kind. The evidence is satisfactory that impulses generated in the nerves of the ampullæ, and probably of the vestibular sacs also, give rise to *sensations of position* both dynamic and static. And it is highly probable that such sensations form a constant basis for our notion of the spatial relations of the head. But the preservation of equilibrium does not depend wholly upon the special sense-organ, as does sight upon the eye. For the muscular and tactile, not to speak of the visual and other senses, supply information in the same direction, and, no doubt, these may to a certain extent vicariously fill the function of the semicircular apparatus when this is abolished.

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[1] Lee: *Journal of Physiology,* xv. p. 311; xvi. p. 192.

[2] Rawitz: *Zoölogischer Jahresbericht,* 1896.

[3] *Journal of Physiology,* xv. p. 311, xvi. p. 192.

F. SMELL.

The complex paired cavity of the nose is divisible into a lower respiratory and an upper olfactory tract, the mucous membrane over each of which is distinctive. The covering of the respiratory tract is known as the *Schneiderian* or *pituitary* membrane; its surface is overlaid with cylindrical ciliated epithelium, the ciliary current of which is directed posteriorly toward the pharynx.

The Schneiderian membrane lines the lower two-thirds of the septum, the middle and inferior turbinated bodies, and the bony sinuses which communicate with the nasal chamber. The membrane upon the turbinated bodies and the lower part of the septum is composed largely of erectile tissue.

The function of the respiratory tract is threefold: it restrains the passage of solid particles into the lungs; it warms the air inspired to approximately the temperature of the body; and it gives up moisture sufficient nearly to saturate the air.

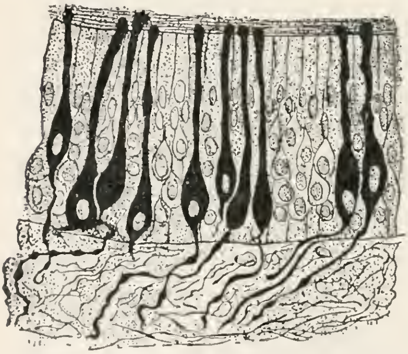

FIG. 203.—Section of olfactory mucous membrane (after V. Brunn): the olfactory cells are in black.

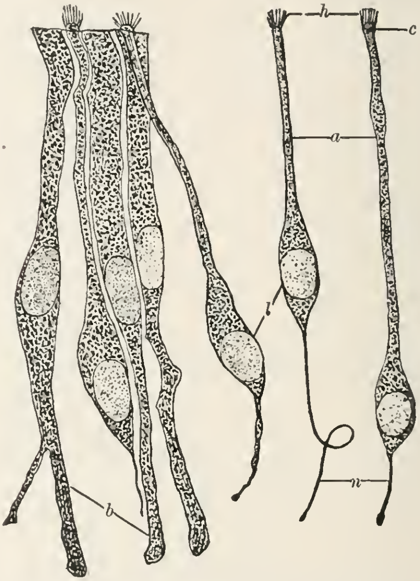

FIG. 204.—Cells of the olfactory region (after V. Brunn): *a*, olfactory cells; *b*, epithelial cells; *n*, central process prolonged as an olfactory nerve-fibril; *l*, nucleus; *c*, knob-like clear termination of peripheral process; *h*, bunch of olfactory hairs.

The olfactory mucous membrane, which alone is the peripheral organ for smell, is seated in the upper part of the nasal chamber, away from the line of the direct current of inspired air. The membrane is thick and is covered by an epithelium composed of two kinds of cells, columnar and rod cells. The latter are the true *olfactory cells* (Figs. 203, 204), with which the fibres of the olfactory nerve are known to be connected. These olfactory cells, in fact, are comparable to nerve-cells in that the fibres connected with them, the fibres composing the olfactory nerve, are direct outgrowths from the cells (Fig. 205), essentially similar in every way to the nerve-fibre processes springing from nerve-cells in the nerve-centres. In this respect the olfactory cells differ from the sensory cells in other organs of special sense. The membrane appears to be not ciliated except near its juncture with the Schneiderian membrane, where the columnar cells acquire cilia and gradually pass over into the cells covering the respiratory tract. Substances exciting the sense of smell exist as gases or in a fine state of division in the air inspired. They reach the olfactory mucous membrane by diffusion, assisted by the modified inspiratory movements of "sniffing" and "smelling," and are most acutely perceived when the air containing them is warmed to the body-temperature. The amount of odoriferous matter that may thus be recognized is extraordinarily small; thus, it is said that in one liter of air the odor of 0.000,005 gram of musk and of 0.000,000,005 gram of oil of peppermint can be perceived.[1] The odoriferous particles probably excite the sense of smell by coming into contact with the olfactory epithelium after solution in the layer of moisture covering it. This epithelium is easily thrown out of function, as the common loss of smell when there is a "cold in the head" testifies. When the nostril is filled with water in which an odorous substance is dissolved, no sensation of smell is excited, but it is said that if normal salt-solution, which injures the living tissues less than water, be used as the solvent, the odor can still be perceived. In many lower animals the sense of smell has an acuteness and an importance in their economy unknown in the human race. It is probable that not only do different races have their distinctive odors, but that each individual exhales an odor peculiar to himself, distinguishable by the olfactory organs of certain animals. The classification

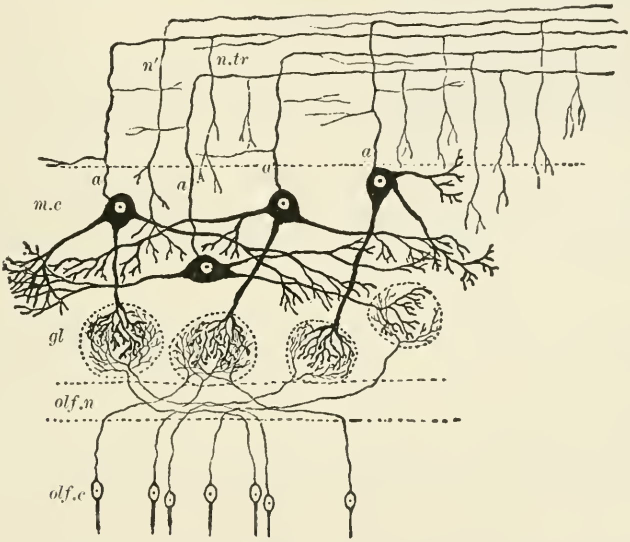

Fig. 205.—Diagram of the connections of cells and fibres in the olfactory bulb (Schäfer, in Quain's *Anatomy*): *olf.c*, cells of the olfactory mucous membrane; *olf.n*, deepest layer of the bulb, composed of the olfactory nerve-fibres which are prolonged from the olfactory cells; *gl*, olfactory glomeruli, containing arborization of the olfactory nerve-fibres and of the dendrons of the mitral cells; *m.c*, mitral cells; *a*, thin axis-cylinder process passing toward the nerve-fibre layer, *n.tr*, of the bulb to become continuous with fibres of the olfactory tract; these axis-cylinder processes are seen to give off collaterals, some of which pass again into the deeper layers of the bulb; *n'*, a nerve-fibre from the olfactory tract ramifying in the gray matter of the bulb.

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[1] Passy: *Comptes-rendus de la Société de Biologie*, 1892, p. 84.

of odors is not very definite, and the relation of odors to one another in the way of contrast and harmony is ill understood. No limited number of primary sensations, as in vision, have been discovered out of which other sensations can be composed. Certain sensations, as those due to the inhalation of ammonia and other irritant gases, are thought to be due to excitement of the nasal filaments of the fifth nerve, and not of the olfactory.

Subjective sensations of smell are sometimes experienced, the result of some irritation arising in the olfactory apparatus itself.

Finally, in man sensations of smell have their most important uses in connection with taste; many so-called "tastes" owe their character wholly or partly to the unconscious excitement of the sense of smell.

G. TASTE.

The peripheral surfaces concerned in taste include, in variable degree, the upper surface and sides of the tongue and the anterior surfaces of the soft palate and of the anterior pillars of the fauces. Other parts of the buccal and pharyngeal cavities are, in most persons, devoid of taste.[1]

The chief peripheral sensory organs of taste are groups of modified epithelial cells, known as *taste-buds* (Fig. 206), seated in certain papillæ of the tasting surfaces. According to some authors, only parts provided with taste-buds can give taste-sensations.[2]

The structure of taste-buds is most easily studied in the *papilla foliata* of the rabbit, a patch of fine, parallel wrinkles found on each side of the back part of the tongue of the animal. The taste-bud is a somewhat globular body seated in the folds of mucous membrane between the furrows of the papilla. It is made up of a sheath of flattened, fusiform cells enclosing a number of rod-like cells each of which terminates in a hair-like process. These cells surround a central pore which opens into a furrow of the papilla. The hair-bearing cells recall the appearance of the olfactory rod-cells, and are probably the true sensory cells of taste, since between them terminate the filaments of the gustatory nerve. In the human tongue taste-buds are confined to the fungiform papillæ, seen often as red dots scattered over the upper surface; to the circumvallate papillæ, the pores of the buds opening into the groove around the papilla; and to an area just in front of the anterior pillar of the fauces, which somewhat resembles the papilla foliata of the rabbit.

The sensory nerves distributed to the tongue include filaments from the glosso-pharyngeal, the lingual branch of the fifth, and the chorda tympani. The relation of these nerves to the sense of taste has been the occasion of much dispute. The weight of evidence probably favors the belief that the glosso-pharyngeal is the nerve of taste for the posterior third of the tongue, while the lingual and, to some extent, the chorda carry taste-impressions from the anterior two-thirds. Clinical cases have been cited to show that all the

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[1] V. Vintschgau: "Geruchsinn," *Hermann's Handbuch der Physiologie*, iii. 2, 1880.

[2] Camerer: *Zeitschrift für Biologie*, 1870, vi. S. 440; Wilczynsky: *Hofmann und Schwalbe's Jahresbericht der Physiol.*, 1875.

gustatory fibres arise from the brain as part of the glosso-pharyngeal nerve, whatever may be their subsequent course to the tongue. On the contrary, other cases have shown a marked loss of taste-sensation following upon lesions of the fifth nerve at or near its origin from the brain, while still others indicate that some of the taste-fibres may arise in the seventh nerve. The point is of practical importance in diagnosis, in the interpretation of loss of taste over any given part of the tongue, but the contradiction in the clinical cases reported has led to the general belief that the origin and course of the gustatory fibres are subject to considerable individual variations.

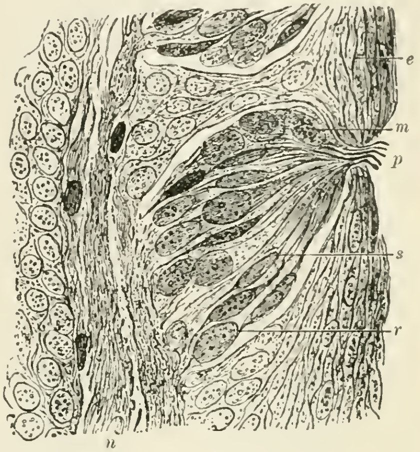

FIG. 206.—Section through one of the taste-buds of the papilla foliata of the rabbit (from Quain, after Ranvier), highly magnified: *p*, gustatory pore; *s*, gustatory cell; *r*, sustentacular cell; *m*, leucocyte containing granules; *e*, superficial epithelial cells; *n*, nerve-fibres.

Our taste-perceptions are ordinarily much modified by simultaneous olfactory sensations, as may easily be demonstrated by the difficulty experienced in distinguishing by taste an apple, an onion, and a potato, when the nostrils are closed. In the condition of anosmia the ability to discriminate between tastes is much below par. Sight has also an important influence, at least in quickening the expectancy for individual flavors. Every smoker knows the blunting of his perception for burning tobacco while in the dark; various dishes having distinctive flavors are said to lose much of their gustatory characteristics when the eyes are bandaged.[1]

The intensity of gustatory sensation increases with the area to which the tasted substance is applied. The movements of mastication are peculiarly adapted to bring out the full taste-value of substances taken into the mouth, and the act of swallowing, by which the morsel is rubbed between the tongue and the palate, has been proved to develop tastes not appreciable by simple contact with the sensory surface. A considerable area in the mid-dorsum of the tongue is said to be devoid of all taste-sensibility.[2]

The sensitiveness of taste-sensation is greatest when the exciting substance is at the temperature of the body. Weber[3] found that when the tongue was dipped during one-half to one minute in water either at the freezing temperature or warmed to 50° C., the sweet taste of sugar could no longer be appreciated by it. It is probable that sapid substances reach the sensory endings of the nerves of taste only after being dissolved in the natural fluids of the mouth, and any artificial drying of the buccal surfaces or alteration of their secretion must affect taste-perceptions.

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[1] *Cf.* Patrick: "Studies in Psychology," Univ. Iowa, 1899, vol. ii.

[2] Shore: *Journal of Physiology*, 1892, vol. xiii. p. 191.

[3] *Archiv für Anatomie und Physiologie*, 1847, S. 342.

The excitement of the taste-nerves appears to depend not so much on the absolute amount of the substance to be detected as on the concentration of the solution containing it. Thus, when, 1 part of common salt to 213 of water was tasted by Valentin,[1] $1\frac{1}{2}$ cubic centimeters of the fluid was sufficient to give a saltish taste; when diluted so that the ratio of salt to water was 1 to 426, 12 cubic centimeters taken in the mouth scarcely gave the salt taste. Sulphate of quinine dissolved in the proportion 1 to 33,000 gave a decided bitter taste, but a solution 1 to 1,000,000 was with difficulty perceived as bitter.

It has generally been conceded that all gustatory sensations may be built up out of four *primary taste-sensations*—namely, *bitter*, *sweet*, *sour*, and *salt*. Some authors even limit the list to tastes of bitter and sweet (V. Vintschgau).

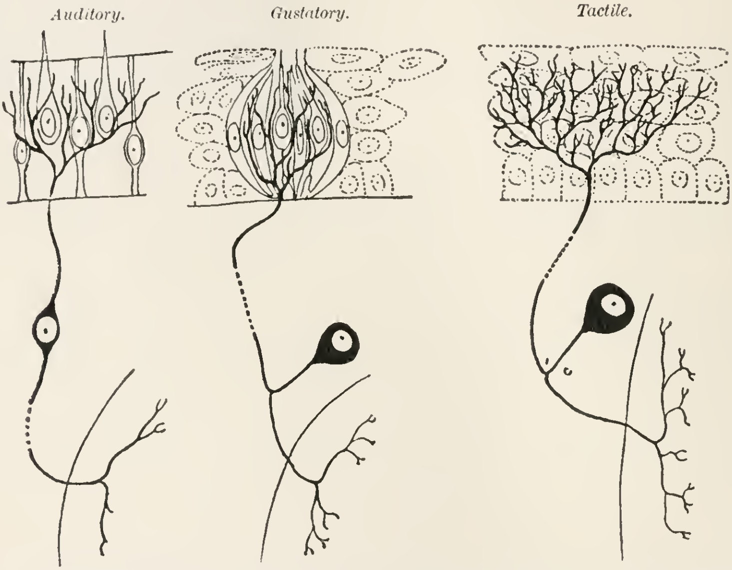

FIG. 207.—Diagram showing the mode of termination of sensory nerve-fibres in the auditory, gustatory, and tactile structures of vertebrata (from Quain, after Retzius). Each sense organ may be considered as essentially constructed of a nerve-cell with two processes, one finding its way centrally to cluster round other nerve-cells or their processes, and the other to terminate in the periphery. In the organ of smell the peripheral process is very short and is directly irritated by foreign particles, the original nerve-cell being represented by the olfactory cell (Fig. 291). In the organs of touch the nerve-cell is found in the ganglion of the posterior spinal nerve-root; the peripheral process is very long and is acted on indirectly through the modified epithelium round which it clusters. The same may be said of the other sense organs. See Quain's *Anatomy*, 10th ed., vol. iii. pt. 3, p. 152.

There is strong reason to believe that corresponding to the four primary taste-sensations there are separate centres and nerve-fibres, each of which, when excited, gives rise only to its appropriate taste-sensation. Substances which arouse the sense of taste are not appreciated in uniform degree over the surface of the tongue. Thus, to V. Vintschgau, at the tip of the tongue acids were perceived acutely, sweets somewhat less plainly, and bitter substances hardly at all. It is generally admitted that sweet and sour tastes are recognized chiefly at the front, and bitter, together with alkaline tastes, by the posterior

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[1] *Lehrbuch der Physiologie*, 1848.

part of the tongue. Strong evidence in favor of the specific difference between various taste-nerves is found in the fact that the same substance may excite a different gustatory sensation according as it is applied to the front or the back of the tongue. Thus, it has been demonstrated that a certain compound of saccharin (para-brom-benzoic sulphimide) appears to most persons to be sweet when applied to the tip of the tongue, but bitter in the region of the circumvallate papillæ.[1]

Oehrwall[2] has examined the different fungiform papillæ scattered over the tongue with reference to their sensitiveness to taste-stimuli. One hundred and twenty-five separate papillæ were tested with succinic acid, quinine, and sugar. Twenty-seven of the papillæ gave no response at all, indicating that they were devoid of taste-fibres. Of the remaining ninety-eight, twelve reacted to succinic acid alone, three to sugar alone, while none were found which were acted upon by quinine alone. The fact that some papillæ responded with only one form of taste-sensation is again evidence in favor of the view that there are separate nerve-fibres and endings for each fundamental sensation; but the figures given in the experiments show that the majority of the papillæ are provided with more than one variety of taste-fibre.

An extract of the leaves of a tropical plant, *Gymnema silvestre*, when applied to the tongue, renders it incapable of distinguishing the taste of sweet and bitter substances; it probably paralyzes the nerves of sweet and bitter sensations. When a solution of cocaine in sufficient strength is painted on the tongue, the various sensations from this member are said to be abolished in the following order: (1) General feeling and pain; (2) bitter taste; (3) sweet taste; (4) salt taste; (5) acid taste; (6) tactile perception (Shore).

That there are laws of contrast in taste-sensation has long been empirically known. Thus, the taste of cheese enhances the flavor of wine, but sweets impair it (Joh. Müller). It is unfortunate, from a hygienic standpoint at least, that in this most important department of the physiology of sensation investigations are almost wholly wanting.

Certain tastes may disguise others without physically neutralizing them; when, for example, sugar is mixed with vinegar, the overcoming of the acid taste is probably effected in the central nerve-organ.[3]

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[1] Howell and Kastle: *Studies from the Biological Laboratory of Johns Hopkins University.* 1887, iv. 13.

[2] *Skandinavisches Archiv für Physiologie*, 1890, vol. ii. S. 1.

[3] Brücke: *Vorlesungen über Physiologie*, 1876.

IV. PHYSIOLOGY OF SPECIAL MUSCULAR MECHANISMS.

A. The Action of Locomotor Mechanisms.

The Articulations.—The form, posture, and movements of vertebrates are largely determined by the structure of the skeleton and the method of union of the bones of which it is composed. There are two hundred bones in the human skeleton, and they are so connected together as to be immovable, or to allow of many varieties and degrees of motion. There are four principal methods of articulation :

1. **Union by Bony Substance (Suture).**—This form of union occurs between the bones of the skull. These bones, which at birth are independent structures connected by fibrous tissue, gradually grow together and make a continuous whole, only a more or less distinct seam remaining as witness of the original condition.

2. **Union by Fibro-Cartilages (Symphysis).**—The bodies of the vertebræ and the sacro-iliac and pubic bones are closely bound together by disks of fibro-cartilage. This material, which is very strong, but yielding and elastic, acts as a buffer to deaden the effect of jars, permits of a slight amount of movement when the force applied is considerable, and restores the bones to their original position on the removal of the force. The spinal column can be thought of as an elastic staff; the capacity for movement differs greatly in different regions, however, partly on account of differences in the thickness of the intervertebral disks as compared with the antero-posterior and lateral diameters of the bodies of the vertebræ, and more especially on account of the method of contact of the superior and inferior vertebral processes. In the cervical region the disks are thick and the diameter of the vertebræ is small, and this permits of considerable bending in all directions and a certain amount of rotation. In the dorsal region a slight amount of bending from side to side and a slight amount of rotation are possible ; but backward bending is inhibited by contact of the articular processes, and forward bending is prevented by the strong articular ligaments. In the lumbar region bending in all directions is more free, but rotation is made impossible by the interlocking of the articular processes.[1]

3. **Union of Fibrous Bands (Syndesmosis).**—Some of the bones, as those of the carpus and tarsus, are connected by interosseous ligaments which, at the same time that they bind the bones together, admit of a certain amount of

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[1] Fick : *Compendium der Physiologie des Menschen*, Wien, 1891.

play, the extent of the movement varying with the character of the surfaces and the length of the ligaments.

4. **Union by Joints (Diarthrosis).**—The adjacent surfaces of most of the bones are so formed as to permit of close contact and freedom of movement in special directions. The parts of the bones entering into the joint are clothed with very smooth cartilage, and the joint-surfaces are lubricated by synovial fluid, a viscid liquid secreted by a delicate membrane which lines the fibrous capsule by which the joint is surrounded. The joint-capsule is firmly attached to the bones at the margin of the articular cartilages, and, at the same time that it completely surrounds and isolates the joint-cavity, it helps to bind the bones together. The bones are further united by strong ligaments, in some cases within and in other cases without the capsule. These ligaments are so placed that they are relaxed in certain positions of the joints and tightened in others; they guide and limit the movements of the joints. The joint-surfaces always touch, although usually the parts in contact change with the position of the joint. If continuous contact of the joint-surfaces is to be maintained and free movement is to take place in special directions, it is evident that the opposing surfaces must not only be so constructed that they shall fit each other with great accuracy, but also have forms especially adapted to the movements peculiar to each of the joints.

The different joints exhibit a great variety of movements and may be classified as follows: gliding joints, hinge joints, condyloid joints, saddle joints, ball-and-socket joints, pivot joints. For a description of the structure and the peculiarities of these joints the student is referred to works on anatomy.[1] The contact of the surfaces of the joint is secured in part by the fibrous capsule, in part by the joint ligaments, and in part by the tension of the muscles. The elastic muscles are attached under slight tension, and, moreover, during waking hours are kept slightly contracted by tonus impulses of reflex origin. Another less evident but no less important condition is the atmospheric pressure. The capsule fits the joint closely and all the space within not occupied by the bones is filled by cartilages, fibrous bands, fatty tissues and synovial fluid. The joint is air-tight, and, as was first demonstrated by the Weber brothers, the atmospheric pressure keeps all parts in close apposition. This force is sufficiently great in the case of the hip-joint to support the whole weight of the leg even after all the surrounding soft parts have been cut through. The proof that the air-pressure gives this support is found in the fact that the head of the femur maintains its place in the acetabulum after all the soft parts which surround the joint have been divided, but falls out of its socket if a hole be bored in the acetabulum and air be permitted to enter the cavity of the joint. Though the air-pressure keeps the bones in constant contact it offers no resistance to the movements peculiar to the joints.

The movements of the bones are effected chiefly by muscular contractions, but the direction and extent of the movements are for the most part determined by the form of the joint-surfaces and the limitations to movement

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[1] *Quain's Anatomy*, vol. ii. pt. 1; *Gray's Anatomy; Morris's Anatomy.*

which result from the method of attachment of the ligaments. The following kinds of movement are possible: (*a*) *angular*, in which the angle formed by the longitudinal axis of two bones changes, as in flexion and extension or abduction and adduction; (*b*) *circumduction*, in which the longitudinal axis of a bone describes the sides of a cone, the apex of which is in the joint; (*c*) *rotation*, in which a bone moves about its longitudinal axis; (*d*) *gliding*, in which a bone so moves as to change its position with reference to its neighbor, without rotation or change of angle. As a matter of fact, most of the movements that are made are the resultant of two or of all of these simple motions. In the *gliding joints*, in which the articular surfaces are nearly flat (as in the case of the joints between the articular processes of the vertebræ, and the carpal and tarsal joints), a sliding movement may occur in various directions, and a rotation movement is possible; but the extent of these movements is very slight, being limited by the strong capsule and ligaments. *Hinge joints* have but a single axis of motion, because the convex and somewhat cylindrical surface of one bone fits quite closely the concave surface of the other, and because of tense lateral ligaments which permit of movements in only a single plane. The joint between the humerus and the ulna at the elbow is an example. In this case only flexion and extension are possible, although a slight obliquity of the surfaces causes the head to move in flexion toward the middle line of the body, which is interpreted by some as a screw movement. In this joint the limits of motion are determined by the contact of the coronoid and olecranon processes of the ulna with the bone in the corresponding fossæ of the humerus, as well as by the resistance of capsule and ligaments. The knee-joint[1] is a less simple form of hinge joint. The presence of the semilunar cartilages and the shape of the joint-surfaces cause flexion to be produced by the combined action of sliding, rolling, and rotation movements. In complete extension the lateral ligaments and the posterior and anterior crucial ligaments are put on the stretch, and there is a locking of the joint, no rotation being possible; in complete flexion, on the other hand, the posterior crucial ligament is tight, but the others are sufficiently loose to allow of a considerable amount of pronation and supination. In the *condyloid joint* the articulating surfaces are spheroidal, as in the case of the metacarpo- and metatarso-phalangeal joints. These exhibit all forms of angular movement and circumduction. In the *saddle-joint* there is a double axis of motion—*e. g.*, the articulation of the trapezium with the first metacarpal bone of the thumb permits of movement about an axis extending from before backward, and another, at nearly right angles to this, extending from side to side. All modes of angular movement are possible with such a joint.

The *ball-and-socket joint*, of which the shoulder- and hip-joints are examples, permits of the greatest variety of movements, any diameter of the head

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[1] W. Braunne and Fischer have studied with mathematical accuracy the construction and movements of many of the joints of the human body. Their articles are published in the *Abhandlungen der math.-phys. Classe der königl. Sächsischer Gesellschaft der Wissenschaften*, Bd. xvii., and others.

of the bone serving as an axis of rotation. The *pivot-joint* allows of rotation only; the atlanto-axial and radio-ulnar joints may be placed in this class.

Method of Action of Muscles upon the Bones.—The bones can be looked upon as levers actuated by the forces which are applied at the points of attachment of the muscles. All three forms of levers are represented in the body; indeed, they may be illustrated in the same joint, as the elbow.

An example of *a lever of the first class*, in which the fulcrum is between the power and the resistance, is to be found in the extension of the forearm in such an act as driving a nail: the inertia of the hammer, hand, and forearm offers the resistance, the triceps muscle acting upon the olecranon gives the power, and the trochlea, upon which the rotation occurs, is the fulcrum. The balancing of the head upon the atlas is another example: the front part of the head and face is the resistance, the occipito-atlantoid joint the fulcrum, and the muscles of the neck the power.

In the case of *a lever of the second order*, the resistance is between the fulcrum and the power; for example, when the weight of the body is being raised from the floor by the hands: the fulcrum is where the hand rests on the floor, the weight is applied at the elbow-joint, and the power is the pull of the triceps on the olecranon. The raising of the body on the toes is another example: the fulcrum is at the place where the toes are in contact with the floor, the resistance is the weight of the body transmitted through the tibia to the astragalus, and the power is applied at the point of attachment of the tendo Achillis to the os calcis.[1]

The raising of a weight in the hand by flexion of the forearm through contraction of the biceps gives an example of *a lever of the third order*, in which the power is applied between the fulcrum and the weight. This form of lever, because of the great length of the resistance arm, as compared with the power arm, is favorable to extensive and rapid movements, and is the most usual form of lever in the body.

The power is applied to best advantage when it is exerted at right angles to the direction of a lever, as in the case of the muscles of mastication and of the calf of the leg. If the traction be exerted obliquely, the effect is the less the more acute the angle between the tendon of the muscle and the bone; for example, when the arm is extended the flexor muscles work to great disadvantage, for a large part of the force is expended in pulling the ulnar and radius against the humerus, and is lost for movement, but as the elbow is flexed the force is directed more and more nearly at right angles to the bones of the forearm, and there is a gain in leverage, which is of course again decreased as flexion is completed. This gain in leverage which accompanies the shortening of the muscles is the more important, since the power of the muscle is greatest when the muscle has its normal length, and continually lessens as the muscle shortens in contraction. There are a number of special arrangements which help to increase the leverage of the muscles by lessening the obliquity of attachment—viz. the enlarged heads of the bones, and in some

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[1] Certain observers would class this movement as an example of a lever of the first class (Ewald: *Pflüger's Archiv*, 1896, Bd. lxiv. S. 53).

cases special processes projecting from the bones, the introduction of sesamoid bones into the tendons, and the presence of pulley-like mechanisms.

The contraction of a muscle causes the points to which it is attached to approach one another, and the direction of the movement is often determined by the direction in which the force of the contracting muscle is applied to the bones. In the case of certain joints, however, the form of the joint-surfaces and the method of attachment of the ligaments limits the direction of movement to special lines; and when this is not the case the movement is usually the resultant of the action of many muscles rather than the effect of the contraction of any one muscle. This question has been made the subject of careful study by Fick.[1]

In the case of many muscles, both of the bones to which they are attached are movable, and the result of contraction depends largely on which of the extremities of the muscles becomes fixed by the contraction of other muscles. Though most muscles have direct influence over only one joint, there are certain muscles which include two joints between their points of attachment, and produce correspondingly complex effects. The accurate adjustment and smooth graduation of most co-ordinated muscular movements is due to the fact that not only the muscles directly engaged in the act, but the antagonists of these muscles take part in the movement. It would appear from the observations of certain writers[2] that antagonistic muscles may be not only excited to contraction, but inhibited to relaxation, and that the tension of the muscles is thereby accurately adjusted to the requirements of the movement to be performed. The importance of the elastic tension and reflex tonic contractions of muscles to ensure quick action, to protect from sudden strains, and to restore the parts to the normal position of rest has been referred to elsewhere.

The shape of the muscle has an important relation to the work which it has to perform. A muscle consists of a vast number of fibres, each of which can be regarded as a chain of contractile mechanisms. The longer the fibre, the greater the number of these mechanisms in series and the greater the total shortening effected by their combined action; consequently, a muscle with long fibres, such as the sartorius, is adapted to the production of extensive movements. In order that a muscle shall be capable of making powerful movements it is necessary that many fibres shall be placed side by side, as in the case of the gluteus: "Many hands, light work."

Standing.—In spite of the ease with which the many joints of the body move, the erect position is maintained with comparatively little muscular exertion. It is an act of balancing in which the centre of gravity of the body is kept directly over the base of support. In the natural erect position of the body the centre of gravity of the head is slightly in front of the occipito-atlantoid articulation, so that there is a tendency for the head to rock forward, as is seen from the nodding of the head of one falling asleep. The centre of gravity of the head and trunk together is such that the line of gravity falls slightly behind a line drawn between the centres of the hip-

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[1] *Hermann's Handbuch der Physiologie*, 1871, Bd. i. pt. 2, S. 241.

[2] Sherrington: *Proceedings of the Royal Society*, Feb., 1893, vol. liii.

joints, which would incline the body to fall backward. The line of gravity of the head, trunk, and thighs falls slightly behind the axis of the knee-joints, and the line of gravity of the whole body slightly in front of a line connecting the two ankle-joints, so that the weight of the body would tend to flex the knee- and ankle-joints.

We cannot here consider in detail the mechanical conditions which limit the movements possible to the different joints in the erect position of the body. Although these conditions help to support the body in the upright position, they are not alone sufficient to the maintenance of this posture, as is shown by the fact that the cadaver cannot be balanced upon its feet. That standing requires the action of the muscles is further proved by the fatigue which is experienced when one is forced to stand for a considerable time. The body may be supported in the standing position in various attitudes. Thus, the soldier standing at "attention" places the heels together, turns the toes out, makes the legs straight and parallel, so as to extend the knees to their utmost, tilts back the pelvis, straightens the spine, and looks directly forward. In this position many of the muscles are relieved from action by the locking of the hip- and knee-joints. The tilting backward of the pelvis causes the line of gravity to fall slightly behind the axis of rotation of the hip-joint and puts the strong ilio-femoral ligament on the stretch, which balances the tendency of the weight of the body to extend the hip. The line of gravity would fall slightly behind the axis of rotation of the knee, and tend to cause flexion; but when the joint is extended, the thigh, because of the horizontal curvature of the internal condyle, receives a slight inward rotation, and the knee cannot be flexed without a corresponding outward rotation. In standing with the feet turned out, this rotation movement is prevented by the same ilio-femoral ligament that locks the hip-joint. The ankle-joint cannot be locked, and the tendency of the body to fall forward is resisted by the strong muscles of the calf of the leg. The erect position of the spine and the balancing of the head have likewise to be maintained by the action of muscles. Although this position gives great stability, it cannot be long maintained with comfort. It is less fatiguing to allow the joints to be a little more flexed, and to keep the balance by the action of the muscles, the position being frequently changed so as to bring fresh muscles into action. Perhaps the most restful standing position is found in letting the weight of the body be supported on one leg, the pelvis being tilted so as to bring the weight of the body over the femur, and the other being used as a prop to preserve the balance. Absolute stability in standing is impossible for any length of time; the body is continually swaying, and a pencil resting on a writing surface placed upon the head is found to write a very complicated curve. There is a normal sway for every individual, and this may become markedly exaggerated under pathological conditions. The maintenance of equilibrium requires that afferent impulses shall continually pass to the co-ordinating centres which control the muscles involved in this act, and if any of these normal impulses fail the sway of the body is increased; for example, it is more difficult to stand steadily when the eyes are closed than when they are open; the absence of the normal sensory impulses from the skin of the feet, the muscles, joints, etc., also makes standing more difficult and tends to increase the sway. The effect of the normal sway of the body is to shift the pressure and strain from point to point and to relieve the different muscles from continuous action.

Locomotion.[1]—The movements of animals were first studied by careful observation, accompanied by more or less accurate direct measurements, and by these simple methods the Weber brothers[2] arrived at quite accurate conclusions as to the nature of the processes, walking, running, jumping, etc. These results were greatly extended by Marey,[3] who employed elaborate recording methods, and exact pictures of all stages of these processes were later obtained through the remarkable revelations of instantaneous photography.[4]

Walking.—During the act of walking, at the same time that the body is propelled forward it is continually supported by the feet, one or the other of which is always touching the ground. Preparatory to beginning the movement the weight of the body is thrown upon one leg, while the other leg is placed somewhat behind it, the knee and ankle being slightly flexed. At the start the body is given a slight forward inclination, then the back leg is extended and impels the body forward. As the centre of gravity progresses so as to be no longer over the supporting leg, it would fall were it not that the back leg is at the same instant swung forward to sustain it. As the body moves forward and its weight is received by the leg which has just been advanced, the leg which has been its support is freed from the weight and becomes inclined behind it. This leg and foot are next extended, the body thereby receiving another forward impulse, and then the hip-, knee-, and ankle-joints flexing slightly, the leg swings forward past the supporting leg and again becomes the support of the body. The forward movement of the body is due in part to a slight inclination which tends to cause it to fall forward, and in part to a push given it by each leg in turn as it leaves the ground.

The amount of work performed by the legs in ordinary walking is comparatively slight, since the swing of the leg is, like that of a pendulum, largely a passive act. Speed in walking is attained by inclining the body somewhat more, by which it is better able to oppose the resistance offered by the air, and by flexing the legs somewhat more, which, by lessening the distance between the hip-joints and the ground, lengthens the step at the same time that it permits the propelling limb in extending to push the body forward with greater force. The more rapid movement of the body is also accompanied by a more rapid forward swing of the leg, the muscles aiding the force of gravity.

The transfer of the weight of the body from one leg to the other in walk-

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[1] Beaunis: *Physiologie humaine*, 1888, vol. ii. p. 269, gives many references to the literature of this subject.

[2] W. and E. Weber: *Mechanik der menschlichen Gehewerkzeuge*, 1836.

[3] *La Méthode graphique*, 1885.

[4] Marey: *Méthode graphique* (*supplement*), 1885; Muybridge: *The Horse in Motion, as Shown by Instantaneous Photography*, 1882.

ing causes an up-and-down and a lateral sway with each step. Were the legs without joints, like stilts, these oscillations would be very great, especially when the step was long; as a matter of fact, they are slight. The tendency for the centre of gravity to move from side to side as the legs alternately push the body forward is partly balanced by the swing of the opposite arm; and the vertical oscillations are minimized by the fact that the leg which is about to receive the weight flexes as the centre of gravity moves forward and comes over it, and extends as it passes on to be received by the other leg. The path taken by the centre of gravity during walking is a complicated one. If referred to the plane in which the body is moving, it describes for one double step an oval; projected on the horizontal and frontal planes, its path has the form of the sign of infinity, $\propto$. The rate of movement influences its position in special parts of the curve.[1]

In *running*, the body is inclined more than in walking, and the legs are more flexed in order that the extension movement of the back leg, which drives the body forward, may be more effective. In running, the body is propelled by a series of spring-like movements and there are times when both feet are off the ground, the back leg leaving the ground before the other touches it.

B. VOICE AND SPEECH.

1. STRUCTURE OF THE LARYNX.

Voice-production.—The human voice is produced by vibration of the true vocal cords, normally brought about by an expiratory blast of air passing between them while they are approximated and held in a state of tension by muscular action. Mere vibration of the cords could produce but a feeble sound; the voice owes its intensity both to the energy of the expiratory blast (Helmholtz)[2] and to the reinforcement of the vibrations by the resonating cavities above and below the cords.

A true conception of the action of the larynx can only be gained by a preliminary study of the organ *in situ*, in its relations with the trachea, pharynx, tongue, extrinsic muscles, and hyoidean apparatus. Removed from its connections, the larynx, in vertical transverse section, is seen to be shaped somewhat like an hour-glass, the true vocal cords forming the line of constriction half way between the top of the epiglottis and the lower border of the cricoid cartilage (Fig. 208). In median vertical section the axis of the larynx above the vocal cords extends decidedly backward, and below the cords the axis is nearly perpendicular to the plane in which they lie. The epiglottis is an ovoid lamella of elastic cartilage, shaped like a shoe-horn, that leans backward over the laryngeal orifice so that the observer must look down obliquely in order to inspect the cavity of the larynx (Fig. 212.) The mucous membrane is thickened into a slight prominence, known as the "cushion," at the base of

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[1] Fischer: *Abhandl. d. math.-physik. Cl. d. Sächs. Gesellsch. d. Wissensch.*, xxv. Nr. i.

[2] Quoted by Grützner: *Hermann's Handb. der Physiologie*, 1879, Bd. 11, Th. 2, S. 14.

the epiglottis. The epiglottis, which is extremely movable in a median plane, may be tilted backward so as to close completely the entrance into the larynx.

Functions of the Epiglottis.—One function of the epiglottis seems obviously to serve as a cover for the superior entrance of the larynx, over which it is said to shut in the act of swallowing. But it is found that deglutition occurs in a normal manner when the epiglottis is wanting or is too small to cover the aperture, the sphincter muscles surrounding the latter being capable of protecting the larynx against the entrance of foreign substances. It is held by some that the epiglottis has an important influence in modifying the voice according as it more or less completely covers the exit to the column of vibrating air. It is also held that the epiglottis acts as a sort of sounding-board, taking up and reinforcing the vibrations of the air-column impinging against it.[1]

Sweeping downward and backward from each edge of the epiglottis is a sheet of mucous membrane, the *ary-epiglottic fold*, which forms the lateral rim of the superior aperture of the larynx and which ends in, and covers posteriorly, the arytenoid cartilages. The rounded prominence on the posterior corner of this fold is made by the cartilage of Santorini, and a second, less marked, swelling external to it, by the *cartilage of Wrisberg* (Fig. 215). Looking down into the larynx, it is seen that its lateral walls approach each other by the development on each side of a permanent ridge of mucous membrane, known as the *ventricular band* or *false vocal cord* (Fig. 208).

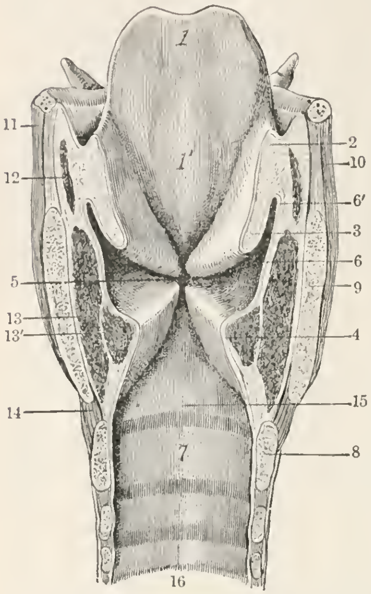

FIG. 208.—Vertical transverse section of the larynx (after Testut): 1, posterior face of epiglottis, with 1′, its cushion; 2, aryteno-epiglottic fold; 3, ventricular band, or false vocal cord; 4, true vocal cord; 5, central fossa of Merkel; 6, ventricle of larynx, with 6′, its ascending pouch; 7, anterior portion of cricoid; 8, section of cricoid; 9, thyroid, cut surface; 10, thyro-hyoid membrane; 11, thyro-hyoid muscle; 12, aryteno-epiglottic muscle; 13, thyro-arytenoid muscle, with 13′, its inner division, contained in the vocal cord; 14, crico-thyroid muscle; 15, subglottic portion of larynx; 16, cavity of the trachea.

Ventricular Bands and Ventricles of Morgagni.—*The ventricular bands or false vocal cords* arise from the thyroid cartilage near the median line, a short distance above the origin of the true cords. They are inserted into the arytenoid cartilages somewhat below the apices of the latter. Their free border is more or less ligamentous in structure. They are brought into contact by the sphincter muscles of the larynx, and thus protect the glottis. It has even been stated that, in paralysis of the true cords, they may be set in vibration and be the seat of voice-formation. So-called "œdema of the glottis" is chiefly due to accumulation of fluid in the wide lymph-spaces found in the false cords.

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[1] Mills: *Journ. of Physiology*, 1883, vol. iv. p. 135.

The ventricular bands are parallel with and just above the true vocal cords, from which they are separated by a narrow slit. They do not, however, reach so near the middle line as the true cords, which can be seen between and below the bands. The ventricular bands project more or less into the cavity of the larynx like overhanging lips, so that each band forms the inner wall of a space closed by the true vocal cords below, and communicating with the cavity of the larynx through the narrow slit above mentioned. The spaces thus bounded internally by the false cords are known as

The Ventricles of Morgagni (Fig. 208).—No complete explanation has been offered as to the purposes served by the ventricles of Morgagni and the false vocal cords. Numerous mucous and serous glands seated in the ventricular bands pour their secretions into the ventricles, whence the fluid may be transmitted by the overhanging lips of the ventricular bands to the true vocal cords; hence, an important function of the former structure, probably, is to supply to the vocal cords the moisture necessary to their normal action. The secretion contained within the ventricle is protected by the ventricular band from the desiccating influence of the passing air-currents. The existence of the ventricular spaces also permits free upward vibration of the true cords. The ventricles of Morgagni in some of the lower animals, as the higher apes, communicate with extensive cavities which serve an obvious purpose as resonating chambers for the voice, and perhaps the preservation of this function in the ventricles themselves is still of importance in the human being. It is not improbable that the ventricular bands find their most important function as sphincters of the larynx, the superior opening of which may be firmly occluded by their approximation. The well-known fact that during strong muscular effort the breath is held from escaping is, according to Brunton and Cash,[1] due to the meeting of the false cords in the middle line. The overhanging shape of the cords allows them to be readily separated by an inspiratory blast, but causes them to be more firmly approximated by an expiratory effort. This mechanism recalls the mode of action of the semilunar valves of the heart.

The true vocal cords arise from the angle formed by the sides of the thyroid cartilage where they meet in front, a little below its middle point, and, passing backward, are inserted into the vocal processes of the arytenoid cartilages. The aperture between the vocal cords and between the vocal processes of the arytenoids is known as the *glottis* or *rima glottidis* (Figs. 214, 215). Since, as will be seen later, the vocal cords may be brought together while the vocal processes of the arytenoids are widely separated at their bases, the space between the cords themselves is sometimes called the *rima vocalis* and that between the vocal processes the *rima respiratoria*.

In the adult male the vocal cords measure about 15 millimeters in length and the vocal processes measure 8 millimeters in addition. In the female the cords are from 10 to 11 millimeters in length. The free edges of the cord are thin and straight and are directed upward; their median surfaces are flattened. Each cord is composed of a dense bundle of fibres of yellow elastic tissue,

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[1] Brunton and Cash: *Journ. Anat. and Phys.*, 1883, vol. xvii.

which fibres, though having a general longitudinal course, are interwoven, and send off shoots laterally into the subjacent tissue. The compact ligament, known commonly as the "vocal cord," forms only the free edge of a reflexion from the side wall of the larynx. This reflexion is wedge-shaped in a vertical, transverse section and contains much elastic tissue and the internal and part of the external thyro-arytenoid muscle (Fig. 208). This whole structure properly forms the vocal cord, and by contraction of its contained muscle its thickness and vibrating qualities may be greatly modified.

Like the trachea, the larynx, with the exception of the vocal cords, is lined by columnar, ciliated epithelium, the direction of whose movement is upward toward the pharynx. The vocal cords are covered by thin, flat, stratified epithelium. The inner surface of the epiglottis, the walls of the ventricles, and the ventricular bands contain much adenoid tissue, the spaces of which are apt to become distended with fluid, giving rise to œdema of those parts. The whole mucous membrane of the larynx, except over the vocal cords, is richly supplied with glands both mucous and serous in character.

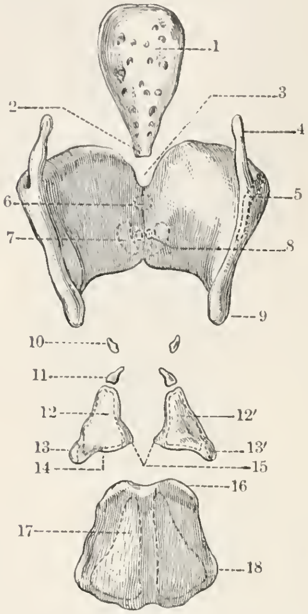

Fig. 209.—Cartilages of the larynx, separated (Stoerk): 1, epiglottis; 2, petiolus; 3, median notch of thyroid; 4, superior cornu of thyroid; 5, attachment of stylo-pharyngeus muscle; 6, origin of thyro-epiglottic ligament; 7, origin of the thyro-arytenoid muscle; 8, origin of true vocal cord; 9, inferior cornu of thyroid; 10, cartilage of Wrisberg; 11, cartilage of Santorini; 12, 12′, arytenoid cartilages, showing attachments of the transverse arytenoid muscle; 13, 13′, processus muscularis, showing attachments of the posterior and lateral crico-arytenoid muscles; 14, base of the arytenoid cartilage; 15, vocal processes of the arytenoids; 16, articular surface for the base of the arytenoid cartilage; 17, posterior view of cricoid cartilage, with outline of attachment of the posterior crico-arytenoid muscle; 18, articular surface for inferior cornu of thyroid cartilage.

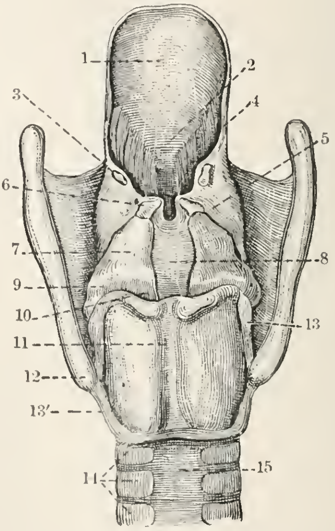

Fig. 210.—Cartilages and ligaments of the larynx, posterior view (after Stoerk): 1, epiglottis; 2, cushion of the epiglottis; 3, cartilage of Wrisberg; 4, ary-epiglottic ligament; 5, 8, mucous membrane; 6, cartilage of Santorini; 7, arytenoid cartilage; 9, its processus muscularis; 10, crico-arytenoid ligament; 11, cricoid cartilage; 12, inferior cornu of thyroid cartilage; 13, posterior superior cerato-cricoid ligament; 13′, posterior inferior cerato-cricoid ligament; 14, cartilages of the trachea; 15, membranous portion of trachea.

Cartilages of the Larynx.—The mechanism of the larynx is supported by a skeleton composed of several pieces of cartilage. The lowermost of these cartilages is the *cricoid* cartilage, so called from its resemblance to a signet ring (Fig. 209). The cricoid cartilage is situated above the topmost ring of the trachea to which it is attached by a membrane. The vertical measurement of the cricoid cartilage is about one inch on its posterior, and one-quarter inch on its anterior surface. Superior to, and partly overlapping the cricoid, is the *thyroid* cartilage, which forms an incomplete ring, being deficient posteriorly (Fig. 209). The free corners of the thyroid behind are prolonged upward or downward into projections known as the *cornua.* The upper pair are attached to the extremities of the greater cornua of the hyoid bone, while by the inner surface of the ends of the lower cornua the thyroid is articulated with the cricoid cartilage and rotates upon it around an axis drawn through the points of articulation. The lower anterior border of the thyroid cartilage is evenly concave, but its upper border has a deep narrow notch in the middle line. The upper half of the thyroid in front projects sharply forward in an elevation known as *Adam's apple* (*pomum Adami*), which is much more marked in adult males than in females. The elliptical space between the cricoid and thyroid cartilages in front is covered by a membrane. Adam's apple, the anterior part of the cricoid ring, and the space between the two, can easily be felt in the living subject; they rise perceptibly toward the head with each swallowing movement.

The arytenoid cartilages are two in number and are similar in shape (Figs. 209, 210). Each cartilage, which has somewhat the form of a triangular pyramid, is seated on, and articulates with, the highest point on the posterior part of the cricoid cartilage some distance from the middle line. Of the free faces of the pyramid, one looks backward, one toward the middle line, and the third outward and forward. Each face is more or less concave. The apex of each arytenoid cartilage is capped by a small body called the *cartilage of Santorini* or, from its bent shape, *corniculum laryngis* (Figs. 209, 210). Outside and in front of the latter is the minute *cuneiform cartilage* or *cartilage of Wrisberg,* enclosed in the ary-epiglottic fold. The lateral posterior corner of the arytenoid cartilage forms a blunt projection which serves for the attachment of muscles, the *processus muscularis.* The anterior, lower, and median part of each cartilage is of especial interest, since it serves for the posterior attachment of the vocal cord; it is known as the *processus vocalis.*

The thyroid and cricoid cartilages and the body of the arytenoids are of hyaline cartilage, and tend to become ossified in middle life. The other cartilages and the vocal processes of the arytenoids are composed of the elastic variety.

The Muscles of the Larynx may be divided into two classes—the *extrinsic* and the *intrinsic;* the former find their origin outside the larynx, and the latter both arise and are inserted within it.

Extrinsic Muscles.—To this group belong the *sterno-hyoid,* the *sterno-thyroid,* and the *omo-hyoid* muscles, which depress the larynx or hyoid bone; the *thyro-hyoid* muscle, which depresses the hyoid bone or elevates the thyroid cartilage. To the elevators of the larynx belong the *genio-hyoid*, the *mylo-hyoid*, the *digastric*, the *stylo-hyoid*, and the *hyo-glossus*. The muscles of the palate and the constrictors of the pharynx enter into coördinated action with the above. When food is passing through the pharyx in the act of swallowing, the hyoid bone is drawn upward and forward, raising the larynx with it; the tongue is thrown backward so that the epiglottis covers the entrance into the larynx, and the constrictors of the larynx contract, completely closing the entrance into that organ.

The *intrinsic muscles* of the larynx are the *crico-thyroids*, the *lateral crico-arytenoids*, the *posterior crico-arytenoids*, the *arytenoid*, the *aryteno-epiglottideans*, and the *thyro-arytenoids;* all being in pairs except the arytenoid, which crosses the middle line. The *crico-thyroid* muscle arises from the front and side of the cricoid cartilage and, passing upward and backward, is inserted into the lower edge of the thyroid cartilage (Fig. 211). The action of the crico-thyroid muscle is to diminish the distance between the thyroid and cricoid cartilages in front, either by depressing the front of the thyroid or by elevating that of the cricoid cartilage, or both. In the first case the distance between the anterior attachment of the vocal cords and the vocal processes of the arytenoid cartilages is increased by movement of the thyroid, and in the second case the same effect is produced by backward rotation of the edge of the cricoid upon which the arytenoid cartilages are seated (Fig. 210). The muscle, therefore, is a tensor of the vocal cords. It is, probably, the mechanism we ordinarily use in raising the pitch of the voice when the vocal machinery has been "set" by the other muscles (see below). If the fingers be placed on the cricoid ring and on the *pomum Adami* while the ascending scale is sung in the middle chest register, both descent of the front of the thyroid and ascent of the cricoid can be made out. The *lateral crico-arytenoid* muscle arises from the upper, lateral border of the cricoid cartilage, and passes upward and backward to be inserted into the outer edge of the arytenoid cartilage, on and in front of the lateral prominence (Fig. 212). Its main action is to wheel the vocal process of the arytenoid toward the middle line and thus approximate the vocal cords. The *posterior crico-arytenoid* is a large muscle, which rises from the median posterior surface of the cricoid cartilage and passes upward and outward to be inserted into the outer surface of the arytenoid cartilage, behind and above the insertion of the lateral crico-arytenoid (Fig. 213). Its action is to turn the vocal processes outward and thus abduct the vocal cords. The posterior crico-arytenoid occupies an important position in the group of respiratory muscles; during vigorous inspiration it is brought into action

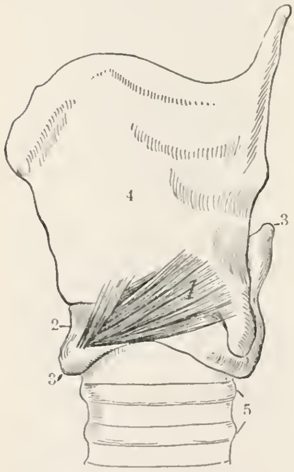

Fig. 211.—Lateral view of the cartilages of larynx with the crico-thyroid muscle (*Quain's Anatomy*, after Willis): 1, crico-thyroid muscle; 2, crico-thyroid membrane; 3, cricoid cartilage; 4, thyroid cartilage; 5, upper rings of the trachea.

and widens the glottis. Paralysis of this muscle is a most serious condition, since it is followed by approximation of, and inability to separate, the vocal cords. The *arytenoid*, or *transverse* or *posterior arytenoid* muscle, the single unpaired muscle of the larynx, is a considerable band passing across the middle line from the posterior surface of one arytenoid cartilage to that of the other (Fig. 213). Its action is to draw the arytenoid cartilages together in the middle line and approximate the vocal processes; its action is essential in closing the glottis. In the resting larynx the arytenoid cartilages are kept apart by the elastic tension of the parts. The *aryteno-epiglottidean*, sometimes called the *oblique arytenoid*, muscles consist of two bundles of fibres seated upon the surface of the arytenoid muscle (Fig. 213). Each muscle arises from the outer posterior angle of the arytenoid cartilage, and, passing upward and inward, crosses in the middle line partly to be inserted into the outer and upper part of the opposite cartilage, partly to penetrate the ary-epiglottic fold as far as the epiglottis, and the remainder to join some fibres of the thyro-arytenoid muscle. The action of the aryteno-epiglottidean muscles is to close the glottis. The *thyro-arytenoid* is a muscle of complex mechanism, usually described as formed of two parts, an external and an internal. The external thyro-arytenoid arises from the lower

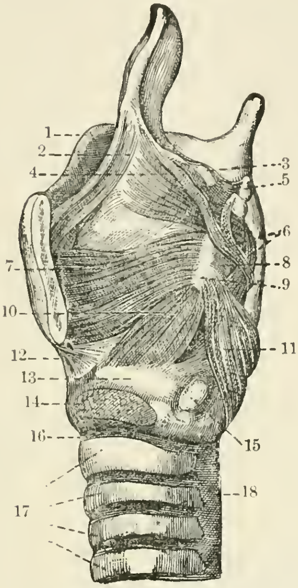

FIG. 212.—Larynx and its lateral muscles after removal of the left plate of the thyroid cartilage (Stoerk): 1, thyroid cartilage; 2, thyro-epiglottic muscle; 3, cartilage of Wrisberg; 4, ary-epiglottic muscle; 5, cartilage of Santorini; 6, oblique arytenoid muscles; 7, thyro-arytenoid muscle; 8, transverse arytenoid muscle; 9, processus muscularis of arytenoid cartilage; 10, lateral crico-arytenoid muscle; 11, posterior crico-arytenoid muscle; 12, crico-thyroid membrane; 13, cricoid cartilage; 14, attachment of crico-thyroid muscle; 15, articular surface for the inferior cornu of the thyroid cartilage; 16, crico-tracheal ligament; 17, cartilages of trachea; 18, membranous part of trachea.

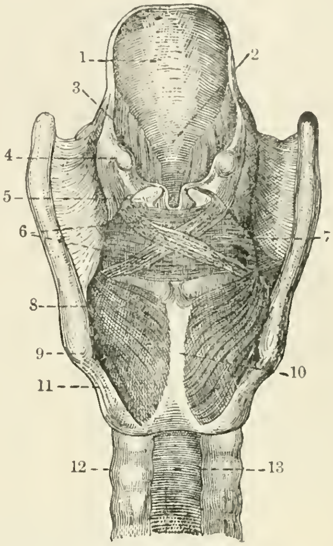

FIG. 213.—Larynx with its muscles, posterior view (Stoerk): 1, epiglottis; 2, cushion; 3, ary-epiglottic ligament; 4, cartilage of Wrisberg; 5, cartilage of Santorini; 6, oblique arytenoid muscles; 7, transverse arytenoid muscle; 8, posterior crico-arytenoid muscle; 9, inferior cornu of thyroid cartilage; 10, cricoid cartilage; 11, posterior inferior cerato-cricoid ligament; 12, cartilaginous portion; 13, membranous portion of trachea.

part of the angle of the thyroid cartilage; its fibres pass, for the most part, backward and somewhat upward and outward to be inserted into the outer edge of the arytenoid cartilage and its lateral *processus muscularis* (Figs. 208, 214). Some of its bundles of fibres, however, have different directions, and a portion of them pass upward into the ventricular bands. The internal *thyro-arytenoid*, wedge-shaped in transverse section, lies between the muscular division just described and the vocal ligament, by which its thin median edge is covered. The internal thyro-arytenoid arises from the anterior angle of the thyroid cartilage and is inserted into the *processus vocalis* and the outer face of the arytenoid cartilage. Certain fibre-bundles of this, as of the external division of the muscle, pass in various directions, some of them being inserted into the free border of the vocal cord. The action of the muscle is, on the whole, to draw the arytenoids forward and thus relax the vocal cords; but, by its contraction, the cords may also be approximated and their thickness, and probably their elasticity, extensively modified.

Specific Actions of the Laryngeal Muscles.—To sum up the various effects of the muscular action on the larynx: A *sphincter action* of the larynx is brought about by the combined contraction of all the muscles with the exception of the crico-thyroids and the posterior crico-arytenoids; *the vocal cords are adducted and the glottis narrowed* by the transverse and oblique arytenoids, the external thyro-arytenoids, and the lateral crico-arytenoids; *the vocal cords are abducted and the glottis widened* chiefly or wholly by the posterior crico-arytenoids; *the vocal cords are made tense* by contraction of the crico-thyroids; *the vocal cords are slackened* by the combined action of the sphincter group and especially by the external thyro-arytenoids.

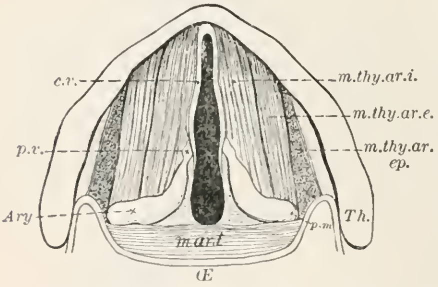

Fig. 214.—Diagram to illustrate the thyro-arytenoid muscles; the figure represents a transverse section of the larynx through the bases of the arytenoid cartilages (redrawn from Foster): *Ary*, arytenoid cartilage; *p.m*, processus muscularis; *p.v*, processus vocalis; *Th*, thyroid cartilage; *c.v*, vocal cords; *Œ* is placed in the œsophagus; *m.thy.ar.i*, internal thyro-arytenoid muscle; *m.thy.ar.e*, external thyro-arytenoid muscle; *m.thy.ar.ep*, part of the thyro-ary-epiglottic muscle, cut more or less transversely; *m.ar.t*, transverse arytenoid muscle.

It will easily be seen that in the larynx, as in the skeleton at large, the efficiency of any single muscle involves the action of accessory muscles; thus, contraction of the crico-thyroid could have little effect in tightening the vocal cords were not the arytenoid cartilages fixed by contraction of the posterior crico-arytenoid and arytenoid muscles.

Nerve-supply of the Larynx.—The larynx receives its nerve-supply from the superior and the inferior or recurrent laryngeal nerves. The extremely sensitive surface of the mucous membrane of the organ above the vocal cords is supplied by sensory filaments of the superior laryngeal nerve. The superior laryngeal also supplies motor fibres to the crico-thyroid muscle, whose action as a tightener of the vocal cords is peculiar. All the other muscles of the larynx receive their motor impulses from the inferior laryngeal nerve. Much of the nervous mechanism of the larynx is still in dispute.

Laryngoscopic Appearance of the Larynx.—Much may be learned by inspection of the larynx during life by means of the laryngoscopic mirror. It is not difficult for an observer to examine his own larynx by placing himself before a second mirror in which may be seen the image reflected from the laryngoscope. To inspect the larynx the tongue must be held well out so as to pull forward the epiglottis, then the structures below appear in the laryngoscopic mirror in reversed position. Beneath the middle of the epiglottis the cushion may be seen as a slight swelling, and continuing downward and backward from the edges of the cartilage, may be seen the ary-epiglottic folds, each marked at its extremity by two rounded nodules, the cartilages of Wrisberg and Santorini (Fig. 215). In quiet breathing the glottis is nearly stationary and opened to the extent of from 3 to 5 millimeters. The vocal cords bounding it look white and glistening in contrast with the red color of the general mucous membrane. The cartilages of Santorini are several millimeters apart, and a sheet of mucous membrane reaches from one to the other. The ventricular bands are seen as red shelves reaching to the outer margin of the shining cords and separated from the latter by a dark line which is the entrance into the ventricles of Morgagni.

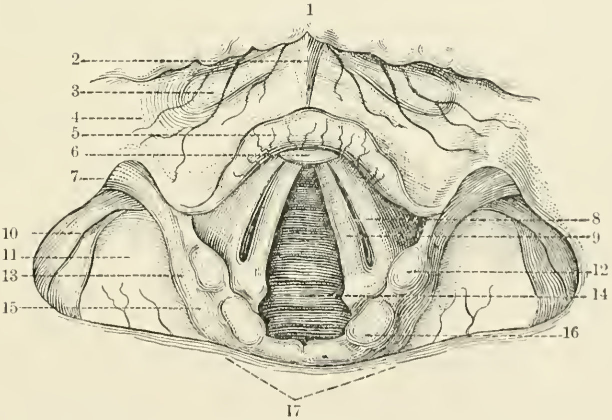

Fig. 215.—The laryngoscopic image in easy breathing (Stoerk): 1, base of the tongue; 2, median glosso-epiglottic ligament; 3, vallecula; 4, lateral glosso-epiglottic ligament; 5, epiglottis; 6, cushion of epiglottis; 7, cornu major of hyoid bone; 8, ventricular band, or false vocal cord; 9, true vocal cord; opening of the ventricle of Morgagni seen between 8 and 9; 10, folds of mucous membrane; 11, sinus pyriformis; 12, cartilage of Wrisberg; 13, aryteno-epiglottic fold; 14, rima glottidis; 15, arytenoid cartilage; 16, cartilage of Santorini; 17, posterior wall of pharynx.

When a deep inspiration is taken the glottis is widely opened, even to the extent of half an inch; an angle is formed between the vocal process of the arytenoid and the vocal cord, the space between the cartilages of Santorini is widened, and the rings of the trachea, and even its bifurcation may be seen below. With the succeeding expiration the glottis again becomes narrow. When the voice is sounded the picture at once changes. The space between the cartilages of Santorini is obliterated, the vocal processes and cords are brought together, and the whole rim of the glottis or the vocal cords alone, according to the pitch of the note, may be seen to vibrate.

2. The Voice.

The vocal machinery consists of—(1) the motive power or breath; (2) the larynx, which forms the tone; (3) the chest, the pharynx, the mouth, and the nose, which color the tone; and (4) the organs of articulation.[1]

The production of voice is undoubtedly accomplished by the vibration of the vocal cords which have previously been approximated in the middle line and made tense through action of the nerve-muscular apparatus already described. A blast of air from below pressing against the cords so adjusted, causes them to separate and fall into vibration. We have to distinguish in voice the three features of *loudness*, *pitch*, and *quality*.

The *loudness* of the tone depends on two factors: (1) the strength of the tone-producing blast as determining not only the amplitude of vibration of the vocal cords, but also the energy with which the air is expelled; (2) the resonance of the two chambers between which the vocal cords are suspended, the chest below and the cavities of the head above, whose walls and contained air, by their sympathetic vibration, powerfully reinforce the oscillations imparted to them.

The *pitch* of the voice is determined by the thickness, tension, and length of the vocal cords, conditions which regulate the pitch of the note obtained from any vibrating string. The thickness and the elastic quality of the cords are probably largely under the control of the thyro-arytenoid muscle. The principal tensor of the cords is the crico-thyroid muscle. Other muscles, as described above, may so fix the arytenoid cartilages that their vocal processes may be prevented from taking part in the vibration of the cords throughout the whole and also, possibly, throughout part only of their length. This dampening of the vocal processes of the arytenoids may be accomplished either by pressure applied to them throughout their whole length, in which case the posterior part of the glottis is closed, or they may be pressed together at the tips alone, leaving the respiratory glottis open as a triangular aperture.

Quality.—Variation in the *quality* of the voice depends on the fact that vibrations of the vocal cords are composite in character, giving rise to notes made up of a fundamental tone combined with upper partial tones (see p. 383). By reason of the varied adjustments that may be imparted to it, the larynx is capable of producing many more qualities of tone than is any artificial instrument.[2] Change in the size and shape of the resonance-chamber above and below the vocal cords produces a corresponding change in their fundamental notes and, therefore, in the partial tones of the voice which they reinforce by sympathetic vibration (see p. 385). According to Helmholtz,[3] the difference in quality between the various vowel sounds of the human voice depends on

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[1] C. H. Davis: *The Voice*, 1879.

[2] Helmholtz: *Sensations of Tone*, trans. by Ellis, 1885, p. 98.

[3] *Op. cit.*, p. 104.

the number and relative prominence of the various overtones determined by altering the shape and size of the nasal and buccal resonance-chambers.

By a simple experiment the production of voice by the vocal cords can easily be illustrated. Take a glass tube, about $\frac{1}{2}$ inch in diameter and of convenient length, and press one end firmly against the palmar surfaces of the proximal phalanges of two fingers at their line of division when they are brought together. By blowing smartly into the other end of the tube, a musical note will be produced by the vibration of the folds of the skin between which the air is forced. By relaxing the pressure with which the fingers are held together, the length of the vibrating segment of skin is increased and its tension diminished; its note is accordingly lowered. The reverse conditions are produced when the fingers are held together tightly and the tube applied firmly; the pitch of the note is then raised. In these ways the pitch of the note may be varied through two octaves, which is the range of a good singing voice. Various upper partials of the note so produced may be made prominent by sympathetic resonance, if the vibrating air-stream is sent across the opening of a wide-mouthed bottle, of about a pint capacity. The air within the bottle is thrown into sympathetic vibration when its fundamental tone is contained in the note emitted through the fingers; when the volume of the air is diminished by slowly pouring water into the bottle, the fundamental tone of the resonator is changed, and it responds to one after another of the partials contained in the musical note.

The marvellous adjustment of muscular action by which, at will, notes may be struck of definite pitch and quality, is evidence of an elaborate nervous machinery for the larynx, not only on the efferent side but, possibly through a muscular sense, on the afferent side as well. The various phenomena of aphasia, and the anatomical importance of the cerebral areas devoted to the elaboration of speech, point in the same direction. The relations between the centres for speech and hearing are most intimate. The ear plays a constant part, as a critical medium, in the tuition of the vocal organs in either speech or song. So-called "dumbness" is the result, usually, not of defects in the vocal organs, but of lack of hearing and, hence, of inability to control by the ear the pitch or quality of the vocal notes.

The voice and the larynx of the child fall naturally in a group with those of the female as contrasted with the adult male. At the age of puberty a boy's larynx becomes congested and undergoes rapid development. The voice changes rapidly from the juvenile to the adult quality. During this change, the voice frequently "breaks" or rapidly returns from the newly-acquired chest register to the head or falsetto notes of childhood (see p. 433). In boys who are castrated a good while before the age of puberty is reached, the larynx does not undergo its characteristic development, and the voice remains of a peculiar quality, much valued in some countries in the rendition of vocal music. The practice of castration for æsthetic purposes has, accordingly, in certain districts, long been in vogue. In the female the changes in the larynx and in the voice at puberty are much less marked than in the male.

Arrangements for Changing the Pitch of the Voice.—As has frequently been mentioned, the vocal cords are stretched, and the pitch of their note is elevated, by contraction of the crico-thyroid muscle. But the change that is thus produced in the tension of the vocal cords is by no means capable of accounting for the full range of pitch which falls within the compass of the voice. When the arytenoid and the crico-arytenoid muscles sufficiently contract, the vocal processes are brought tightly together and their vibration is prevented. Voice-production must then be limited to the vocal cords themselves, and the stretching action of the crico-thyroids may begin anew and reach its maximum with the glottis so set that only its ligamentous borders can vibrate. It can also be seen that the vocal cords themselves may be shortened functionally, or even be broken up into segments, or the main body of the cord be changed in thickness, by contraction of the complex thyro-arytenoid muscles; each such condition would be accompanied by a change in the rate of vibration. We are probably justified in assuming that, when the musical scale is sung, the lowest notes are produced by vibration of the glottic borders throughout their full length, and the elevation of pitch is affected by the gradually-increased tension of the vocal ligaments through the action of the crico-thyroid muscle. This contraction having reached its maximum, the muscle probably relaxes, only to contract again after the vibrating segments of the glottis are shortened by a partial or complete clamping together of the vocal processes in the manner described above. There are thus two or three, or more, adjustments which may be imparted to the vibrating mechanism of the larynx, each of which is distinguished by giving rise to a note of different pitch that may further be altered by action of the crico-thyroid muscle. It might be anticipated that the voice whose pitch was gradually elevated in the manner described would suffer some alteration in quality at those points in the scale where there is a change in the *set* of the larynx producing a shortening of the vibrating segment. Such, indeed, is the fact.

Registers.—Long before the invention of the laryngoscope, and before anything definite was known of the method of voice-production, it was recognized that in ascending the musical scale there occur certain breaks, as it were, where the voice changes in quality as well as in pitch. It is an object in musical education to render these breaks as little prominent as possible. The kinds of voice included between these breaks were distinguished as the vocal "registers." There is no general agreement among musicians as to how many registers are compassed by the voice, and the nomenclatures used to distinguish them differ in the most confusing fashion. According to some authors, the range of the voice is included within two registers only; more commonly three distinct registers are described, to which, in certain cases, a fourth is said to be probably added. The most common designation of the lowest register is the "chest voice," though it has also been called "thick"[1] as distinguished from the "thin" register; another term applied to it is the "long-reed" register as con-

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[1] Browne and Behnke: *Voice, Song, and Speech*, 1890, p. 135.

trasted with the "short-reed" register.[1] The middle register of all voices is by some authors (Garcia,[2] Mme. Seiler[3]) denominated the "falsetto," while other writers use this term to distinguish certain higher notes of the male voice of a peculiar quality not in ordinary use. The third and highest series of vocal sounds is usually known as the "head" register.

The lowest or chest register is that used in ordinary life. It is so called from the strong vibrations of the chest-wall which may be felt while the voice is sounded. In passing to the higher register the chest vibration is found to diminish and that of the head bones to increase; in the one case the cavity of the head acts strongly as a resonance chamber, and in the other that of the thorax. According to Madame Seiler, in the lowest register both the vocal ligaments and the vocal processes of the arytenoids vibrate. In the middle register the vocal processes are clamped together and the vibration of the ligaments seems confined chiefly to their sharp edges; while in the highest register the ligaments themselves appear to be damped throughout the greater part of their length, the vibrations being confined to the edges of an oval slit at their anterior ends (Fig. 216). Within any definite register the quality of individual voices is determined by the size and elasticity of the parts of the larynx, and probably also by peculiarities of the resonating chambers; voices are accordingly classified as base, tenor, alto, and soprano.

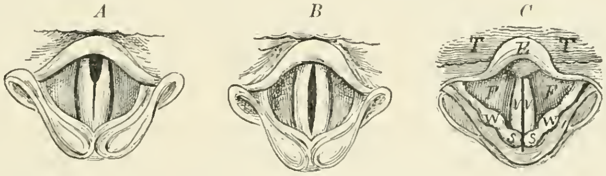

FIG. 216.—The voicing (female) larynx (after Browne and Behnke). *A*, Small or highest register. *B*, Upper thin or middle register. *C*, Lower thin or middle register: *T,T*, tongue; *F,F*, false vocal cords; *S,S*, cartilages of Santorini; *W,W*, cartilages of Wrisberg; *V,V*, vocal cords.

A Whistling Register.—A friend and former pupil of the author's has the remarkable power of emitting from the larynx notes which are indistinguishable in quality from an ordinary whistle. He writes, "The whistle cannot be made to 'slide' into vocal tones of any sort, nor can any other tones be produced simultaneously with it. Its range is about one and a half octaves, or half an octave less than my singing voice.

"The lips have nothing to do with the sound except as their position changes the resonance-quality of the tone by 'reinforcement' or otherwise, for I can whistle almost as readily with the teeth closed and the lips wide parted as with the jaws and lips firmly closed as in the ordinary position. Any other movement of the air-column destroys the sound at once." Some years ago the author made a laryngoscopic examination of this larynx while it was in the act of whistling. No notes were written at the time, but the picture remembered is that of vocal cords closely approximated, except for an oval slit between their anterior and middle portions, as in singing head tones, the cords vibrating chiefly along their free edges.

Speech.—*Language* consists, in general, of a combination of short musical sounds, *vowels* or *sonants*, which are produced purely by vibration of the vocal

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[1] Mackenzie: *Hygiene of the Vocal Organs*, 1891, p. 55.

[2] Garcia: *Lond., Edin., and Dub. Mag.*, vol. x. 1855, p. 218. (Quoted by Seiler.)

[3] Seiler: *op. cit.*

cords, together with superadded noises or modes of obstruction, *con-sonants,* produced by action of the mouth-parts. The vowel sounds usually carry the accent of syllables, and the consonants, for the most part, are sounded only with, or represent peculiar modes of obstructing the former. No classification of vocal signs can be made in which exceptions do not form important *addenda* to general rules.

Articulation is the modification of sound in speech, usually effected by action of the lips, the tongue, the palate, or the jaws, and the place of articulation depends, in any definite case, on the mode in which a sound is formed. Its use as an expression of thought is the chief physiological distinction between man and the lower animals. Distinctness of articulation, so essential to clearness of language, not to mention its æsthetic value, depends on the accuracy of the muscular adjustments used in forming sounds, especially consonantal sounds.

The *speaking* is distinguished from the *singing voice* partly by the fact that most sounds in the first case are articulate or formed in the mouth, while in the latter their quality is only there modified. In singing the tone is sustained at the same pitch for a considerable interval, while in speaking the voice is continually sliding up and down on the vowel sounds. In speaking the consonantal noises and obstructions are more prominent because of their more abrupt formation.[1, 2]

Vowel sounds owe their origin to vibration of the vocal cords, and their quality to the selective resonance of the cavities above the cords. In sounding the series of vowels, *a, e, i, o, u* (pronounced ah, a, e, o, oo), it is found that the form and size of the mouth-cavity, the position of the tongue, the position of the soft palate separating or allowing communication between the nasal and pharyngeal cavities, undergo a progressive change (Fig. 217). Helmholtz has shown that the vowel sounds owe their differences of quality to the varied resonance of the mouth-cavity, dependent on its shape, through which now one, now another, of the overtones in the note produced by vibration of the vocal cords is reinforced.[3] This result is dependent on the fact that when the mouth is set in position for the formation of the various vowel sounds the pitch of its

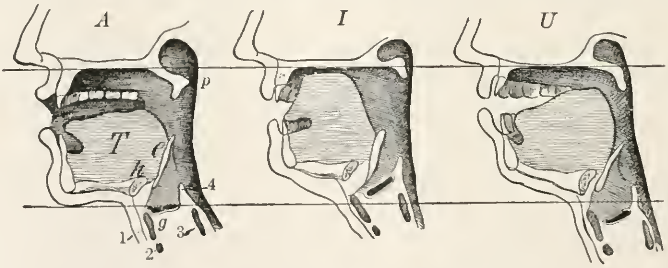

FIG. 217.—Section of the parts concerned in phonation, and the changes in their relations in sounding the vowels *A* (^{ah}), *I* (^{ee}), *U* (^{oo}) (after Landois and Stirling): *T*, tongue; *p*, soft palate; *e*, epiglottis; *g*, glottis; *h*, hyoid bone; 1, thyroid; 2, 3, cricoid; 4, arytenoid cartilage.

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[1] Browne and Behnke: *op. cit.*, p. 28.

[2] Monroe: *Manual of Physical and Vocal Training*, 1869, p. 51.

[3] Helmholtz: *loc. cit.*

fundamental note, or the rate of vibration to which it sympathetically responds, varies accordingly.[1] That the resonance of the mouth cavity changes with its shape is illustrated in the various pitch of the notes produced by flipping the edge of an incisor tooth, the cheek, or Adam's apple with the finger-nail, while the mouth assumes the positions for production of the different vowels.

Vowels whose normal pitch is low, as *o*, *u*, cannot be sounded easily in the higher part of the musical scale; conversely, high-pitched vowels, as *e* in *feet*, lose their character in the lower part of the scale. Language is, therefore, much less distinct in song than in speech.[2]

It has already been stated that the difference in quality of musical notes depends upon the number and relative intensity of their partial tones, each of which is separated from the fundamental tone by a fixed interval. Since the mouth parts have a fairly fixed position for each vowel sound, the buccal cavity reinforces by sympathetic resonance tones of definite vibration rates. When a given vowel is sounded in different parts of the musical scale, now one, now another partial tone is reinforced, according as its pitch harmonizes with the prime tone of the mouth cavity, so that the interval between the resonated partials and their fundamental tone may change, with corresponding change in the quality of the vowel sound. That is, the resonated partial depends not only on its relation to the fundamental, but also on its vibration rate.[3] This feature of vocal resonance distinguishes the human larynx from most musical instruments. That the ground is not covered by these facts was shown by Auerbach,[4] who demonstrated that the strength of upper partials in vowel sounds depends also on the strength of their production by the vocal cords and, therefore, upon their relation to the fundamental tone. That is to say, the quality of a vowel is dependent not only on the *absolute* vibration numbers of its upper partials, according to which they are or are not reinforced by the position of the mouth, but also on the *relative* position of these upper partials as compared with the fundamental tone.

The peculiar æsthetic value of the human voice is dependent on the fact that, on account of its varied powers of adjustment, the larynx is capable of producing many more kinds of tone-quality than any artificial instrument. Helmholtz[5] found no less than sixteen overtones to accompany the fundamental.

The posture of the mouth-parts differs markedly when set for the various principal vowel sounds; but as we know that each vowel sound has several modifications or gradations so that a tone may pass by an easy glide from one to another, so the form of the mouth passes by insensible steps from one vowel position to another. It will be seen later that several articulate sounds play the part now of vowels, now of consonants, according to their position in the syllable or mode of formation. There has also been shown reason for believing that the form of the chest cavity and the tension of its walls are factors in determining the pitch of its fundamental tone; so that through the varied

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[1] Helmholtz: *op. cit.*, p. 108.

[2] *Op. cit.*, p. 114.

[3] *Op. cit.*, p. 118.

[4] Quoted by Grützner: *op. cit.*, p. 179.

[5] *Op. cit.*, p. 103.

sympathetic resonance of the thorax the reinforcement of laryngeal tones may here be altered somewhat, as in the mouth itself.[1,2]

Whispering is a mode of speech in which noise largely replaces pendular musical vibrations. The glottis remains more or less widely open and the vocal cords are not tense; the vibrations are produced both in the larynx and in the buccal-pharyngeal chambers. Vowel sounds may be produced in whispering as well as in true voice because, from the multitude of irregular vibrations, those waves are reinforced which make up the vowel sounds determined by the set of the mouth. Gentle whispering requires much less effort than does speaking, and inspiratory whispering is less easily distinguished from expiratory than is the strained voice of inspiration from the natural sound of expiration. Consonants, as already indicated, may sometimes play the part of vowels, but pure consonants do not appear in syllables except in combinations with vowels, which combinations always carry the syllable accent.

Consonants.—The distinction between consonants and vowels lies in the fact that the tones of the latter are produced by vibration of the vocal cords, the parts above which act only as resonance-boxes and modify the sound, and never offer marked obstruction to the exit of air; whereas in the formation of consonants there is some adjustment in the mouth-passage either in the nature of a local narrowing, by which a peculiar noise is added to the vocal sound, or in the nature of a sudden closing or opening of the air-channel by which a characteristic noise is likewise added to the vocal sound. In other words, the parts above the larynx *make* the sounds of consonants but only *modify* those of vowels.[3] No sharp line of separation can be drawn between vowels and consonants, since certain characters, according to their associations, now fall into one, now into another class. In the classification of consonantal sounds much confusion exists, dependent chiefly on the fact that several letter characters change their modes of formation and expression with their place in the syllable. The same facts, also, are expressed by different authors by different nomenclatures, and sounds occur in one language that are not found in another. Adopting the general classification of Grützner,[4] we may divide consonants into the following three groups:

1. *Semi-vowels* or *liquids*, which can be used either as vowels or consonants; this group includes the sounds *m*, *n*, *ng*, *l*, and *r*. In expressing the function of a consonant, the letter is not to be sounded as if it stood alone, but its character given as actually expressed in a syllable; thus the sound of *p* is not *pee*, but is the abbreviated labial expression, as in *pack* or *piece* when all the letters are eliminated after the first. Of the liquids the *n*, *m*, and *ng* (sometimes called "resonants") have the nature of vowels when final (as in *him*, *hen*, *being*), and are then produced by vibration of the vocal cords, the lips having previously been closed for the *m*, and the tongue applied to the roof of the mouth to cut off the exit of air for *n* and *ng*; the expelled air escapes altogether through the nose, which acts as a resonance-chamber. Used as conso-

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[1] *Op. cit.*, p. 93.

[2] Sewall and Pollard: *Journal of Physiology*, 1890, vol. xi., p. 159.

[3] Grützner: *op. cit.*, p. 196.

[4] *Op. cit.*, p. 197.

nants, as in *make* and *no, m* and *n* are seen to have the characters of the second group,—Explosives. *L* is pronounced somewhat like *n*, but air is allowed to escape through the mouth on each side of the tongue; it may be produced either with voice or without voice (in whispers). It may have vowel characters as in *play*. *R* is characterized as a *vibrative* and may have several seats of articulation, as by the thrill of the tip of the tongue against the hard palate, or that of the hind part of the tongue against the soft palate, or even by the coarse vibration of the vocal cords themselves. In the first two cases it may be sounded either with or without voice. Its vowel nature is shown in such words as *pray*.

2. *Explosives*, which are produced either when an obstruction is suddenly offered to or removed from the exit of air from the mouth; at the same time a characteristic noise is produced. They may be subdivided according to the place of articulation into *labials* (*p*, *v*); *linguo-palatals* (*t*, *d*); *gutturals* (*k*, *g*). The similarity in the method of formation of *p* and *b*, *t* and *d*, *k* and *g*, is striking. They are frequently characterized as being formed *with* or *without* voice; that is, *b*, *d*, and *g* require voice for their distinct recognition, and when whispered they are easily mistaken for *p*, *t*, *k*, which latter do not require voice (vibration of the vocal cords) for their recognition. A consonant, then, is said to be formed *with voice* when it can be rendered distinctly only by an accompanying vibration of the vocal cords, *without voice* when articulated clearly without laryngeal aid. The former are sometimes called *sonants*, the latter *surds*. This classification only approximates the truth, for the suddenness and energy with which the obstruction to the breath is removed determines our recognition of the consonant irrespective of voice.[1]

Table of Consonantal Elements.[2]

PLACE OF ARTICULATION.	ORAL.				NASAL.
	Momentary.		Continuous.		Continuous.
	Surds (without voice).	Sonants (with voice).	Surds (without voice).	Sonants (with voice).	Sonants (with voice).
Lips	p	b	. . . . . .	w	m
Lips and teeth	. . . .	. . . . . .	f	v	
Tongue and teeth	. . . .	. . . . . .	th(in)	th(y)	
Tongue and hard palate (forward)	t	d	s	z, r	n
Tongue and hard palate (back)	ch	j	sh	zh, r	
Tongue, hard palate, and soft palate	. . . .	. . . . . .	. . . .	y, l	
Tongue and soft palate	k	g	. . . .	. . . . . .	ng
Various places	h				

3. *Friction* sounds or *frictionals*, often called *aspirates*, are all noises produced by the expired blast passing through a constriction in its passage, at which point a vibration is set up. No obstruction being offered to the sound, they are known as *continuous* as distinguished from the *momentary* sounds of

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[1] Grützner, *op. cit.*, pp. 211, 213.

[2] *Webster's International Dictionary*, 1891, p. lxvi.

group 2. They may be divided into *labio-dental frictionals, f* (without voice); *v, w* (with voice); the *lingual frictionals s, th* (as in *them*); *sh, ch* soft (without voice); *z, j* (with voice). The sound of *h* may be regarded as due to the vibration of the separated vocal cords. It is peculiar, however, in appearing to be formed in any part of the vocal chamber; when it is formed the mouth parts take on no peculiar position, but assume that of the vowel following the *h*, as *hark*, *hear*, etc.

V. REPRODUCTION.

The principles and problems of Physiology that have been already presented in this work, comprising nutrition and the functions of the muscular and the nervous systems, have reference to the individual man or woman. Through the normal activity of those functions and their appropriate coördination the individual lives his daily life and performs his daily tasks as an independent organism. But man is something more than an independent organism; he is an integral part of a race, and as such he has the instincts of racial continuance. The continuance of the race is assured only by the production of new individuals, and the strength of the human reproductive instinct is indicated in some measure by the large proportion of energy that is expended by woman in the bearing of children and by both sexes in the nurture and education of the young. The function of reproduction is not limited to the daily life and well-being of independent organisms. It has a deeper significance than that. Its essence lies in the fact that it has reference to the species or race. Many of its problems are, therefore, broad ones; they include not only the immediate details of individual reproduction, but larger ones relative to the nature and significance of reproduction and of sex, and to heredity. In the following discussion, while attention will be given chiefly to the facts of individual reproduction, some of the broader applications of the facts will be indicated.

A. REPRODUCTION IN GENERAL.

In all forms of organic reproduction the essential act is the separation from the body of an individual, called the parent, of a portion of his own material living substance, which under suitable conditions is able to grow into an independent adult organism.

Among living beings two methods of reproduction are recognized, the asexual and the sexual methods. Both are widespread among animals and plants, but the asexual method is the more primitive of the two and is relatively more frequent in low organisms. The sexual method, the only one present in the production of new individuals among the higher animals, has evidently been acquired gradually, and has probably been developed from the asexual method.

Asexual Reproduction.—Asexual reproduction, or *agamogenesis*, is the chief method of reproduction among unicellular plants and animals, and throughout the plants and in the lower multicellular animals it is important. Among various species it takes various forms, known as fission or division, gemmation or budding, endogenous cell-formation or spore-formation or multiple fission; but all the varieties are modifications of the simplest form, fission or division. In fission, found only in unicellular organisms and typified in *Amœba*, the protoplasm of the single cell, together with the nucleus, becomes divided into two approximately equal portions which separate from one another. In the process no material is lost, and two independent nucleated organisms result, each approximately half the size of the original. The parent has become bodily transformed into the two offspring, which have only to increase in size by the usual processes of assimilation in order themselves to become parents. In higher organisms, even where sexual processes alone prevail in the production of new individuals, the asexual method has persisted in the multiplication of the individual cells that constitute the body; embryonic growth is an asexual reproductive process, a continued fission, differing from the amœboid type in the facts that the resulting cells do not separate from one another to form independent organisms, but remain closely associated, undergo morphological differentiation and physiological specialization, and together constitute the individual. Likewise in the adult the production of blood-corpuscles and of epidermis, the regrowth of lost tissues, and the healing of wounds are examples of asexual cell-reproduction. From the standpoint of multicellular growth Spencer and Haeckel have happily termed the process of asexual reproduction in unicellular organisms "discontinuous growth."

Sexual Reproduction.—Sexual reproduction, or *gamogenesis*, occurs in unicellular organisms, where it is known as conjugation, and it is the prevailing form of reproduction in most of the multicellular forms. In most of the invertebrate and vertebrate animals it is the sole form of reproduction of individuals. In its simple form of conjugation, typified in the minute monad, *Heteromita*, it consists of a complete fusion of the bodies of two similar individuals, protoplasm and nuclei, followed by a division of the mass into numerous spore-like particles, each of which grows into an adult *Heteromita*. In the higher infusorian, *Paramœcium*, the fusion of the two similar individuals is a partial and temporary one, during which a partial exchange of nuclear material takes place; this is followed by separation, after which each individual proceeds to live its ordinary life and occasionally to multiply by simple fission.

In the highly specialized sexual reproduction of higher animals, including man, the individuals of the species are of two kinds or sexes, the male and the female, with profound morphological and physiological differences between them; in each the protoplasm of the body consists of two kinds of cells, somatic cells and germ-cells, the former subserving the nutritive, muscular, and nervous functions of daily life, the latter subserving reproduction. The germ-cells of the male, called *spermatozoa*, are relatively small and active, those of the female, called *ova*, are relatively large and passive; the reproductive process consists of a fusion of a male and a female germ-cell, the essential part being a fusion of their nuclei; and this is followed by continued asexual cell-division and growth into a new individual. Among both plants and animals it is not difficult to find a series of forms showing progressively greater and greater deviations from the typical asexual toward the typical sexual method of reproduction, and the existence of such a series is indicative of the derivation of the latter from the former type.

Origin of Sex, and Theory of Reproduction.—It is obvious that the production of new individuals is necessary to the continued existence of any species. It would be interesting to know the origin and significance of the two existing methods of reproduction. Apropos of the asexual process, Leuckart, and especially Herbert Spencer, have pointed out that during the growth of a cell the mass increases as the cube, but the surface only as the square, of the diameter—*i. e.* the quantity of protoplasm increases much more rapidly than the absorptive surface. It follows from this that during the growth of a unicellular organism a size will ultimately be reached beyond which the cell will not be able to absorb sufficient food for the maintenance of the protoplasm. In order that growth may continue beyond this point, a division of the cell, which ensures a relative increase of surface over mass, is absolutely necessary. Fission is, therefore, a necessary corollary of growth, and, although we are ignorant of the details of its mechanism, it is conceivable that the method of asexual reproduction arose through causes connected with growth.

The explanation of sexual reproduction is much more difficult, for here, in addition to the budding off of the germ-cells from the parental bodies, which has probably the same fundamental cause as fission in unicellular forms, we must account for the differentiation into sexes, the existence of special sexual cells, and the fusion of the male and the female germinal substance; in short, we must account for the conception of sexuality itself and all that it implies.

Regarding the origin of sexuality itself, as to the question whether sexuality is an original and fundamental attribute of protoplasm or has been acquired, we may say at once that at present we know really nothing. Yet, whatever view is held as to the origin of sexuality, it seems entirely probable that the method of reproduction known as sexual is a derivative of the method known as asexual—the latter is primitive, the former has arisen from it. From the wide distribution and prominence of the former among vital phenomena we must believe, with biologists generally, that sexual differentiation and sexual processes have arisen from natural causes, and for the reason that sexual reproduction is of advantage to living beings and to species. In what way it is of advantage, however, is disputed. Three views, all of which have evidence in their favor and which are not mutually exclusive, are at present engaging the attention of scientific men. The first to be mentioned is the theory advocated by Hensen, Edouard van Beneden, and Bütschli, according to whom the fusion of the cells in sexual reproduction exists for the purpose of rejuvenating the living substance. The power possessed by cells of dividing asexually is limited; in time the protoplasm grows old and degenerates; its vital powers are weakened, and without help the extinction of the race must follow. But the mingling of another strain with such senescent protoplasm gives it renewed youth and vigor, restores the power of fission, and grants a new lease of life to the species. From his observations upon the Infusoria, Maupas[1] has brought forward valuable evidence which has been quoted in favor of this view. *Stylonychia* normally produces by fission 130 to 180 generations or individuals, *Onychodromus* 140 to 230, and *Leucophrys patula* 300 to 450, after which conjugation is necessary to continued division. If conjugation be prevented, the individuals become small, their physiological powers become weakened, their nuclei atrophy, and the chromatin disappears; all of which changes are evidence of the oncoming of senile degeneration, and this ultimately results in death. Analogous to this is doubtless the fact, pointed out by Hertwig,[2] that in sexual animals an unfertilized ovum within the oviduct soon becomes over-mature and enfeebled, and subsequent fertilization, even though possible, is abnormal. Even if the idea of "rejuvenescence" be regarded as fanciful and as a comparison rather than an explanation, it seems to be a principle of nature that occasional fusion of one line of descent with another is necessary to continued reproduction and continued life.

A second theory, defended by Hatschek and Hertwig, argues that sexual reproduction prevents variation, and thus preserves the uniformity of the race. The mingling of two different individuals possessing different qualities must give rise to an individual intermediate between the parents, but differing from them. Such differences between parents and offspring are numerous, but in a single generation are minute, and they are easily obliterated by a subsequent union, which latter in turn gives rise to other minute differences. Hence sexual reproduction, although constantly producing variations, as constantly eradicates them, and, by striving always toward the mean between two extremes, tends toward homogeneity of the species. The essential truth of such a view seems obvious.

A third theory, advocated by Weismann and Brooks, is quite the opposite of the last, and maintains that the meaning of sexual reproduction lies in the production of variations. "The process furnishes an inexhaustible supply of fresh combinations of individual variations." These minute variations, seized upon by natural selection, are augmented and made serviceable, and a variety, better able to cope with the conditions of existence, results. The transformation, not the homogeneity, of the species is thereby assured. The two latter views are not necessarily mutually exclusive. Both claim that fertilization brings into evidence variations. It is quite conceivable that subsequent fertilizations may obliterate some and augment others, the result of union being the algebraic sum of the characteristics contributed by the two sexes.

Primary and Secondary Characters.—In the human species, as in all the higher sexual animals, the characters of sex, anatomical, physiological, and psychological, are divisible into two classes, called primary and secondary. Primary sexual characters are those that pertain to the sexual organs themselves and to their functions. They are naturally the most pronounced of all

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[1] E. Maupas: *Archives de Zoologie expérimentale et générale*, 2e série, vii., 1889.

[2] O. und R. Hertwig: *Experimentelle Studien am thierischen Ei vor, während und nach der Befruchtung*, i., 1890.

sexual attributes. Secondary sexual characters comprise those attributes that are not directly connected with the sexual organs, but that, nevertheless, constitute marked differences between the sexes; such are the greater size and strength of man's body as compared with woman's, the superior grace and delicacy of woman's movements, the deeper, rougher voice of man, and the higher, softer voice of woman. In reality, all secondary sexual characters are accessory to the primary ones, and the greater portion of the present article will be devoted to a discussion of the latter. The primary sexual characters of the male centre in the production of spermatozoa and the process of impregnation, those of the female in the production of ova and the care of the developing embryo.

Sexual Organs.—Sexual organs are classified into essential and accessory organs. The essential organs are the two *testes* of the male and the two *ovaries* of the female. The accessory organs of the male comprise the *vasa deferentia*, the *seminal vesicles*, the *urethra*, the *penis*, the *prostate gland*, *Cowper's glands*, and the *scrotum* and its attached parts. The accessory organs of the female comprise the *oviducts* or *Fallopian tubes*, the *uterus*, the *vagina*, the various external parts included in the *vulva*, and the *mammary glands*. During the greater part of life the sexual organs perform but a portion of their duties; only at intervals, and in some individuals never, do they complete the cycle of their functions by engaging in the reproductive process itself. In the following account we shall discuss first the habitual physiology of the organs of the male and of the female, and later their special activities in the reproductive process.

B. The Male Reproductive Organs.

The male reproductive organs, already mentioned, have as their specific functions the production of the essential male germ-cells, the spermatozoa, the production of a fluid medium in which the spermatozoa can live and undergo transportation, the temporary storing of this seminal fluid, and its ultimate transference to the outside world or to the reproductive passages of the female.

The Spermatozoon.—Spermatozoa were first discovered by Hamm, a student at Leyden, in 1677. Hamm's teacher, Leeuwenhoek, first studied them carefully. They were long believed to be parasites, even until near the middle of the present century, when their origin and fertilizing function were established. Spermatozoa are cells modified for locomotion and entrance into the ovum. Human spermatozoa are slender, delicate cells, averaging 0.055 millimeter ($\frac{1}{450}$ of an inch) in thickness, and consisting of a head, a middle-piece, and a tail (Fig. 218). The *head* (*h*) is flattened, egg-shaped, with a thin anterior edge and often slightly depressed sides. It terminates anteriorly in a slender, projecting, and sharply pointed thread or spear. It consists of a nucleus composed of a dense mass of chromatin and covered by an excessively thin layer of cytoplasm. von Bardeleben[1] claims the number of chromosomes in the chromatin after maturation to be eight.

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[1] K. v. Bardeleben: *Verhandlungen der anatomischen Gesellschaft; Anatomischer Anzeiger;* 1892, vii.

The *middle-piece* (*m*) is a short, cytoplasmic rod, probably containing a centrosome. The *tail* (*t*) is a delicate filiform, apparently cytoplasmic structure, and analogous to a single cilium of a ciliated cell. The tail is tipped by an excessively fine, short filament, the *end-piece* (*e*). The most abundant of the solid chemical constituents of the spermatozoon is nuclein, probably in the form of nucleic acid, which is found in the head. Other constituents are proteids, protamine, lecithin, cholesterin, and fat.

Fig. 218.—Human spermatozoa (after Retzius): *A*, seen *en face*; *h*, head; *m*, middle piece; *t*, tail; *e*, end-piece; *B*, *C*, seen from the side.

The structure and power of movement of the spermatozoon plainly show it to be adapted to activity. It is not burdened by the presence of food-substance within its protoplasm. It is the active element in fertilization; it seeks the ovum, and it is modified from the form of the typical cell for the special purpose of fertilization. The nucleus is the fertilizing agent. The head is plainly fitted for facilitating entrance into the ovum. The tail is a locomotor organ capable of spontaneous movements, and, after expulsion of the semen, it propels the cell, head forward, through the liquid in which it lies. The movement is a complex one, and is effected by the lashing of the tail from side to side, accompanied by a rotary movement about the longitudinal axis. The rate of movement has been variously estimated at from 1.2 to 3.6 millimeters in the minute. Spermatozoa taken directly from the testis are quiescent; normally they begin to move when mixed with the secretions of the accessory sexual organs.[1] Toward heat, cold, and chemical agents spermatozoa behave like ciliated cells.

Ripe spermatozoa appear to be capable of living for months within the male genital passages, where they are probably quiescent. Outside of the body they have been kept alive and in motion for forty-eight hours. It is not certain how long they may remain alive within the genital passages of the human female. Dührssen[2] claims to have found motile spermatozoa in the oviduct at least three and one half weeks after coition. It seems not improbable that within the female organs their environment is favorable to a somewhat prolonged existence. In this connection it is of interest to know that spermatozoa capable of fertilizing have been known to live within the *receptaculum seminis* of a queen bee for three years.

Spermatozoa are produced in large numbers. Upon the basis of observations in several individuals, Lode[3] computes the average production per week as 226,257,000, and in the period of thirty years from twenty-five to fifty-five years of age the total production as 339,385,500,000. This excessive production is an adaptation by nature that serves as a compensation for the

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[1] Cf. Walker: *Archiv für Anatomie und Physiologie*, Anatomischer Abtheilung, 1899, S. 313.

[2] Dührssen: *Centralblatt für Gynäkologie*, 1893, xvii. S. 592.

[3] A. Lode: *Pflüger's Archiv für die gesammte Physiologie*, 1891, l.

small size of the cells and the small chance, of every cell finding an ovum. Without large numbers fertilization would not be ensured and the continuance of the species would be endangered.

Maturation of the Spermatozoon.—Considerable theoretical interest attaches to the question of the real morphological value of the spermatozoon. It is undoubtedly a cell, and has arisen by division from one of the testicular cells, called the spermatocyte or sometimes the mother-cell of the spermatozoon. But is it the morphological equivalent of one of the mother-cells? In most animals, and probably also in man, each spermatocyte gives rise to four spermatids, which grow directly into four spermatozoa. The process of derivation of the spermatozoa may be called, by analogy with the process in the ripening of the ovum, *maturation.* The details and essence of the process have been much discussed. Van Beneden found in an interesting worm, *Ascaris,* that the number of chromosomes in the nucleus of a single spermatozoon is only half that in the original testicular cell; that is, the process of maturation of the spermatozoon consists in a reduction of the chromosomes by one-half. This discovery has since been extended to many other forms, including mammals and man,[1] and it has been shown further that the mature spermatozoon contains only one-half of the number of chromosomes characteristic of the tissue-cells of the species in question. In the light of the subsequent process of fertilization these facts are interesting. Following Hertwig and Strasburger, who regard the chromatic substance of the nucleus as the bearer of the hereditary qualities, many biologists now interpret this halving of the chromatin as a provision for the reduction of the hereditary mass, which later will be restored to its full amount by union with the egg. As we shall see, the maturation of the ovum follows a somewhat similar course, and, since the process has been more fully studied there, we shall reserve further discussion until that subject is reached (p. 451).

Semen.—Semen consists of spermatozoa, together with liquid and dissolved solids, coming partly from the testes themselves, but secreted chiefly by the accessory sexual glands—namely, the glands within the *vasa deferentia,* the seminal vesicles, the prostate gland, and Cowper's glands. It is a whitish, viscid, alkaline fluid, with a slight characteristic odor. The amount passed out at any one time has been estimated at between 0.5 and 6 cubic centimeters. Its chemical composition has not been examined exhaustively. Besides water, it contains approximately 18 per cent. of solid substances, which comprise nuclein, protamine, proteids, xanthin, lecithin, cholesterin, and other extractives, fat, and sodium and potassium chlorides, sulphates, and phosphates. Under proper treatment colorless crystals, called Böttcher's crystals, may be obtained from semen. They appear to be a phosphate of a nitrogenous base, which has been called *spermine.* Interest in the semen centres in its histological rather than its chemical features. The fluid portion serves as a vehicle for the transportation of and possibly also for the nutrition of the ripe spermatozoa. Colorless particles, called

[1] v. Bardeleben: *loc cit.*

seminal granules, exist in semen. They are possibly parts of nuclei of disintegrated cells. Comparatively little is known of the composition or the specific function of the individual secretions contributed by the various organs. The disintegration of the nutritive cells of the testis probably furnishes some of the nutritive substance of the liquid. Prostatic secretion is viscid, opalescent, and usually alkaline, and contains 1.5 per cent. of solids, comprising mainly proteids and salts. It contributes at least a portion of the substance of Böttcher's crystals to the semen, and their partial decomposition is said to be responsible for the characteristic odor of the seminal fluid. The secretion from the seminal vesicles is fairly abundant, is albuminous, and in some animals at least, such as the rodents, seems to contain fibrinogen. This enables the fluid to clot after its reception in the female passages, and thus to prevent loss of spermatozoa. Camus and Gley[1] find that this coagulation is caused by a specific ferment present in the prostatic fluid. Cowper's glands secrete a mucous fluid. By careful experiments upon white rats Steinach[2] has shown that removal of the seminal vesicles and the prostate gland, while not diminishing sexual passion and the ability to perform the sexual act, including the actual discharge of spermatozoa, prevents entirely the fertilization of the ova; removal of the seminal vesicles alone markedly weakens the fertilizing power of the semen. Under normal circumstances the secretions of these accessory glands are essential to the motility of the spermatozoa,[3] and they may have other important functions. Ivanoff,[4] however, has been able to impregnate dogs, rabbits, and guinea-pigs artificially by injecting into the vagina spermatozoa taken directly from the epididymis and mixed with a 0.5 per cent. solution of sodium carbonate.

The Testis.—The testes (Fig. 219, *t*) are compound tubular glands with a unique structure. Formed early in embryonic life as solid structures, with the seminiferous tubules (*ts*) represented by solid cords of cells, they remain in the embryonic condition until the time of puberty. Some of the cells, the mother-cells of the spermatozoa, then begin actively to divide, and the result of division with differentiation is the mature spermatozoa. These latter accumulate at the centre of the tubules, the walls being formed largely of the dividing cells or immature spermatozoa. Other cells do not produce spermatozoa, but seem to disintegrate and give rise to the nutritive fluid and nuclear particles that are found mixed with the sperm-cells. From the time of puberty on, usually throughout life, this cellular activity proceeds, the rate and regularity probably varying greatly with individuals and depending largely on the frequency of discharge of the semen. Spermatozoa may be wanting in old men, but they have been found in individuals at eighty or ninety years of age. The spermatozoa accumulate within the seminal

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[1] Camus and Gley: *Comptes rendus de la Société de Biologie*, 1896, p. 787, and 1897, p. 787.

[2] E. Steinach: *Pflüger's Archiv für die gesammte Physiologie*, 1894, lvi. Cf. also Rehfisch: *Deutsche medicinische Wochenschrift*, 1896, xxii. S. 245; and Lode: *Sitzungsber. d. Kais. Akad. d. Wiss. Wien. Math. naturw. Cl.*, 1895, civ., Abth. iii.

[3] Cf. Walker: *Archiv für Anatomie und Physiologie*, Anatomischer Abtheilung, 1899, S. 313.

[4] Ivanoff: *Journal de Physiologie et de Pathologie générale*, 1900, ii. p. 95.

tubules, and by the constant formation of others behind them are gradually pushed outward along the ducts.

The Ducts of the Testis.—The ducts of the testis (Fig. 219) comprise a succession of tubes of different morphological and physiological values. They are approximately twenty-five feet in length, and are named, in order, *tubuli recti, rete vasculosum, vasa efferentia, canal of the epididymis, vas deferens,* and *ejaculatory duct.* The *tubuli recti* (*tr*) and *rete vasculosum* (*rv*), being mere channels for the passage of spermatozoa, present no special physiological features. The *vasa efferentia* (*ve*) and the *canal of the epididymis* (*e*) contain smooth muscular tissue in their walls, and, moreover, are lined by ciliated epithelium, the cilia causing a movement outward; both of these features doubtless aid in the outward passage of the spermatozoa. The excretory duct of the testis, or *vas deferens* (*vd*), with its offshoot, the seminal vesicle, is more important physiologically. It is nearly two feet in length, with a diameter throughout the greater part of its course of one-tenth of an inch. Near its termination, however, it is larger and sacculated, and resembles the seminal vesicle; it is known here as the *ampulla of Henle.* Its epithelium is not ciliated, but its walls contain a very thick, plain muscular layer consisting of outer longitudinal and inner circular fibres. In the walls of the ampulla of Henle exist small tubular glands. The *vas deferens* is an important storehouse for the spermatozoa. The glands near its termination supply a part of the liquid of the semen. The muscles in its walls, by contracting, aid in the seminal discharges. The *seminal vesicle* (*vs*) is a branched diverticulum from the vas deferens. In structure it is not radically unlike the ampulla of Henle, its walls containing muscular layers and glands. An important function is to contribute liquid to the semen. Of all the organs the seminal vesicles contribute probably the greatest share of liquid. Microscopic examination has somewhat weakened the old belief that the vesicles are storehouses for spermatozoa, but Rehfisch[1]

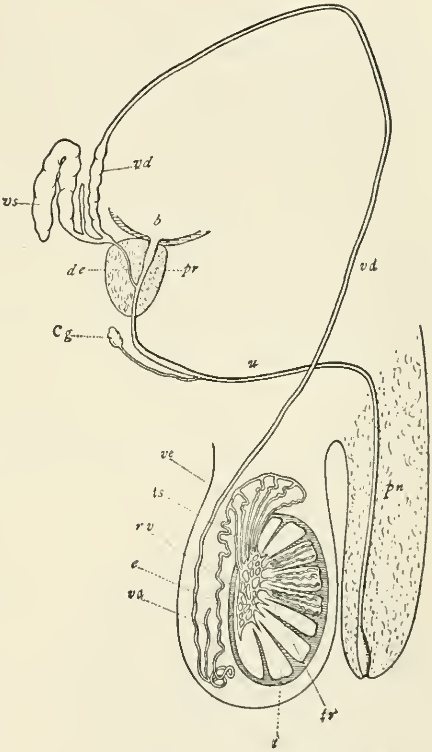

FIG. 219.—Diagram of the male productive organs; *t*, testis; *ts*, seminiferous tubules; *tr*, tubuli recti; *rv*, rete vasculosum; *ve*, vasa efferentia; *e*, canal of the epididymis; *va*, vas aberrans; *vd*, *vd*, vas deferens; *vs*, seminal vesicle: *de*, ejaculatory duct; *pr*, prostate gland; *b*, urinary bladder; *Cg*, Cowper's gland; *u*, urethra; *pn*, penis.

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[1] Rehfisch: *Deutsche medicinische Wochenschrift*, 1896, xxii. S. 245.

finds the anatomical relation of the vesicle to the vas deferens in the human being to be such that liquids injected into the testicular end of the vas deferens pass first into the vesicle before going out the urethra; and he believes strongly that the vesicles exert the double function of serving as storehouses for spermatozoa and finding liquid for the semen. The *ejaculatory duct* (*de*) on each side is a short, thin-walled muscular tube, passing partly through the substance of the prostate gland and serving to convey the semen to the urethra.

The Urethra.—The *urethra* (Fig. 219, *u*), the common excretory duct for the urine and the semen, is commonly described as consisting of three parts, named, respectively, the prostatic, the membranous, and the spongy portions. The first is characterized by the presence of the prostate gland, the second by the absence of special features, and the third by the presence of Cowper's glands and the penis. Throughout its length the wall of the urethra contains plain muscular tissue arranged longitudinally within and circularly without; and, except at the external opening, the small racemose mucous *glands of Littré.* Its wall is hence contractile and its lumen is kept moist. Beyond these its special physiological features are given it by the organs above mentioned.

The Prostate Gland.—The *prostate gland* (Fig. 219, *pr*) is a compound tubular gland whose alveoli are mingled with a large quantity of plain muscular tissue. It completely surrounds the urethra at the base of the bladder, and opens into it by numerous small ducts situated about the openings of the *vasa deferentia.* Its function is to contribute prostatic fluid to the semen. The composition of this fluid and its specific use so far as it is known have been already mentioned (p. 446).

Cowper's Glands.—*Cowper's glands* (Fig. 219, *Cg*), two in number, are tubulo-racemose glands, the ducts of which open into the spongy portion of the urethra by two orifices situated some two inches below the openings of the *vasa deferentia.* Their viscid secretion is thought to be one of the components of the seminal fluid, but its specific function is unknown. It has been suggested that Cowper's fluid cleanses the urethra of urine and of semen, instead of contributing actually to the seminal fluid.

The Penis.—The *penis* (Fig. 219, *pn*) has as its constant function merely the conveying of the urine to the outside world, and for this purpose it has no special features beyond those belonging to the urethra, which runs throughout its whole length. Specifically, however, it is the intromittent organ, and serves to convey the semen into the genital passages of the female. This function is based upon its power of erection, and this power is dependent upon the presence of the erectile tissue which constitutes the bulk of the organ. The erectile tissue is arranged in the form of three long cylindrical masses imperfectly separated from, but parallel to, one another and extending lengthwise. Of these, the two *corpora cavernosa* lie at the sides, and meet each other in the middle line along the upper side of the penis; the *corpus spongiosum* lies in the middle line below, and is pierced throughout its length by the urethra. At its proximal end each corpus is enlarged into a bulbous part, and is covered by a layer of muscular fibres constituting a distinct muscle—the bulbs of the *corpora cavernosa* by the *ischio-cavernosi* (*erectores penis*), that of the *corpus spongiosum* (called *bulbus urethræ*), by the *bulbo-cavernosus* (*accelerator urinæ*). At its distal end each *corpus cavernosum* terminates bluntly, while the *corpus spongiosum* projects farther and enlarges to form the extremity of the organ, the *glans penis*. Each corpus is spongy in consistence, being formed of a trabecular framework of white and elastic connective tissue and plain muscular fibres, with cavernous venous spaces, and it is covered by a tough fibrous tunic. When the spaces are distended with blood the whole organ becomes hard, rigid, and erect in position. The mechanism of erection will be studied more in detail later (p. 463). The penis, especially toward its termination, is beset with end-bulbs, Pacinian bodies, and other nerve-terminations, which make it particularly sensitive to external stimulation.

C. THE FEMALE REPRODUCTIVE ORGANS.

The female reproductive organs, already mentioned, have as their specific functions the production of the essential female germ-cells, the *ova*, and their transference to the uterus, and, if unfertilized, to the outside world; if the ova are fertilized, other specific functions are the protection and nutrition of the developing embryo, its ultimate transference to the outside world, and the nutrition of the child during early infancy.

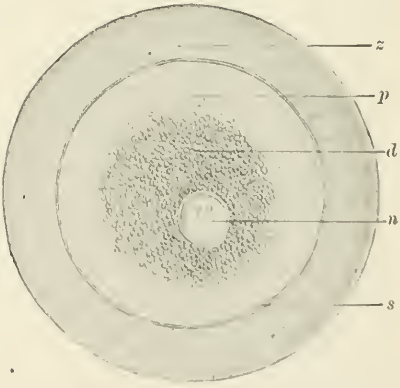

FIG. 220.—Human ovum (modified from Nagel): *n*, nucleus (germinal vesicle) containing the ameboid nucleolus (germinal spot); *d*, deutoplasmic zone; *p*, protoplasmic zone; *z*, zona radiata; *s*, perivitelline space.

The Ovum.—The human ovum was discovered in 1827 by von Baer, and it was he who first completely traced the connection between ova in the generative passages and ova in the Graafian follicles of the ovary. The conception of ova as the essential female element had, however, long been held, and Harvey's dictum of the seventeenth century, that everything living is derived from an egg (*omne vivum ex ovo*), is well known. The human ovum, as it comes from the ovary, is a spherical, protoplasmic cell (Fig. 220), averaging with the *zona radiata*, approximately 0.2 millimeter ($\frac{1}{127}$ inch) in diameter. As in other cells, the cell-body may be distinguished from the nucleus, the protoplasm of the former being called *cytoplasm*. In its finer structure the cytoplasm consists of an excessively delicate network of protoplasmic substance. As in other mammalian eggs, it probably contains, adjoining the nucleus, a minute, specially differentiated portion, consisting of a single or double *centrosome* surrounded by an *attraction sphere* (Fig. 221, *A*). For some distance inward from the border the cytoplasm is pure and transparent, and this portion is often called the protoplasmic zone

(Fig. 220, *p*). Throughout the centre of the cell, however, it is obscured by the presence of an abundance of yolk-substance, or *deutoplasm*, from which the corresponding part of the ovum is sometimes called the deutoplasmic zone (*d*). Deutoplasm is non-living substance; it consists of granules of yolk imbedded in the meshes of the cytoplasmic network, and, like its analogue, the yolk of the hen's egg, it serves as food for the future cells of the embryo.

A comparison of the respective amounts of food in the human and the fowl's egg, with the manner of embryonic development, is suggestive. The chick develops outside the body of the hen, and, therefore, requires a large supply of nutriment, which it finds in the yolk and the white of the egg. The child develops within the mother's body and receives its nourishment from the maternal blood; hence the supply of food within the egg is only enough to ensure the beginning of growth, special blood-vessels being formed to facilitate its continuance.

The *nucleus* (*n*), frequently called by its early name, the *germinal vesicle*, is spherical, and usually occupies a slightly eccentric position. Its protoplasm consists of a network composed of two kinds of material: the more delicate, slightly staining threads are the *achromatic substance*, the coarser, deeply staining portion, the *chromatic substance* or *chromatin*. The former is continuous with, and probably of exactly the same nature as, the cytoplasm. The chromatin is peculiar to the nucleus, and at certain stages in the nuclear history is resolved into distinct granules or filaments, the *chromosomes* (Fig. 221, *A*), the number of which in the human ovum before maturation is thought to be sixteen. There is every reason for believing that the chromatin is the bearer of whatever is inherited from the mother. The nucleus is limited by a nuclear membrane, and contains a strongly marked *nucleolus*, which has likewise retained its original name of *germinal spot*. There is probably no proper cell-wall, or *vitelline membrane*, such as is said to exist in many mammalian and other eggs. The ovum is, however, surrounded by a thick, tough, transparent membrane of ovarian origin, about 0.02 millimeter ($\frac{1}{1270}$ inch) in thickness, and called the *zona radiata* or *zona pellucida* (Fig. 220, *z*). It is pierced by a multitude of fine lines radiating from the surface of the zona to the ovum; these are thought to represent pores, to contain fine protoplasmic processes of the surrounding ovarian cells, and thus to serve as channels for the passage of nutriment to the egg. Between the *zona radiata* and the ovum a narrow space, the perivitelline space (*s*), exists. Attached to the outside of the *zona radiata* are usually patches of cells derived from the *discus proligerus* of the Graafian follicle of the ovary, which may form a complete covering and constitute the *corona radiata*. They disappear soon after the egg is discharged from the ovary.

Regarding the chemistry of the mammalian ovum little is known definitely, and of the human ovum nothing whatever except by inference from the eggs of lower animals. The protoplasmic basis undoubtedly resembles other undifferentiated protoplasm in its general composition, with an abundance of proteid among its solid constituents. Deutoplasm is a rich mixture of food-substance in concentrated form, and contains among its solids probably vitellin, nuclein, albumin, lecithin, fats, carbohydrates, and inorganic salts.

The form and the structure of the egg suggest the part that it plays in reproduction. It is not locomotor; in fertilization it is the passive element; it remains in its place and is sought by the spermatozoon. Its nucleus is the equivalent of that of the spermatozoon. Its form renders easy the entrance of the male element. Its bulk consists largely of food in a very concentrated form, and, as development proceeds, it supplies this food to the growing cells.

In lower forms of animal life, where eggs are fertilized outside the body of the parent in the water into which they are set free, they are usually produced in enormous numbers. Some fail of fertilization, while others are destroyed by enemies, and the large number is a compensatory adaptation by nature for their poor chance of survival. In mammals and man, however, ova have a much better opportunity of being fertilized and of developing into adults, and their number is correspondingly reduced. Their relative fewness, as compared with the spermatozoa, is in harmony with their larger size and the fact that, while awaiting fertilization, they are carefully protected within the body of the mother.

Maturation of the Ovum.—Attention has been called to the maturation of the spermatozoon. The ovum undergoes an analogous process of ripening, which has been studied very carefully, and from its theoretical interest has given rise to a large amount of discussion. Maturation begins approximately as the ovum is leaving the ovary, and is not completed until after the ovum has received the spermatozoon, although the exact time-relations in the human species are not yet determined. It consists of a mitotic division of the nucleus, essentially like mitosis (karyokinesis) in ordinary cell-division, and an expulsion of one portion from the cell. This occurs twice in succession. The cast-off bits of protoplasm are known as *polar bodies*. The details of the process of maturation are as follows (Fig. 221): In all animals the nucleus of the ovarian ovum, or oöcyte, at the time of its formation receives from its mother-cell the same number of chromosomes as the ordinary tissue-cells contain. These constitute its chromatic reticulum. As the oöcyte prepares for maturation the chromatin is resolved into masses, the number of which is one-half that of the somatic chromosomes. In a large number of species, such as many of the worms, the insects, and the crustaceans, each chromatic mass constitutes a group of chromosomes, usually four in each group, which is called a "quadruple-group" or "tetrad" (*B*). The number of tetrads is hence one-half the number of original chromosomes, while the total number of chromosomes in the nucleus at this stage is double the original number. The nucleus moves from its position in the interior of the egg toward the surface, and the nuclear membrane begins to disappear. At the same time the two minute cytoplasmic structures, the centrosomes, which lie close beside the nucleus, separate and take up positions at a considerable distance apart from each other, in some cases even upon opposite sides of the nucleus. The

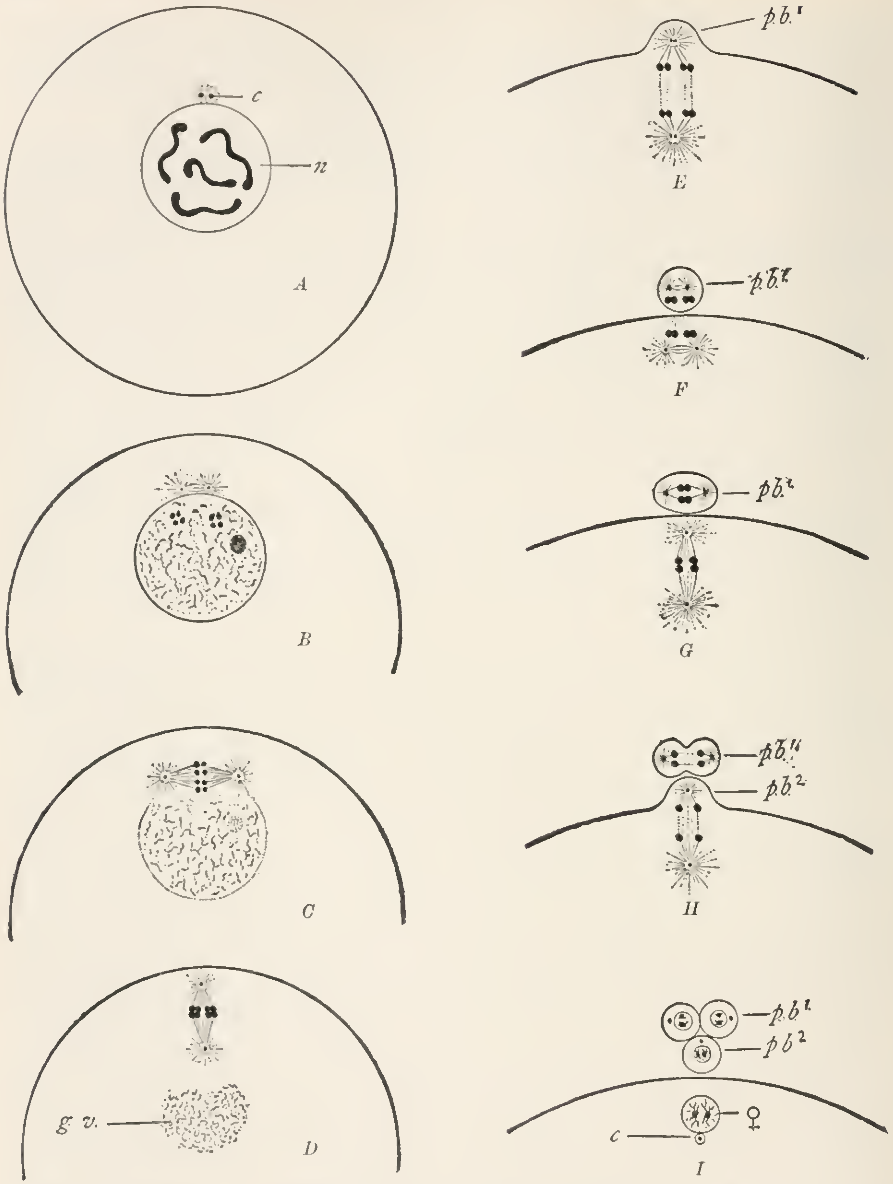

FIG. 221.—Stages in the maturation of the ovum; diagrammatic (mainly from Wilson): *A*, the original ovarian ovum; *n*, its nucleus, containing four chromosomes; *c*, its double centrosome, surrounded by the attraction sphere; in *B* much of the chromatin has begun to degenerate; the rest has become arranged into two quadruple groups of chromosomes, or tetrads; the formation of the spindle and the asters has begun; in *C* the first polar amphiaster, bearing the chromosomes, is completed; in *D* the amphiaster has become rotated and has travelled toward the surface of the ovum; *g. v.* the degenerated remains of the nucleus; in *E* the division of the tetrads into double groups of chromosomes, or dyads, has begun, and the first polar body, $p. b^1$, is indicated; in *F* the first polar body, containing two dyads, has been extruded; the formation of the second polar amphiaster has begun; in *G* the first polar body is preparing to divide; the second polar amphiaster is fully formed; in *H* the division of the dyads into single chromosomes in both the first polar body and the egg has begun, and the second polar body, $p. b^2$, is indicated; in *I* the formation of the polar bodies is completed; ♀, the egg-nucleus, containing two small chromosomes, one-half the original number. In fertilization the spermatozoon will bring in two additional chromosomes, thus restoring the total number of four.

substance lying between them—either the cytoplasmic network or the achromatic substance of the nucleus—loses its reticular appearance, becomes filamentous, and arranges itself in the form of a spindle with the threads extending from pole to pole (*C, D*). The groups of chromosomes become attached to the spindle threads midway between the poles. At each pole there may lie a centrosome, and about it the cytoplasm may become arranged in the form of a star, the *aster*, though these structures are not universal among species. The spindle with the two asters is known as the *polar amphiaster*, and the complicated structure seems to be formed, as in ordinary cell-division, for the sole purpose of dividing the nucleus into two portions. This is now performed (*E*): each quadruple-group of chromosomes splits into two, and these, known as "double-groups," or "dyads," separate from each other and pass toward the poles of the spindle. The nucleus is thus divided into halves. While the division has been proceeding, the spindle has wandered halfway outside the egg, and, when it is completed, one of the resulting nuclear halves, comprising one-half of the full number of dyads, together with the centrosome and the aster, finds itself entirely extruded from the egg and lying within the perivitelline space. It is known as the *first polar body* (*F, p.* b^1). The diminished nucleus within the ovum proceeds at once to undergo a second mitotic division (*G, H, I*); each of the remaining dyads divides into two single chromosomes, which are separated from each other; and a *second polar body* (*p.* b^2), containing one-half the number of single chromosomes characteristic of the tissue-cells, is extruded. Apparently the two polar bodies are of no further use. In many animals the first divides into two, but sooner or later both degenerate and disappear. The remnant of the nucleus left within the egg, much reduced in size, wanders back to the interior. In the mammals no true tetrads are formed, and a considerable interval of time elapses between the formation of the two polar bodies, during which the spermatozoon enters the egg. But in them the process of maturation is the same in essence as in the lower animals. In all species the chromosomes are reduced to one-half the number belonging to the ovarian ovum; in many species they are then resolved again into scattered chromatic substance. The nucleus develops a membrane and again enters the resting stage. It is known henceforth as the *egg-nucleus*, or *female pronucleus*, and it awaits the coming of the spermatozoon. According to most observers, its centrosome gradually degenerates and disappears.

Thus the curious process of maturation of the ovum is different in detail from that of maturation of the spermatozoon. In the latter the spermatocyte divides into four functional spermatozoa; in the former the oöcyte divides into two functionless polar bodies (or, by subdivision of the first, three, which have been called abortive eggs) and one functional ovum. It is entirely probable, however, that the essence of the process is exactly the same in the two cases, and lies in the reduction of the number of the chromosomes. The three important facts have now been demonstrated in a large number of species, viz.—that in the maturation of both the ovum and the spermatozoon the number of chromosomes is halved, that the number in the two mature germ-cells is the same, and that this number is one-half that of the chromosomes of the somatic cells. It is wholly probable that these facts are universal in sexual reproduction. Each mature germ-cell, therefore, while in reality a cell, is, when compared with the somatic cells, incomplete. The subsequent union of the two in fertilization restores the chromosomes to their normal number. Inasmuch as the chromatin is probably the all-important constituent of the germ-cells, the bearer of the paternal and the maternal inherited characteristics, the phenomena of maturation are of great interest. Many biologists follow Hertwig and Strasburger in regarding maturation as an adaptation for the prevention of the constant increase in quantity of the hereditary substance that would otherwise take place with every union of ovum and spermatozoon. Without a reducing process the quantity of chromatin in cells would become in a very few generations inconveniently great. The most striking feature of maturation, however, is the halving of the number of chromosomes. The significance of this is not clear. Nevertheless it is evident that maturation is a preparation of each germ-cell for union with its mate.[1]

The Ovary; Ovulation.—The ovaries (Fig. 222, *o*) are often spoken of as glands, but they are not glands according to the ordinary histological and physiological use of the term. They are solid organs with a structure peculiar to themselves, and their function is the production of ova. Their stroma consists of fine connective tissue with numerous connective-tissue cells. The ova are developed in the interior within cavities called, from their discoverer, *Graafian follicles* (*Gf*), from primitive ova that are modified cells of the germinal epithelium of the embryo. It has been calculated that a single human ovary at the age of seventeen years contains 17,600 primitive ova,[2] but that not more than 400 of these arrive at maturity.[3] Each Graafian follicle is lined by an epithelial layer several cells thick, the *membrana granulosa*, and is filled with a clear, serous, viscid liquid, the *liquor folliculi*. Imbedded in the epithelium upon one side is usually a single ovum, completely surrounded by the cells and forming a prominent hillock which projects well into the cavity of the follicle. The epithelium immediately surrounding the ovum is the *discus proligerus*. Within the discus the ovum grows and becomes surrounded by the *zona pellucida*. In the process of growth the Graafian follicle approaches the surface of the ovary, and finally comes to form a minute rounded vesicular projection covered only by the ovarian epithelium. When fully ready for discharge, the wall of the follicle becomes ruptured, probably by the increasing pressure of the contained liquid, and the ovum with its *zona pellucida* and a portion or all of the *discus proligerus*, now called the *corona radiata*, is cast out upon the surface of the

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[1] For a critical discussion of maturation, see Wilson: *The Cell in Development and Inheritance*, 1900, 2d ed., New York.

[2] Heyse: *Archiv für Gynäkologie*, 1897, liii. S. 321.

[3] Henle: *Handbuch der Anatomie*, 1873.

ovary to be taken up by the Fallopian tube. The empty follicle undergoes changes and becomes the *corpus luteum* (*c.l*). Usually the *corpus luteum* degenerates within a few days and ultimately disappears. If, however, pregnancy follows ovulation, it grows very large, perhaps because of the congested state of the reproductive organs, and remains for months before the retrograde metamorphosis sets in. Not all Graafian follicles reach maturity and burst, for many, after developing to a considerable size, undergo degenerative changes, characterized by liquefaction and disappearance of their contents.

The discharge of the ovum is known technically as *ovulation*. In most animals ovulation is a periodic phenomenon accompanying certain seasons, and is marked by general sexual activity. In woman and many domesticated animals the relation to the seasons no longer exists, but too little is known of the causes and time-relations of the phenomenon and its general bearings upon other physiological processes, notably upon menstruation in woman. A large but not wholly decisive literature upon the subject in the human being has been written. It is a common belief, originating in the seventeenth century, that ovulation in woman is a periodic phenomenon occurring regularly every month and contemporaneous with the occurrence of the menstrual flow, and numerous post-mortem observations of the presence in the ovary of freshly-discharged Graafian follicles at the menstrual period afford evidence of the frequent coincidence of the two phenomena. But ovulation at the time of menstruation, though probably usual, is not exclusive of ovulation at other

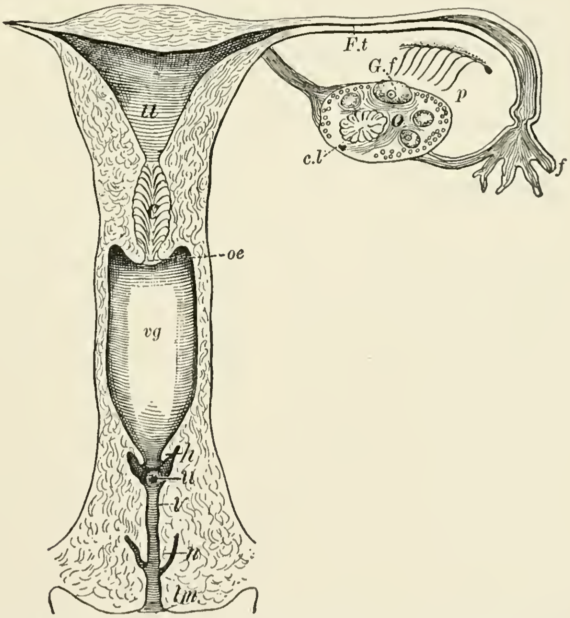

FIG. 222.—Diagram of the female reproductive organs (modified from Henle and Symington): *o*, ovary; *G.f*, Graafian follicle containing an ovum; *c.l*, corpus luteum; *p*, parovarium; *f*, fimbriated end of *F.t*, Fallopian tube; *u*, body, and *c*, cervix of uterus; *o.e*, os uteri externum; *vg*, vagina; *h*, hymen; *u*, opening of urethra; *v*, vulval cleft; *n*, labia minora, or nymphæ; *l.m*, labia majora.

times, for intermenstrual observations of fresh ovarian scars are not rare, and prove without doubt that discharge of an ovum may occur at any time between two successive periods (see under Menstruation, p. 457). Graafian follicles develop even during infancy; most of them, and perhaps all, retrograde without discharging their ova, but the occasional instances of pregnancy at the ages of seven, eight, or nine, prove that ovulation may occur during childhood. Ovulation usually begins at puberty, its commencement thus coinciding with that of menstruation, and continues until the climacteric. After the climacteric it may occur in exceptional cases, although here, as before puberty, retrogressive degeneration of the Graafian follicles is the rule. It is commonly believed that ovulation is at a standstill during both pregnancy and lactation. The undoubted possibility of a pregnancy originating during lactation would, however, seem to prove the possibility of ovulation during the latter period. It is not decided whether removal of the uterus does away wholly with ovulation.

The Fallopian Tube.—Each of the *Fallopian tubes* (Fig. 222, *F. t*), or *oviducts*, opens into the peritoneal cavity about one inch from the corresponding ovary. Around the opening is an expanded fringe of irregular processes, the *fimbriæ* (*f*), one of which is attached to the ovary. The length of the tube is between three and four inches, and the opening into the uterus is extremely small. The chief structures in the walls of the oviducts that are of physiological interest are the double layer of plain muscle, an outer longitudinal and an inner circular coat, longitudinal fibres from which pass also into the fimbriæ; and the cilia with which the tube is lined throughout, and which are present also upon the inner side of the fimbriæ. The direction of the ciliary movement is from the ovary toward the uterus. The primary function of the Fallopian tubes is to convey ova from the ovary to the uterus; they also convey spermatozoa in the reverse direction; and within them the union of ovum and spermatozoon usually takes place.

The mechanism of the receipt of the ovum by the tube is not fully understood. After ovulation the ovum is slightly adherent to the surface of the ovary by the agency of the viscid *liquor folliculi*. It is possible, but it has not been proved, that in the human being, as has been seen in some animals, the expanded, fimbriated end of the Fallopian tube clasps the ovary when the egg is discharged. The passage of the ovum into the tube is probably brought about by the cilia lining the fimbriæ. Once within the tube, the ciliary action, assisted perhaps by contraction of the muscular fibres in the walls, carries the ovum slowly along toward and finally into the uterus. In some mammals the passage occupies three to five days; the time in woman is not definitely known, but is thought to be from four to eight days.

The Uterus.—The *uterus* (Fig. 222, *u*), or *womb*, receives the ovum from the Fallopian tube and passes it on, if unimpregnated, to the vagina; on the other hand, it receives from the vagina spermatozoa and transmits them to the Fallopian tubes; it is the seat of the function of menstruation; when impregnation has taken place, it retains and nourishes the growing embryo, and ultimately expels the child from the body. Its structure accords with these functions. Its thick walls consist largely of plain muscular tissue arranged roughly in the form of three indistinctly marked layers. Of these, the external and the middle coats are thin; the fibres of the former are arranged in general longitudinally, those of the latter more circularly and obliquely. The third, most internal layer, which is regarded by some as a greatly hypertrophied *muscularis mucosæ*, forms the greater part of the uterine wall. Its fibres are arranged chiefly circularly; toward the upper part they become transverse to the Fallopian tubes, and at the cervix longitudinal fibres lie within the circular ones. The individuality of the muscular layers and uniformity in the course of the fibres is largely interfered with by the numerous blood-vessels of the uterine walls. The uterus is lined by an epithelium composed of columnar ciliated cells, except in the lower half of the cervix, where a stratified non-ciliated epithelium exists. The direction of the ciliary movement in woman, as in other mammals, is toward the *os uteri*.[1] The mucous membrane is thick, and contains very numerous, branching, tubular glands, which are lined by ciliated epithelium and have a tortuous course, terminating in the edge of the muscular layer. They secrete a viscid, mucous liquid. Between the glands are branched connective-tissue cells, which are not unlike the connective-tissue cells of embryonic structures, and wandering cells. Lymph-spaces and blood-capillaries exist. The development of the tissue goes on slowly up to the time of puberty, and, as we shall see, after puberty the mucous membrane is subject to constant change.

Menstruation.—Except during pregnancy the most striking activities of the uterus are associated with that peculiar female function which, from its monthly periodicity, is called *menstruation*. The most obvious external fact of this phenomenon is the discharge every month of a bloody, mucous liquid through the vagina; the most obvious internal facts are the bleeding and the degeneration and disappearance of a portion of the mucous membrane of the body of the uterus. This curious process, though having analogies in lower animals, occurs most markedly in the human female, and from before the time of Aristotle to the present, among both primitive and civilized races, its significance has been the cause of much speculation. The detailed phenomena of menstruation are not as well known as they should be. Experimentation is practically out of the question, and the opportunities of careful post-mortem study of normal healthy uteri at different stages are rare. The main facts are as follows:

Some days before the flow occurs the mucous membrane of the body of the uterus begins to thicken, partly by an active growth of its connective tissue elements and partly by an excessive filling of its capillaries and veins with blood. The cause of this swelling is not known. It continues until the membrane has doubled or trebled in thickness, and, according to some authorities, the uterine cavity becomes a mere slit between the walls. Then occurs an infiltration of blood-corpuscles and plasma, probably largely by diapedesis, although possibly assisted by rupture, through the walls of the swollen capil-

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[1] Hofmeier: *Centralblatt für Gynäkologie*, 1893, xvii. S. 764.

laries into the connective-tissue spaces beneath the epithelial lining of the uterine wall. The epithelium is thus pressed up from beneath, and begins rapidly to undergo fatty degeneration in places, and to disappear. The immediate cause of the degeneration is not definitely known. The connective-tissue elements and the upper portion of the glands are involved to some extent in the degenerative change. The capillaries, thus laid bare, burst, and the dark blood oozes forth and, mixed with disintegrated remains of the uterine tissues, with the mucous secretion of the uterus and the vagina, and with the escaped lymph, passes away, drop by drop, from the body. There is great difference of opinion as to the extent of the destruction of uterine tissue. On the one extreme side are those who claim that the loss of tissue is normally wholly trivial and secondary, the hyperæmia and the bloody glandular discharge being the important events. Other authorities, equally extreme, have observed a disappearance of the whole mucous membrane except the deepest layers containing the bases of the glands; this is probably pathological. From all the evidence an opinion inclining toward the former view seems most reasonable—namely, that usually and physiologically only the superficial portion of the mucous membrane disintegrates, and this only in spots.[1] Differences in the amount undoubtedly occur. Occasionally it happens that the membrane, instead of disintegrating, comes away in pieces of considerable size. The term *decidua menstrualis* is applied to the lost coat. The flow continues upon an average four days or more. From observations upon 2080 American women Emmet[2] finds the average duration of the flow at puberty to be 4.82 days, the average in later life 4.66 days. The amount of blood discharged can be determined only with great difficulty. It probably varies greatly, but is commonly estimated at from 100 to 200 cubic centimeters (4 to 5 ounces). The blood is slimy, with abundant mucus; usually it does not coagulate. Epithelium cells, red corpuscles, leucocytes, and detritus from the disintegrated tissues, occur in it, and it has a characteristic odor. As the flow ceases a new growth of connective-tissue cells, capillaries, glands, and from the glands superficial epithelium, begins, and the mucous membrane is restored to its original amount. Whether a resting period follows before the succeeding tumefaction occurs is not definitely known, but it seems probable. The durations of the various steps in the uterine changes are not well known, and probably vary in individual cases. Minot[3] suggests the following approximate times:

Tumefaction of the mucosa, with accompanying structural changes	5 days.
Menstruation proper	4 “
Restoration of the resting mucosa	7 “
Resting period	12 “
Total	28 days.

The menstrual changes in the uterus are accompanied by characteristic phenomena in other parts of the body. The Fallopian tubes are congested,

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[1] See Westphalen: *Archiv für Gynäkologie*, 1896, lii. S. 35; and Mandl: *Ibid.*, S. 557.

[2] T. A. Emmet: *The Principles and Practice of Gynæcology*, 1880, 2d ed.

[3] C. S. Minot: *Human Embryology*, 1892.

and, according to some authorities, their mucous membrane degenerates and bleeds like that of the uterus. The ovaries are likewise congested. As has been stated, it is commonly believed, but not definitely proved, that ovulation accompanies each period. Frequent accompaniments are turgescence of the breasts, swelling of the thyroid and the parotid glands and the tonsils, congestion of the skin, dull complexion, tendency toward the development of pigment, and dark rings about the eyes. The skin and the breath may have a characteristic odor. In singers the voice is often impaired, which is one instance of a general nervous and muscular enervation. Mental depression often exists. Pain is a frequent accompaniment, and nervous and congestive pathological phenomena may, at times, become very pronounced. Recent work has shown that the various phenomena accompanying menstruation are evidences of a profound physiological change, with a monthly periodicity, that the female human organism undergoes, and of which the uterine changes are only a part. Thus, during the intermenstrual period there is a gradual increase of nervous tension and general mobility, of vascular tension manifested by turgescence of the blood-vessels, a gradual increase of nutritive activity manifested by increased production and excretion of urea and increased temperature, and a gradual increase of the heart's action in strength and rate.[1] These various activities of the organism usually attain a maximum a few days before the menstrual flow begins and then undergo a rapid fall, which reaches a minimum toward the close of the flow; a second lesser maximum may occur a few days after the flow ceases. All organic activities that have been carefully investigated show evidences of such a monthly rhythm. It is not known that the male possesses such a period.

The first menstruation is usually regarded as the index of the oncoming of puberty or sexual maturity, and in temperate climates occurs usually at the age of fourteen to seventeen. Its onset is earlier in warm than in cold climates, in city than in country girls, and varies in time with food, growth, and environment. Exceptionally menstruation may begin in infancy or later than puberty, and it has even been known to be wholly wanting in otherwise normal women. Normally, it ceases during pregnancy, and probably usually during lactation, although there are frequent exceptions to the latter rule. In nearly all cases complete removal of the ovaries puts an end to menstruation. Removal of the ovaries and Fallopian tubes diminishes the number of exceptional cases. The final cessation of menstruation, which is a gradual process extending over several months, usually marks the climacteric (menopause), or end of the sexual life, and occurs usually at the age of forty-five to forty-eight. Exceptionally the flow may cease early in life or extend to extreme old age.

Comparative Physiology of Menstruation.—The comparative physiology of menstruation, although it has been studied only incompletely in a few domesti-

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[1] *Cf.* Mary Putnam Jacobi: "The Question of Rest for Women during Menstruation," *Boylston Prize Essay*, 1876; C. Reinl: *Sammlung klinische Vorträge*, 1884, No. 243; O. Ott: *Nouvelles archives d'obstétrique et de gynécologie*, 1890, v.; and A. E. Giles: *Transactions of the Obstetrical Society of London*, 1897, xxxix. p. 115.

cated animals and some monkeys,[1] sheds some valuable light upon the phenomenon in woman. In animals lower than man, in a wild state, the desire and power of reproduction are usually limited to seasonal periods. At such times conception is possible, and probably usually takes place. Such periods are known as "rut," "heat," and "œstrus." During the rest of the year sexual activities are in abeyance. Domestication, with its artificial conditions of regular food-supply, warmth, and care, has increased productiveness (Darwin) and rendered the reproductive periods more frequent. If impregnation be prevented, as is often the case in domesticated animals, the periods of "heat" appear for a while with great frequency and regularity (monkey, mare, buffalo, zebra, hippopotamus, at intervals of four weeks; cow, three weeks; sow, fifteen to eighteen days; sheep, two weeks; bitch, twelve to sixteen weeks). They are characterized by general nervous excitement, desire and power of conception, congestion and swelling of the external genital organs, and a uterine discharge. The latter is scanty, mucous, and bloody, the amount of blood increasing in ascending the evolutionary scale. The histological processes occurring in the uterus have been studied carefully by Retterer in the dog and by Heape in the monkey. In the latter the processes seem to be nearly identical with those of man. In the dog, growth and congestion of the mucosa occur, and are followed by rupture of the capillaries, extravasation of blood, and degeneration of the tissues; but it is doubtful whether the epithelium is actually shed. It is generally believed that "heat" in the lower mammals is accompanied by ovulation. It is not necessarily so in monkeys. The phenomena of "heat" are thus closely similar to those of human menstruation, the similarity being most marked in the monkeys. In addition to these more hidden phenomena there is present sexual desire, which in the human female is largely absent at such periods, although it may be pronounced just before and just after the actual flow.

Theory of Menstruation.—The significance of menstruation is in great dispute. All modern theories agree in regarding it as associated in some way with the function of childbearing. The flow was early believed to be a means employed by the body to get rid of a plethora of nutriment. This was followed by the well-known hypothesis, put forward especially by Pflüger (1865). According to this hypothesis,[2] the menstrual bleeding and the uterine denudation occur for the purpose of providing a fresh uterine surface to which the egg, if impregnated, can readily attach itself, just as, in grafting, the gardener provides a wounded surface upon which the young scion is set, or, in uniting two membrane-covered tissues, the surgeon first wounds or freshens their surfaces. This conception of menstruation is not now commonly accepted. Pflüger regards the mechanism of the uterine process to be as follows: The constant growth of the ovarian cells and the consequent swelling of

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[1] *Cf.* A. Wiltshire: *British Medical Journal,* March, 1883; E. Retterer: *Comptes rendus des séances et mémoires de la société de biologie,* 1892; W. Heape: *Philosophical Transactions of the Royal Society,* 1894, (B), vol. 185, pt. i.; and *Proceedings of the Royal Society,* 1897, lx. p. 202.

[2] E. F. W. Pflüger: *Untersuchungen aus dem physiologischen Laboratorium zu Bonn,* 1865.

the ovary subject the ovarian nerve-fibres, and through them the spinal cord, to a constant slight stimulation. Through the summation of the stimuli within the cord a reflex dilatation of the vessels in the genital organs is produced. The excessive blood-supply leads in turn to the tumefaction of the uterus, and frequently to the ripening of a Graafian follicle. The bleeding follows, and at the same time or slightly later the rupture of the follicle occurs, provided the latter be sufficiently advanced in growth. The menstrual flow and ovulation are, therefore, two phenomena conditioned usually by the same cause, namely, the menstrual congestion, yet either may occur without the other. Pflüger's hypothesis accounts clearly for the absence of menstruation after removal of the ovaries. Numerous other theories have been proposed, no one of which can be said to be widely and generally accepted. The present tendency in belief is as follows : Ovulation and menstruation are in great part independent phenomena ; they may or they may not coexist ; the uterine growth is a preparation for the future embryo ; the tissue of the *decidua menstrualis* is the forerunner of the *decidua graviditatis* (p. 471) ; if an ovum, whenever it is discharged, be fertilized, it attaches itself to the thickened uterine wall, the tissues become the *decidua graviditatis,* pregnancy follows, and the *decidua* is not discharged until the time of parturition ; if, however, fertilization does not take place, there is no attachment, the tissues degenerate and become the *decidua menstrualis,* and the flow occurs. The suggestion of Jacobi[1] is not an extreme one : "The menstrual crisis is the physiological homologue of parturition." Its periodicity, which is approximately that of a tropical month (27.32 days), has been the subject of much hypothesis. In a suggestive paper based upon much careful statistical study Arrhenius[2] ascribes it to the influence of atmospheric electricity, which he finds to undergo a periodic variation of similar length. Regarding the mechanism of menstruation the above hypothesis of Pflüger seems not unreasonable, and, moreover, seems to be supported by the experiments of Strassmann,[3] who by pressure artificially produced in the ovary by means of injections into it of salt solution, produced hyperæmia and swelling of the uterine mucous membrane, congestion of the external genitals, and mucous and bloody discharges.

The mystery of menstruation largely ceases when we recognize what is undoubtedly a fact, that the phenomenon is a highly developed inheritance from our mammalian ancestors, and that, although in the human race under the influence of civilization and social life it has largely lost its technical sexual significance, it is, nevertheless, primarily a reproductive phenomenon derived directly from the lower females. Nature has endowed the latter, in a manner yet unknown, with reproductive periods that are pronounced in the wild state and are coincident with certain of the seasons. A primitive seasonal period may perhaps still be shown in woman by the greater proportion of births that take place during the winter months than at other times of the year : this sig-

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[1] Mary Putnam Jacobi : *American Journal of Obstetrics,* 1885, xviii.

[2] Arrhenius : *Skandinavisches Archiv für Physiologie,* 1898, viii. S. 367.

[3] Strassmann : *Archiv für Gynäkologie,* 1896, lii. S. 134.

nifies greater sexual activity during the months of spring, as is the case in most animals.[1]

Domestication has, however, interfered with the original plan of nature. It has rendered the lower forms more prolific and has made more frequent their reproductive periods. Civilization has done exactly the same for woman. It has rendered her more prolific and has made more frequent her reproductive periods. It is wholly probable that the menstrual periods of woman are the homologues of the frequent reproductive periods of the lower forms. It has been seen that the latter are characterized by the same kind of phenomena that exist in the former; the characteristic human menstrual phenomena are least developed in the lower mammals, much more so in the monkey, and are most pronounced in the human female. For what purpose this evolution of function has taken place we do not know. Below the human species conception is confined to these times of "heat;" in woman it is possible at other than her menstrual periods. In this respect woman is more highly endowed than her mammalian ancestors.

The Vagina.—The *vagina* (Fig. 222, *vg*) is the broad passage from the uterus to the external organs. Its walls consist of smooth muscle fibres, arranged both circularly and longitudinally. It is lined by stratified scaly epithelium and is surrounded by erectile tissue. Its walls contain few glands. Its specific functions are connected solely with the reproductive process; in copulation it receives the penis and the semen. Its cavity is the pathway outward for the products of menstruation and, in parturition, for the child.

The Vulva and its Parts.—The *vulva* (Fig. 222) comprises the genital organs that are visible externally—viz. the *mons Veneris*, the *labia majora* (*l.m*), the *labia minora* or *nymphæ* (*n*), the *clitoris*, which is the diminutive homologue of the penis of the male, and the *hymen* (*h*), or perforated curtain that guards the entrance to the vagina and is usually ruptured at the time of the first coition. The vulva receives the openings of the vagina, the urethra (*u*), and the ducts of Bartholini's glands. Its parts are capable of turgidity through its rich vascular supply, and perform minor ill-defined, adaptive, and stimulating functions in copulation. Their surface is covered by mucous membrane which is moistened and lubricated by a secretion from numerous mucous follicles, sebaceous glands, and the glands of Bartholini. The latter are comparable to Cowper's glands of the male and secrete a viscid liquid.

The Mammary Glands.—The mammary glands, being active only during the period of lactation, may best be studied in connection with that function (see Vol. I., p. 261).

Internal Secretion.—*A priori*, the reproductive organs can scarcely be regarded as organs that are quiescent during the greater part of life and pas-

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[1] "The largest number [of human births] almost always falls in the month of February, ... corresponding to conceptions in May and June. . . . . Observations tend to show the largest number of conceptions in Sweden falling in June; in Holland and France, in May–June; in Spain, Austria, and Italy, in May; in Greece, in April. That is, the farther south the earlier the spring and the earlier the conceptions."—Mayo-Smith: *Statistics and Sociology*, 1895.

sively await the reproductive act. The view that they are more than this is supported by some, although slight, experimental evidence. Notwithstanding the fact that removal of the testis or the ovary in adult life is often unaccompanied by great somatic changes, the profound effects of early castration upon development, in both the male and female, show that upon the presence of the sexual organs depends the appearance of many of the secondary sexual characters—characters which apparently are independent of those organs, and yet of themselves distinguish the individual as specifically masculine or feminine. The mode of dynamic reaction of the sexual organs upon the other organs can at present be little more than hinted at. It is entirely probable that such reaction is either nervous or chemical, or perhaps it is both combined. Regarding the former little is known. Regarding the latter certain facts point to a possible normal and constant contribution of specific material by the reproductive glands to the blood or lymph, and thus to the whole body. Such a process is spoken of as *internal secretion.* This subject is discussed more fully in Vol. I. p. 273.

D. THE REPRODUCTIVE PROCESS.

Thus far attention has been given to the general functions of the reproductive organs. We come now to the special phenomena connected with the reproductive process itself, and have to trace the history of the spermatozoon, the ovum, and the embryo. It should be borne clearly in mind that the essential part of the reproductive process is the fusion of the nuclei of the two germ-cells. Investigation is making it more and more probable that the spermatozoon and the ovum, although so different in appearance and general behavior, are fundamentally and in origin both morphologically and physiologically equivalent cells. In the processes of their growth and maturation they are secondarily modified, the one into an active locomotive body, the other into a passive nutritive body. The modifications in both are confined, however, to the cell-protoplasm (cytoplasm and centrosome); the essential parts, the nuclei, remain unmodified and both morphologically and physiologically equivalent down to the time of their fusion in the process of fertilization. The many and complex details of the reproductive process exist for the sole purpose of bringing together these two minute masses of chromatin.[1]

Copulation.—Copulation is the act of sexual union, and has for its object the transference of the semen from the genital passages of the male to those of the female. It is preceded by erection of the penis and turgidity of the organs of the vulva. These latter occurrences are in the main vascular phenomena, and are brought about by a distention of the cavernous spaces of the erectile tissues with blood. The vascular phenomena are, however, accompanied by complex nervous and muscular activities. As regards the penis, the arteries supplying the organ relax and allow blood to flow in quantity to the *corpora cavernosa* and the *corpus spongiosum.* Simultaneous relaxation of the smooth

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[1] Compare Th. Boveri: "Befruchtung," Merkel und Bonnet's *Ergebnisse der Anatomie und Entwickelungsgeschichte,* 1892, i.

muscle fibres scattered throughout the trabecular framework of the corpora increases the capacity of the blood-spaces. Furthermore, the *ischio-cavernosus* (*erector penis*) and *bulbo-cavernosus* muscles contract and compress the proximal or bulbous ends of the corpora and the outgoing veins. The result of this combined muscular relaxation and contraction is a free entrance of blood into and a difficult exit from the vascular spaces; this leads to a swelling and distention which aid further in compressing the venous outlets and, being limited by the tough, fibrous tunics of the corpora, result in making the organ stiff, hard, erect in position, and well adapted to its specific function. During the process of erection the cresta of the urethra or *caput gallinaginis*, which is an elevation extending from the cavity of the bladder into the prostatic portion of the urethra and containing erectile tissue, becomes turgid and, by the aid of the contraction of the *sphincter urethræ*, effectually closes the passage into the bladder. Erection is a complex reflex act, the centre of which lies in the lumbar spinal cord and may be aroused to activity by nervous impulses coming from different directions. Impulses may originate in the walls of the ducts of the testis from the pressure of the contained semen or in the penis from external stimulation of the nerve-endings in the skin, in both cases passing along the sensory nerves of the organs to the spinal centre; or they may originate in the brain and pass downward through the cord, the impulses in this case corresponding to sexual emotions. The centrifugal paths for the arteries are along the *nervi erigentes*, which are true vaso-dilator nerves, and in the mammals, where experiment has proved their existence, pass from the spinal cord along the posterior lumbar (monkey) or anterior sacral (monkey, dog, cat) nerves to their arterial distribution. The *ischio-* and *bulbo-cavernosus* muscles are under the control of their motor nerve supply, consisting of branches of the perineal nerve.

In the female, anatomists recognize the homologues of the male erectile parts as follows: the *clitoris* with its *corpora cavernosa* and *glans* as the homologue of the penis, the two *bulbi vestibuli* as that of the bulb of the *corpus spongiosum*, the *pars intermedia* perhaps as that of the *corpus spongiosum* itself, and the *erector clitoridis* muscle as the homologue of the *erector penis* (*ischio-cavernosus*). The mechanism of erection is similar to that in the male, and the result is a considerable degree of firmness in the external genital organs.

The sexual excitement attendant upon copulation is usually much greater in man than in woman, and culminates in the sexual orgasm, when the emission of semen from the penis into the vagina occurs. It will be remembered that the prepared semen is stored in the ducts of the testes. The discharge of the fluid is a muscular act which begins probably in the *vasa efferentia* and the canal of the *epididymis*, and sweeps along the powerful muscular walls of the *vasa deferentia* in the form of a series of peristaltic waves. The seminal vesicles also contract, and the mixed liquid and spermatozoa are poured through the ejaculatory ducts into the prostatic portion of the urethra. The muscles of the prostate expel the prostatic fluid and help to pass the semen onward. The glands of Cowper possibly add their contribution. But the final urethral discharge is effected especially by powerful rhythmic contractions of the already partially contracted striped muscles, viz. the *ischio-* and *bulbo-cavernosi*, the *constrictor urethræ*, and probably the anal muscles, the result of the complex series of actions being to expel the semen with some force into the upper part of the vagina close to the *os uteri*. Ejaculation is a reflex act. The centre lies in the lumbar spinal cord; the centripetal nerves are the sensory nerves of the penis, stimulation of the glans being especially effective; the centrifugal nerves are the nerves to the various muscles. In the female during ejaculation the glands of Bartholini pour out a mucous liquid upon the vulva. There is possibly a downward movement of the uterus, brought about by contraction of its round ligaments and accompanied perhaps by a contraction of the uterine walls themselves. But all muscular and erectile activity, as well as sexual passion, is usually less pronounced in woman than in man.

Locomotion of the Spermatozoa.—The union of the spermatozoon and the ovum probably takes place usually in the Fallopian tube not far from its ovarian end, and to this place the spermatozoa at once proceed. Their mode of entrance into the uterus is not wholly clear; it is quite generally believed, but without conclusive experimental proof, that relaxation of the uterus immediately after copulation exerts a suction upon the liquid which aids in its passage through the os and the cervix. It is possible that active contraction of the vaginal walls assists. Spermatozoa have been found in the uterus a half hour after coition.[1] The main agency in the locomotion of the spermatozoa through the body of the uterus and the Fallopian tubes, and probably also from the vagina into the uterus, is the spontaneous movement of the spermatozoa themselves. By the lashing of their tails they wriggle their way over the moist surface, being stimulated to lively activity probably by the opposing ciliary movements in the epithelium lining the passages. Kraft[2] has shown in the rabbit that, when spermatozoa in feeble motion are placed upon the inner surface of the oviduct, not only are they thrown into active contractions, but they move against the ciliary movement, *i. e.* up the oviduct. The capacity of the male cells thus to respond by locomotion in the opposite direction to the stimulating influence of the ciliary cells over which they have to pass, is an interesting adaptation. Probably this is the directive agency that enables the spermatozoa to follow the right path to the ovum, while the ovum, being in itself passive, is by the same ciliary movement brought toward the active male cell. The time occupied in the passage of the spermatozoa is unknown in the human female, but is probably short; in the rabbit spermatozoa have been known to reach the ovary within two and three-quarter hours after copulation. As has been seen, spermatozoa are probably capable of living within the genital passages for several days, when, if ovulation has not taken place, they perish. If, however, an ovum appears, they at once approach and surround it in great numbers, being apparently attracted to it in some myste-

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[1] Schuworski: Abstract in *Monatsschrift für Geburtshülfe und Gynäkologie*, 1896, iv. S. 275.

[2] H. Kraft: *Pflüger's Archiv für die gesammte Physiologie*, 1890, xlvii.

rious manner. The work of Pfeffer,[1] who found that in the fertilization of ferns malic acid within the female organs attracts the spermatozoids to their vicinity, suggests strongly that also among animals the attraction may be a chemical one, the ovum containing or producing something for which the spermatozoon has an affinity. If so, the meeting of the two germ-cells is an illustration of a widespread principle of nature known as *chemotaxis*, or *chemotropism.* Experimental evidence upon the subject in animals is wanting.

Fertilization.—It will be remembered that the ovum and the spermatozoon undergo in their growth the process of maturation, and that this process consists essentially of a loss of one-half of the chromosomes of their nuclei. The germ-cells thus matured meet, as we have seen, in the distal half of the Fallopian tube and fuse into one cell, the process of fusion being called *fertilization* or *impregnation.* The details of fertilization have not been observed in the case of the human being, and the following account is generalized from our knowledge of the process in other mammals and lower animals. In its broad outlines fertilization is probably the same in all animals, the differences being confined to details.

The ovum at the time of fertilization is surrounded by the *zona radiata* alone, the *corona radiata* having been lost. The spermatozoa swarm about the *zona*, lashing their tails and attempting to worm their way through it. Several may succeed in reaching the perivitelline space, but for some unknown reason in most cases one only penetrates the substance of the ovum; the others ultimately perish. In mammalian ova there is no micropyle, and apparently the successful spermatozoon may enter at any point, the protoplasm of the egg rising up as a slight protuberance to meet it (Fig. 223, A). In some animals the tail is left outside to perish; in others it enters, but then disappears; in no case does it appear to be of further use. The head and probably the middle-piece are of vital importance. The head, now known as the *sperm-nucleus* or *male pronucleus*, proceeds by an unknown method of locomotion toward the centre of the egg, and becomes enlarged by the imbibition of liquid (Fig. 223, B). The matured nucleus of the ovum, or *egg-nucleus,* also moves slowly toward the future meeting-place of the two nuclei, which is near the centre of the egg. The two finally meet (Fig. 224, C) and together form a new and complete nucleus, called the *first segmentation-nucleus* (Fig. 224, D). This body has the conventional nuclear structure—namely, an achromatic network with the chromatic reticulum mingled with it—and the whole is covered by a nuclear membrane. From the observations of Van Beneden, Rückert,[2] Zoja,[3] and others, it seems to be a fact that the male and the female chromosomes do not fuse together, but remain distinct from each other, perhaps throughout all the tissue-cells. The chromosomes, it will be perceived, are now restored to the original number present in either germ-cell before its maturation, hence in the human being perhaps sixteen, one-half of them

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[1] W. Pfeffer: *Untersuchungen aus dem Botanischen Institut zu Tübingen*, 1884, i.

[2] J. Rückert: *Archiv für mikroskopische Anatomie*, 1895, xlv.

[3] R. Zoja: *Anatomischer Anzeiger*, 1896, xi.

having come, however, from the male cell and one-half from the female cell. On the commonly accepted theory that they constitute the hereditary substance, the first segmentation-nucleus contains within itself potentially all the inherited qualities of the future individual.

While the head of the spermatozoon is making its way through the substance of the egg there appears beside it a minute cytoplasmic body, the *centrosome*, and around the latter cytoplasmic filaments arrange themselves in the form of a star, the whole body being known as the *sperm-aster* (Fig. 223, B). We have previously recognized such a structure in the ovum at the time of maturation, and have found it functional in the formation of the polar bodies; after maturation it disappears. The sperm-aster accompanies the sperm-nucleus, becomes gradually enlarged, and finally comes to lie, a large and prominent body, beside the segmentation-nucleus. The origin of its centrosome has been greatly disputed. Some investigators maintain that it is formed anew in the egg; but the prevalent opinion at present seems to be that it comes from the spermatozoon in immediate relation to the middle-piece, and hence is exclusively of male origin.

Fig. 223.—Stages in the fertilization of the egg (after Wilson). The drawings were made from sections of the eggs of the sea-urchin, *Toxopneustes variegatus*, Ag.

A. The surface of the egg has become elevated to form *c*, the entrance-cone for the spermatozoon; the head (*h*) and the middle-piece (*m*) of the latter have entered the egg.

B. Five minutes after entrance of the spermatozoon. The head, now the male pronucleus, has rotated 180 degrees, and has travelled deeper into the ovum. The cytoplasm of the latter has become arranged in a radiate manner about the middle-piece of the spermatozoon, now the centrosome, to form the sperm-aster; the egg-nucleus, now the female pronucleus, is approaching the sperm-nucleus; its chromatin forms an irregular reticulum.

There results from fertilization, it is perceived, a single cell complete in all its essential parts. This is the starting-point of the new individual. A pause or resting period usually follows fertilization, and then growth begins.

Segmentation.—The process of growth is a complex process of repeated cell-division, increase in bulk, morphological differentiation, and physiological division of labor.

Cell-division is largely, if not wholly, indirect or mitotic. The term *segmentation*, or *cleavage*, of the ovum is conveniently applied to the first few divisions, although the details of segmentation are not different fundamentally from those manifested later in the division of more specialized cells. Each division may be resolved into three definite acts, which, however, overlap each other in time. The first act is characterized by the appearance of two centrosomes, each with its astral rays, in place of the one already existing (Fig. 224, C). The two take positions beside the nucleus (Fig. 224, D) and await the time when they can exert their specific function. We have spoken of the difference of opinion regarding the origin of the original centrosome of fertilization. The origin of the two centrosomes present in segmentation has likewise been disputed. The question is of considerable theoretical interest in connection with the problem of the physical basis of inheritance. Certain observers have claimed that the centrosomes have a double origin, one being derived from the male and one from the female germ-cell. Upon this theory sexuality is shown by the cytoplasmic centrosomes as well as by the nuclear chromosomes, and the inference is possible that cytoplasm, as well as nucleus, transmits hereditary qualities. This double origin of the centrosomes is not supported by trustworthy evidence. Other observers, following Boveri, maintain that the centrosome of the sperma-

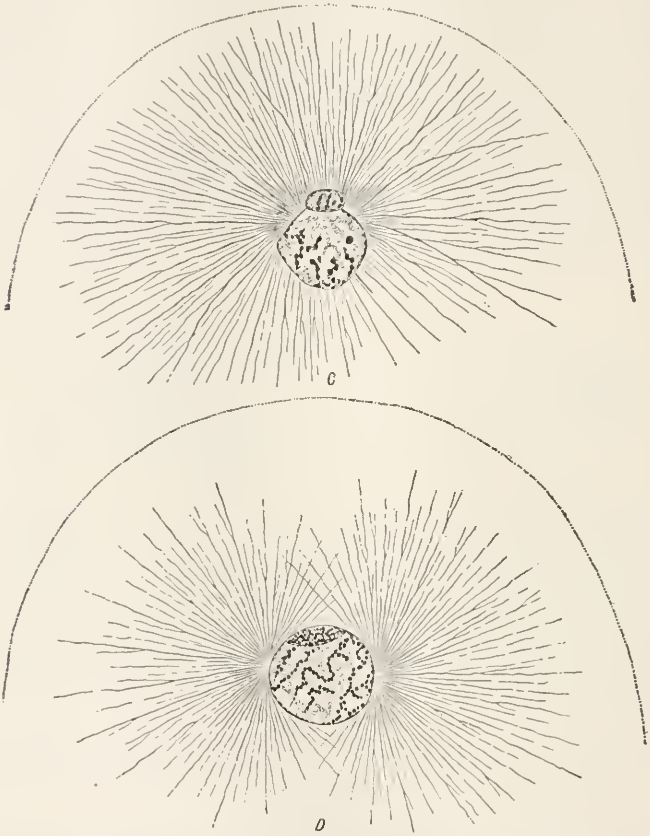

Fig. 224.—Stages in the fertilization of the egg (continued from Fig. 223).

C. Ten minutes after entrance of the spermatozoon. The male and the female pronuclei have met near the centre of the egg and the fusion has begun; the former has become enlarged and its chromatin has become loosely reticulated. The sperm-aster has become enormously enlarged. The single centrosome has been divided into two, which lie upon either side of the sperm-nucleus.

D. Still later after entrance of the spermatozoon. The two pronuclei have united to form the first segmentation-nucleus. The sperm-aster has become divided into two asters, which have moved to opposite poles of the nucleus. The egg is now ready to undergo segmentation.

tozoon divides into the two segmentation-centrosomes, the latter hence being exclusively of male origin. Still others believe that the sperm-centrosome disappears, its place being taken by two new centrosomes derived from the cytoplasm of the egg. The evidence available at present does not allow a decision to be made between these two latter views.[1] According to both of them, however, the cleavage-centrosomes are not male and female, and cannot be regarded as bearers of inherited characteristics. These observations not only allow, but tend to strengthen, the prevailing view of the exclusive hereditary rôle of the nucleus. (See below under Heredity, p. 493.)

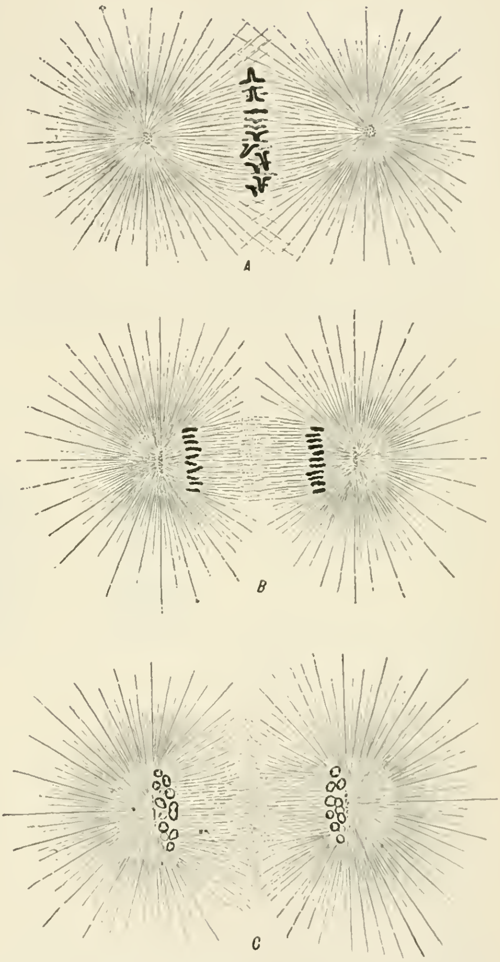

Fig 225.—Stages in the segmentation of the egg (after Wilson). The drawings were made from sections of eggs of the sea-urchin, *Toxopneustes variegatus*, Ag.

A. The nuclear membrane has disappeared. Within the nucleus a distinction between the chromatic and the achromatic substance has been made, the former existing as clearly defined chromosomes aggregated in the centre to form the equatorial plate, the achromatic substance existing as delicate filaments extending in the form of a spindle from pole to pole.

B. Each chromosome has become split into two, and the latter are being pulled toward the poles.

C. The divergence of the chromosomes has ceased and the latter are becoming converted into vesicular masses beside the centrosomes. The spindle is becoming resolved into ordinary cytoplasm.

The second act of segmentation is more complicated than the first, and consists of a halving of the nucleus. The nuclear membrane gradually disappears. The achromatic network resolves itself into long cytoplasmic filaments arranged in the form of a spindle, and meeting at the two centrosomes (Fig. 225, A). The spindle, centrosomes, and asters form the body known as the *amphiaster*. The chromatic substance becomes changed into the definite rod-like *chromosomes*, which are collected in the equatorial zone of the spindle, and constitute the *equatorial plate*. Each chromosome proceeds to split lengthwise, and the two halves move toward the two centrosomes (Fig. 225, B). The cause of this movement is not known. The

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[1] For a critical review of this and other problems in fertilization and segmentation see E. B. Wilson: *The Cell in Development and Inheritance*, 1900, 2d ed., New York.

original idea of Van Beneden,[1] that the astral rays are contractile and mechanically pull apart the half-chromosomes, is supported by considerable but unconvincing evidence. The idea appears to be growing that by reason of chemical changes taking place in the centrosomes the half-chromosomes are attracted to the two poles of the spindle.[2] Strasburger[3] suggests that this attractive influence is chemotaxis. In the process of division each nuclear half obtains half of the original male and half of the original female chromatin, and hence contains inherited potentialities of both parents. After division each half gradually assumes the structure of a typical resting nucleus with its accompanying aster (Fig. 226).

The third act of segmentation consists of a simple division of the cytoplasm into two equal parts, the separation taking place along the plane of nuclear division (Fig. 226, D). Each part contains one of the new nuclei, and the result of the first division is the existence of two cells, two blastomeres, in place of the one fertilized ovum. The beginning of differentiation is often shown even as early as this, for one blastomere is often somewhat larger and less granular than the other.

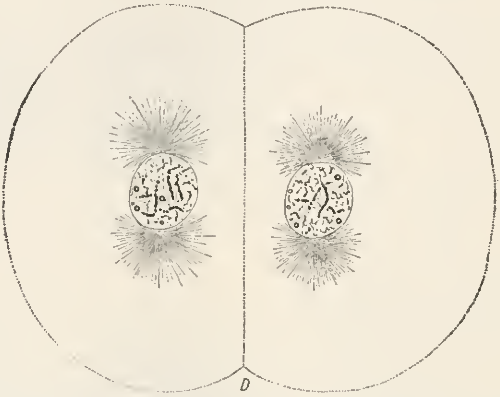

FIG. 226.—Stages in the segmentation of the egg (continued from Fig. 225).

D. The vesicular chromatic masses have become converted into two typical resting nuclei, each with a chromatic network. The single aster, formerly connected with each nuclear mass, has become divided into two, which have taken positions at opposite poles of the nuclei. The division of the cytoplasm is complete, and the two resulting cells, or blastomeres, are resting, preparatory to a second division in a plane at right angles to that of the first.

Each blastomere proceeds now to divide by a similar mitotic process into two, the result being four in all, and by subsequent divisions, eight, sixteen, and more, the divisions not proceeding, however, with mathematical regularity. By such repeated mitotic processes the original fertilized ovum becomes a mass of small and approximately similar cells, the *morula*, from which by continued increase in the number of the cells, morphological differentiation, and physiological division of labor, the embryo with all its functions is destined to be built up.

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[1] Van Beneden: *Archives de Biologie*, 1883, iv.

[2] *Cf.* Bütschli: *Verh. Naturhist. med. Ver. Heidelberg*, 1891; and E. B. Wilson, *op. cit.*

[3] Strasburger: *Anatomischer Anzeiger*, 1893, viii.

Polyspermy.—It happens occasionally that two or more spermatozoa enter the ovum; such a phenomenon is known as *dispermy* or *polyspermy*, according to the number of entering sperms. Each sperm with its nucleus and centrosome becomes a male pronucleus and proceeds to conjugate with the female pronucleus. In the case of dispermy the one female and the two male pronuclei fuse together; each centrosome gives place as usual to two, making four in all, which take up a quadrilateral position about the first segmentation-nucleus; the chromatic figure consists of two crossed spindles; and the egg segments at once into four instead of two blastomeres. Analogous phenomena result from more complex cases of polyspermy. In such double- or multi-fertilized eggs development may proceed to some distance, but typical larval forms are not produced, and death occurs early.

During cleavage the ovum proceeds, after the manner of the non-fertilized ovum, slowly along the Fallopian tube and enters the uterus. Unlike the non-fertilized ovum, however, the morula is not cast out of the body, but remains and undergoes further development. The morphological development of the embryo *in utero* does not fall within the scope of the present article. Some attention may, however, be given to the immediate environment of the developing child and its relations to the maternal organism.

Decidua Graviditatis.—While the segmentation of the ovum is proceeding within the Fallopian tube, the uterus prepares for the future guest by beginning to undergo a profound change, probably being stimulated to activity reflexly by centripetal impulses originating in the walls of the tube through contact with the ovum. This change comprises an enlargement of the whole uterus and a great and rapid growth in thickness of its mucosa and its muscular coat. At first the alterations are not unlike the phenomena of growth preceding the menstrual flow, but, as they proceed, they become much more profound than those. The supply of blood to the walls is greatly increased, the vessels forming large irregular sinuses within the mucosa. The supply of lymph is increased. The glands become tortuous and dilated into flattened cavernous spaces, and their walls atrophy, the epithelium breaking down except in their deepest parts. The mucosa is thus converted into a spongy tissue, the framework of which contains numerous large irregular cells, derived probably from the original connective tissue and called *decidual cells.* The musculature is greatly thickened by an increase, partly in number and partly in size, of its constituent fibres, and the nerve-supply is increased. These general structural changes proceed through the early part of gestation and are accompanied by special changes to be discussed later. It is not definitely known how far the alterations have gone before the advent of the segmented ovum into the uterus. With the latter instead of the unimpregnated ovum present in the Fallopian tube, the hypertrophied uterine mucosa does not break away as in menstruation, but remains, and henceforth is called the *decidua graviditatis*, special names being given to special parts. Entering the uterus, the ovum attaches itself in an unknown manner to the wall of the womb. The part of the mucous membrane that forms its bed is henceforth known as the *decidua serotina;* as the seat of the future placenta, it is physiologically the most interesting and important portion of the uterine mucosa. The surrounding cells and tissues are stimulated to active proliferation and grow around and over the ovum, completely covering it with a layer, the *decidua reflexa.* The remainder of the uterine lining membrane constitutes the *decidua vera.* Between the reflexa and the vera is the uterine cavity. At first thickened, the reflexa later thins away as the embryo grows, and approaches close to the vera; finally it touches the latter, and the original cavity of the body of the uterus becomes obliterated. By the sixth month the reflexa disappears, either coalescing with the vera or undergoing total degeneration (Minot). During the latter half of gestation the vera itself thins markedly. This atrophy of the comparatively unimportant reflexa and vera, in contrast to the placental hypertrophy of the serotina, is interesting. The arrangement of the parts is well shown in the accompanying illustration (Fig. 227).

The Fetal Membranes.—The segmented ovum absorbs nutriment at first directly from its surrounding maternal tissues, and later through the mediation of the placenta. Its growth and cell-division are active, and it increases in size and complexity. It early takes the form of a generalized vertebrate embryo, and by the fortieth day begins to assume distinctly human characteristics. It becomes surrounded early by the fetal membranes, which are two in number, the *amnion* and the *chorion* or, as it is usually called in other vertebrates, *false amnion.* The *amnion* is a thin, transparent, non-vascular membrane immediately surrounding the embryo (Fig. 227). In origin a derivative of the embryonic somatopleure, later it becomes completely separated from the body of the embryo. The space enclosed by the amnion, the *amniotic cavity,* within which the embryo lies, is traversed by the umbilical cord and contains a serous liquid, the *liquor amnii.* This liquid, highly variable in quantity, averages at full term nearly a liter ($1\frac{3}{4}$ pints). It has in general the composition of a serous liquid. It contains between 1 and 2 per cent. of solids, consisting of proteids (0.06–0.7 per cent.), mucin, a minute and variable quantity of urea, and inorganic salts. Its origin, whether from the fetus, especially from the fetal kidneys, or from the mother, has been much discussed. It may possibly come in small part from the former, but its chief origin is doubtless by transudation from the maternal blood, as is indicated by the ready appearance within the amniotic cavity of solutions injected into the maternal veins, and the fact that the amniotic liquid of diabetic women contains sugar. It bathes the entire surface of the embryonic body, and is, moreover, apparently swallowed into the stomach, as the presence of fetal hairs and epidermal scales within the alimentary canal attests. Its chief functions appear to be those of protecting the fetus from sudden shocks and from pressure, maintaining a constant temperature, and supplying the fetal body with water. The proteid possibly confers upon it a very slight nutritive value, and the minute quantity of urea is perhaps indicative of an unimportant excretory function of the fetal kidneys. As growth proceeds, the amnion expands and becomes loosely attached to the outer fetal membrane, the chorion.

The *chorion* (Fig. 227), or *false amnion*, is formed simultaneously with the true amnion, and like it from somatopleure. It is a thickened vascular membrane, completely surrounding the amnion with the contained embryo. Between it and the amnion there is at first a considerable space, traversed by the umbilical cord and filled with the *chorionic fluid* (which is probably of the same general nature as the amniotic fluid). But later this space is obliterated by the enlargement of the amnion. Externally the chorion presents, at first, a shaggy appearance due to the existence of very numerous columnar processes, called *villi*, extending outward in all directions and joining by their tips the *decidua serotina* and the *decidua reflexa*. Later the villi are aborted except in the region of the serotina, where they become more prominent and constitute an important part of the placenta. The blood-vessels of the chorion

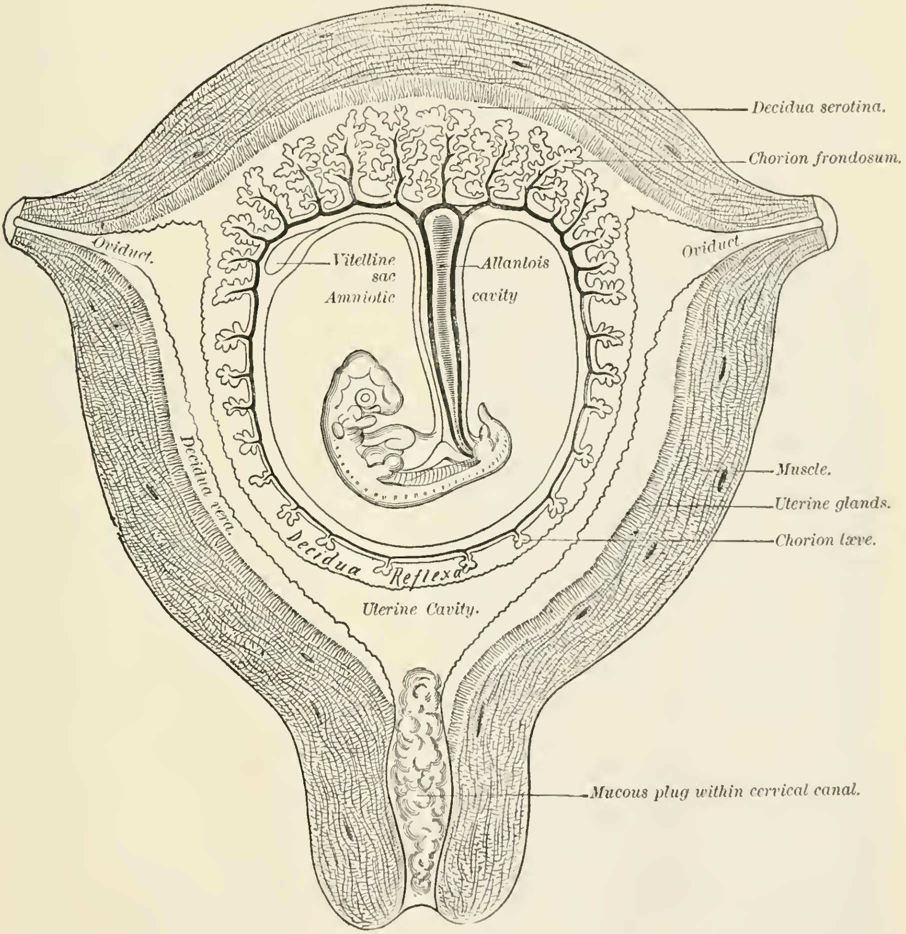

Fig. 227.—Diagram of the human uterus at the seventh or eighth week of pregnancy (modified from Allen Thompson). The fetal villi are shown growing into the sinuses of the decidua serotina and the decidua reflexa; in the latter they are becoming atrophied. They are marked by the black fetal vessels, which can be traced backward along the umbilical cord to the embryo. The placenta comprises the decidua serotina and the chorion frondosum.

are fetal vessels coming from the embryonic structure, the allantois. They comprise the branches and uniting capillaries of the two allantoic or umbilical arteries, and the one (at first two) allantoic or umbilical vein. They are especially well developed within the villi. As growth proceeds, the chorion comes into close contact with the *decidua reflexa*, and, as the latter disappears, with the *decidua vera;* this portion of it is called *chorion læve.* In the region of the *decidua serotina* it enters into the formation of the placenta, and is here called *chorion frondosum.*

The Placenta.—The *placenta* (Fig. 227), or organ of attachment of mother and fetus, is a disk-shaped body, approximately 20 centimeters (7–8 inches) in diameter, attached to the inner surface of the uterine wall, usually either upon the dorsal or the ventral side, and connected by the umbilical cord with the navel of the fetus. It consists of a maternal part, the modified *decidua serotina*, and a fetal part, the modified chorion, intimately united together. The modifications of the serotina consist of a degeneration of the superficial layers of the mucosa, especially of the epithelium and the glands, and the development of very large irregular sinuses at the surface, into which the uterine arteries and veins freely open. It is a disputed question among histologists whether the sinuses are maternal or fetal in origin, or really spaces between maternal and fetal tissues. The modifications of the chorion consist of a great increase in length and complexity of branching of the villi, a great development of their contained blood-vessels, and a firm attachment of their tips to the uneven surface of the serotina, so that their branches come to float freely within the uterine sinuses and to be bathed in uterine blood (Fig. 228). The analogy between the mammalian placental villi and the gills of a fish, also highly vascular and floating in liquid, is striking. We shall see later that the analogy is not only morphological but also physiological, inasmuch as the villi have important respiratory functions. The bulk of the placenta is this intravillous portion, of spongy consistence,

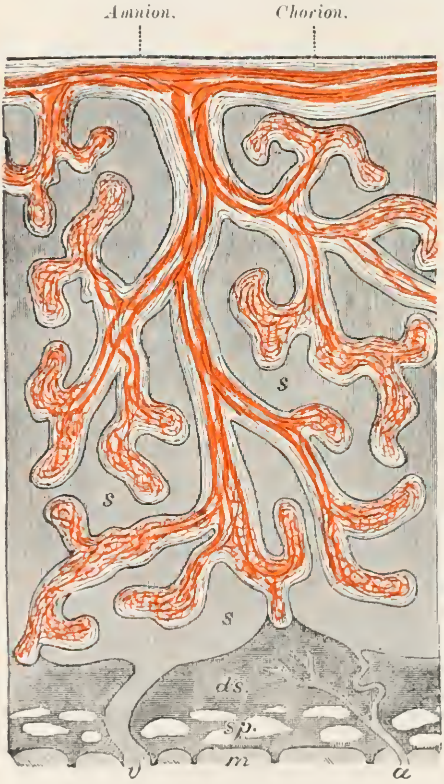

FIG. 228.—Diagram of the placenta (Schäfer): *s*, placental sinuses, into which project the fetal villi, containing the red fetal vessels; *ds*, decidua serotina; *sp*, spongy layer, and *m*, muscular layer, of the uterus; *a*, uterine artery, and *v*, uterine vein, opening into the placental sinuses.

comprising the maternal sinuses permeated by the fetal villi; this is in contact upon the fetal side with the thin unmodified chorion covered within by the amnion, and upon the maternal side with the thin relatively unmodified serotina covered without by the uterine muscle. The pure maternal blood brought by the uterine arteries moves slowly through the sinuses and retires by the uterine veins; the fetal blood is propelled by the fetal heart along the umbilical cord within the allantoic arteries and through the villous capillaries, and returns by the allantoic vein. The two kinds of blood never mix, but are always separated by the thin capillary walls and their thin villous investment of connective tissue and epithelium. Thus the anatomical conditions for ready diffusion are present, and this is the chief means of transfer of nutriment and oxygen from mother to child, and of wastes from child to mother. The physiological rôle of the placenta is, therefore, an all-important and complicated one. The placenta is, technically, the nutritive organ of the embryo.

Nutrition of the Embryo.—We have seen that a fundamental and most striking difference between the minute human ovum and the large egg of the fowl lies in the relative quantity of food contained in the two. The fowl has retained the primitive habit of discharging the ovum from the maternal body, and discharges within its shell at the same time sufficient food for the needs of the developing chick. Evolution has endowed the human mother, in common with other mammals, with the peculiar custom of retaining the offspring within her body until its embryonic life is completed, and of doling out its nutriment molecularly throughout the period of gestation. The store of nutritive deutoplasm with which the egg leaves the ovary is, therefore, only sufficient for the early segmentative activities. Within the Fallopian tube absorption from the surrounding walls doubtless goes on. Arrived in the uterus and imbedded in its decidual wall, the segmented ovum continues to take nutriment from its immediate environing cells. It has been suggested, but without much basis of fact, that the uterine glands, which at this time are greatly dilated, may furnish a nutritive secretion for the use of the embryo; but, *a priori*, it would seem more reasonable that, just as the ovum within the Graafian follicle obtains its food from its surrounding stroma, so within the highly vascular decidua it absorbs directly from the decidual tissue. But that this source soon proves insufficient for the rapid growth is indicated by the early development of the chorion with its villi and the embryonic vascular system. In the youngest known human embryo,[1] believed to be scarcely seven days old, the villi are already well marked. From this time onward throughout gestation the chorion takes an important part in the embryonic nutrition, becoming, as we have seen, an integral part of the placenta. The placenta is *par excellence* the medium of nutritive communication between mother and child.

Let us consider briefly the needs of the embryo. The fetal energies must be directed almost wholly to the all-important functions of growth and preparation for the future independent existence. The organism requires, therefore,

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[1] Peters: *Verhandlungen der deutschen Gesellschaft für Gynäkologie*, 1897, vii. S. 264.

an abundance of food containing all the chief kinds of food-stuffs. With the alimentary canal in its embryonic and functionless state, this food, when it reaches the embryo, must necessarily be already digested and ready for absorption by the cells. A supply of oxygen, not necessarily great in quantity, is also needed. The fetal lungs are not ready for respiration, and the oxygen must come to the blood by another channel than them. Carbonic acid must be got rid of, and through other than pulmonary paths. Urea and its forerunners and other wastes, probably not in great quantity, must be excreted. The fetal kidneys and the skin are probably never very active, as is made reasonably certain by the late external opening of the male urethra, the late development of the cutaneous glands, and the composition of the amniotic liquid, into which they would naturally pour their secretions. Thus the paths of income and outgo that are normal to the individual after birth are only partially open during fetal life; nevertheless, the processes of income and outgo must be performed. The placenta, with its close relationship but non-communication of maternal and fetal blood-vessels, has, therefore, been evolved phylogenetically, and appears early in the course of ontogeny. There is brought to it on the part of the embryo and discharged into the villous capillaries a mixed blood, comprising venous blood from the various capillary systems of the body, and containing, therefore, the carbonic acid and other wastes of venous blood, and a certain proportion of purified blood which has passed directly by way of the *ductus venosus*, the inferior vena cava, the right auricle, the *foramen ovale*, and the left side of the heart to the aorta and the umbilical arteries. There is brought to the placenta on the part of the mother and discharged into the sinuses pure arterial blood, laden with food and oxygen. Through the membrane intervening between maternal and fetal vessels there pass from the fetus carbonic acid and other wastes, and from the mother food (sugar, fats, proteids, etc.) and oxygen. Back to the fetal liver and heart goes the nutritive and arterialized blood, and back to the maternal excretory organs the vessels convey the fetal wastes. The placenta is thus a peculiar organ intermediate between the living cells of the embryo on the one hand and the digestive organs, lungs, kidneys, and skin, of the mother on the other. Little is known of the actual details of the placental process. The structure of the intervening cells indicates that the interchange may be after a manner analogous to that taking place in the lungs, rather than to that of a typical secreting gland—*i. e.* that known physical processes, such as diffusion and filtration, play a prominent rôle. It has been shown by several investigators that the fetus may be poisoned by carbonic oxide and strychnine, and may receive other harmless diffusible substances that are introduced in solution into the maternal circulation. The mother may be affected similarly from the fetal circulation. But, as in the case of the lungs, so the placental membrane can scarcely be regarded as acting in the same passive way as a lifeless membrane would act (compare Respiration). As accessory to the main nutritive source it has been suggested that a diapedesis of maternal leucocytes into the fetus may take place.

The uterine glands are thought by some to afford a nutritive secretion to the sinuses, and to the amniotic liquid has been ascribed a nutritive function. Theoretically, these various means are not impossible, but true placental diffusion must be regarded as the chief principle at work. The result is that the mother relieves the child of all the labor of nutrition except that connected directly with the latter's own cellular and protoplasmic metabolism. The fetal energies are, therefore, free to be expended in the process of growth, while gestation profoundly affects the maternal organism.

Physiological Effects of Pregnancy upon the Mother.—As might have been expected, there is probably not one organic system within the mother's body that is not more or less altered by pregnancy, often morphologically, but especially in regard to function. And such normal alterations pass so gradually and so frequently into genuine pathological conditions that it is sometimes difficult to draw the line between the two. The most marked changes are connected with the body of the uterus, and have already been described. The walls of the *cervix uteri* become hypertrophied, though to a less degree than the body, and their glands secrete a quantity of mucus that forms a plug completely closing the passage-way of the cervix (Fig. 227). The rest of the reproductive organs from the uterus outward become involved in the increased venous hyperæmia. The walls of the vagina become infiltrated with serous liquid. The parts of the vulva partake in the general tumefaction. From the second month of gestation onward the mammary glands undergo gradual development as a preparation for the *post-partum* lactation. The increase in size of the laden uterus brings gradually increasing pressure to bear upon the abdominal viscera, and thus mechanically causes functional derangements of the digestive and the urinary organs. The stretching of the abdominal skin results in localized ruptures of the connective tissue of the cutis, the characteristic scars forming the *striæ gravidarum*, which persist after pregnancy. Other organic changes are, however, more profound than these mechanical ones. In accordance with the increased nutritive labor thrown upon the mother, the total quantity of blood in her body is increased, if we can reason from determinations made upon the lower animals.[1] The condition of the blood has been disputed. The old belief was that the blood of pregnancy is more watery and contains less hæmoglobin than at other times. This is perhaps true for the earlier months, but Schroeder[2] and others have shown that the proportion of hæmoglobin and the number of red corpuscles rise above the normal during the later stages. The work of the maternal heart is increased during gestation. It is maintained by some that the heart beats more rapidly—according to Kehrer,[3] over eighty times in the minute. It has also been thought, mainly from the results of percussion and from sphygmographic tracings, that the left ventricle is hypertrophied during pregnancy. Post-mortem examination confirms this inference. Pregnancy necessarily throws

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[1] O. Spiegelberg und R. Gscheidelen: *Archiv für Gynäkologie*, 1872, iv.

[2] R. Schroeder: *Ibid.*, 1890-91, xxxix.; Wild: *Ibid.*, 1897, liii. S. 363.

[3] F. A. Kehrer: *Ueber die Veränderungen der Pulscurve im Puerperium*, 1886.

increased labor upon both the liver and the kidneys, and these organs are prone to functional disorders. Gastric disturbances are marked by frequent vomiting. A tendency to increased pigmentation in the skin is present. The nervous system is affected, manifesting its alterations both by nutritional disturbances and by mental irritability, depression of spirits, disordered senses, easily passing into temporary pathological states, and occasionally by feelings of heightened well-being. The body-weight usually increases independently of the added weight of the embryo.

Duration of Gestation.—For centuries the duration of gestation in woman has been commonly regarded as 280 days. The beginning of pregnancy, the union of the ovum and the spermatozoon, however, presents no obvious signs by which it may be recognized, and hence the actual length of pregnancy in the human female is no more known than in other mammals. The obstetrician is obliged, therefore, to use artificial schemes in computing its probable length. Several tables have been published of the time elapsing between a single coition resulting in pregnancy and the terminal parturition. Veit,[1] in collecting 503 such cases reported by several obstetricians, finds the duration to be from 265 to 280 days in 396 cases, and longer in the remaining 107 cases, the variation thus being marked. It is obvious that the date of the effective coition can rarely be known. One of the first and most evident signs of pregnancy is the non-appearance of the menses, and, probably largely from the long-prevailing idea of the close relation existing between ovulation and menstruation, it has been customary to regard gestation as dating from the last menstruation. Following Naegele, obstetricians estimate the date of parturition as 280 days from the first day of the last menstruation; and this simple but artificial rule is doubtless approximately correct.

In accordance with modern biological theories, it must be supposed that for each species there has been developed a gestative period of a length most favorable to the continuance of the species; this has been a matter of natural selection. But this principle does not account for the termination of the period in any individual case. The proximate cause of the oncoming of birth must be sought in more specific anatomical or physiological phenomena. This cause has been sought long, and not wholly successfully. Among the agents suggested may be mentioned the pressure which the uterine tissues, the ganglia of the cervix, and the adjacent nerves, receive between the fetal head and the pelvic wall, the stretching of the uterine wall, the fatty degeneration of the deciduæ, the thrombosis of the placental vessels, the venosity of the fetal blood due to the growing functional importance of the fetal right ventricle acting as a stimulus to the placental area, and a gradual increase in irritability of the uterus as the nerve-supply of the organ increases. Some of these, such as the fatty degeneration of the deciduæ and the placental thrombosis, are not constant phenomena, and the others are not definitely proved to be efficient causes. It is probable that, with the uterus undoubtedly irritable, in different

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[1] J. Veit: *Müller's Handbuch der Geburtshülfe*, 1888, 1.

cases different stimuli act to inaugurate the process of birth, and *a priori* several of the above causes seem not improbable ones.

Parturition in General.—Parturition, birth, or labor, is the process of expulsion of the developed embryo, the membranes, and the placenta from the body of the mother. It is executed by contraction of the muscles of the so-called *upper segment* of the uterus and those of the abdominal walls. The *lower segment* of the uterus, comprising approximately that portion of the body lying below the attachment of the peritoneum, the cervix, the vagina, and the vulva, are largely, if not wholly, passive in parturition. The obstetricians have found it convenient to divide labor into three stages, although physiologically these are not sharply differentiated from each other. The first stage is characterized by the dilatation of the *os uteri*, the second by the expulsion of the fetus, the third by the expulsion of the after-birth. The customary position of the fetus within the uterus at the end of pregnancy is that in which the head is downward or nearest the *os*, the back toward the ventral and left side of the mother, and the arms and legs folded upon the trunk.

First Stage of Labor.—For several weeks toward the close of pregnancy there are occasional periods when rhythmic muscular contractions pass over the uterine walls. These are mostly painless, and apparently are not in themselves of special functional importance. The first stage of labor is ushered in by various phenomena, prominent among which are an increase in the intensity of the contractions, their painfulness, and their frequency and continuance. In women they are confined practically to the upper segment of the uterus and its attached ligaments, ceasing at a circular ridge that projects inward and is called the "contraction ring." For some reason, at present disputed, the lower segment of the uterus, and the cervix, are passive. The contractions are probably peristaltic in character, as in lower animals. Schatz[1] has graphically recorded the uterine movements by means of a bladder filled with water and introduced into the uterus. During the earlier part of parturition the contractions gradually increase in intensity up to a maximum which they then maintain. Their rhythm is somewhat irregular; the duration of each contraction averages about one minute, and a pause, which ensues between successive contractions, extends from one and one-half to several minutes. The relaxation of the muscle-fibres during the period of rest is incomplete, the result being that the fibres enter gradually into a tonically contracted state. Each contraction is accompanied by a pain, localized in the early part of labor in the uterus alone, but later extending outward, upward into the abdomen, and downward into the thighs. The pains of labor vary greatly in intensity in individuals, but are usually more intense during the first gestation than during later ones. They are due chiefly to direct mechanical stimulation of the sensory uterine and other nerves by compression, tension, and even laceration.

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[1] F. Schatz: *Archiv für Gynäkologie*, 1885–86, xxvii. Compare O. Schaeffer: *Experimentelle Untersuchungen über die Wehenthätigkeit des menschlichen Uterus, ausgeführt mittelst einer neuen Pelotte und eines neuen Kymographion*, Berlin, 1896; abstract in *Centralblatt für Gynäkologie*, 1896, xx. S. 85.

As a result of the tonic contraction of the uterine walls, gradually increasing with each new peristaltic wave, the uterus becomes gradually narrower in diameter and longer, and the walls press more and more firmly upon the bag of amniotic liquid containing the embryo. Schatz finds that the uterine pressure under the uterine contractions rarely reaches and never exceeds 100 millimeters of mercury. The direction of least resistance to this pressure lies along the cervical canal, the walls of which do not take part in the uterine labor. With each succeeding contraction this canal is forced wider open and the uterine contents are pressed tightly downward and into the cervix. The head of the embryo is preceded by a bulging portion of the membrane, filled with liquid and forming a distinct bladder-like advance-guard. This bag appears at the *os uteri*, its contents increase under the increasing pressure, and in the majority of cases, when the os is fully expanded, it bursts and allows the amniotic liquid to escape to the exterior. In some cases the rupture is delayed until the second stage of labor, and rarely the child is born with the membranes intact.

Second Stage of Labor.—The uterine contractions frequently cease for a period following the rupture of the membrane. They then begin anew with increased force, and are accompanied by a new feature, namely, analogous vigorous rhythmic contractions of the muscles of the abdominal walls. These, following deep inspiration and accompanied by forced attempts at expiration with a closed glottis, diminish the longitudinal and the lateral diameters of the abdominal cavity, compress the abdominal organs, and help to augment greatly the uterine pressure. At the beginning of the second stage the force of the contractions is expended mainly upon the head of the embryo, which lies like a plug in the cervical canal. This is squeezed gradually through the os into the vagina, followed by the more easily passing trunk and limbs. The contractions are frequent, vigorous, and painful, the pains reaching a maximum as the sensitive vulva is put upon the stretch and traversed. The vertex is usually presented first to the exterior, the head and body following as the successive contractions of the maternal muscles develop sufficient power to overcome the resistance offered to their passage by the surrounding walls. In the human female the vaginal muscles do not appear to engage in the expelling act, the uterine and the abdominal muscles alone sufficing and finally forcing the child wholly outside the mother's body. In this gradual manner, painful and dangerous alike to mother and child, the maternal organism forces the offspring to forsake its sheltering and nutritive walls and begin its independent existence.

Third Stage of Labor.—During the later expulsive contractions of the second stage the placenta, being greatly folded by the diminution in the uterine surface of attachment, is loosened from the uterine wall by a rupture taking place through the loose tissue in the region of the blood-sinuses. The child, when born, is joined to the loosened placenta by the umbilical cord, until the latter is tied and cut by the obstetrician. The muscular contractions, now almost painless, continue through the third stage, and the placenta is torn from its attachment, everted, and carried gradually outward. The lining membrane of the uterus from the placenta outward and for a considerable depth is gradually torn free from the deeper parts through the spongy layer, and with the attached chorion and amnion follows the placenta. As a rule, this after-birth appears at the vulva within fifteen minutes after the expulsion of the child; it consists of the placenta, the amnion, the chorion, the *decidua reflexa*, and a considerable portion of the *decidua vera.*

Previous to the third stage slight bleeding from laceration of the passages occurs. But with the loosening of the placenta and the accompanying rupture of the placental vessels the maternal blood flows freely and continues to flow from the uterine wall, chiefly from the placental area, until the after-birth is discharged. The average loss of blood amounts to about 400 grams. At the close of the third stage of labor the uterine contractions have so far proceeded that the organ is compressed into a hard compact mass, the ruptured vessels are contorted and compressed, and the bleeding is thereby largely stopped. For several hours, however, slight hemorrhage continues as an accompaniment of the *post-partum* contractions, but finally this ceases with the formation of a blood-clot over the wounded surface.

The third stage of labor may continue through one or two hours. It is customary, however, for the obstetrician speedily to put an end to it by assisting the removal of the after-birth.

Nature of Labor.—Our knowledge of the nature of the muscular phenomena of labor is incomplete. The uterine contractions are in part automatic and in part reflex, but to what extent the former, and to what the latter, is not known. Rein[1] found that in the rabbit after section of all uterine nerves normal conception, pregnancy, and birth may occur. In some animals uterine movements may continue after removal of the organ from the body. Such and other observations indicate the existence of an automatic contractile power resident in the organ itself. Since nerve-cells are not found in its walls, it seems probable that the automatism resides in the muscle tissue. The uterus is, moreover, very sensitive to direct stimulation, even after excision. In animals higher than rabbits a connection with the lumbar spinal cord seems essential to normal labor. Goltz[2] obtained in dogs conception, pregnancy, and delivery after section of the spinal cord at the height of the first lumbar vertebra. In paraplegic women, with conduction in the cord broken in the dorsal region, delivery is possible. A centre for uterine contraction must hence be supposed to exist in the lumbar cord. Centripetal and centrifugal fibres exist in both sympathetic and spinal nerves, and reflex uterine contractions are readily obtained by stimulation of the central ends of the divided nerve-trunks. According to Langley and Anderson,[3] in the cat and the rabbit both the longitudinal and the circular muscular coats and the arteries of the uterus are supplied with motor nerve-fibres mainly by the third, fourth, and fifth lumbar nerves; the fibres pass to the sympathetic system, and

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[1] G. Rein: *Pflüger's Archiv für die gesammte Physiologie*, 1880, xxiii.

[2] Fr. Goltz: *Ibid.*, 1874, ix.

[3] Langley and Anderson: *Journal of Physiology*. 1895–96, xix. p. 122.

nearly all of them go to the inferior mesenteric ganglia and thence by the hypogastric nerves to the uterus. Stimulation of the uterus itself, the vagina, the vulva, the sciatic and the crural nerves, and various sensory regions, notably the nipples, causes reflex contractions of the uterus. The same result occurs upon stimulation of various portions of the brain, such as the medulla oblongata, the cerebellum, the pons, the corpora quadrigemina, the optic thalamus, the corpus striatum, and even the corpus callosum. In woman psychic influences may call forth or inhibit uterine contractions. How largely the well-known stimulating effects of the blood in asphyxia and of drugs, like ergot, are due to central, and how largely to direct uterine influence is undecided. The regular co-ordinated course of labor and many experimental facts make it probable that, normally, reflex influences constitute a large part of the process, the centripetal impulses arising within the uterus itself, probably largely from the pressure upon the walls of the lower segment and the cervix. In fact, it is customary to speak of labor as a complex reflex action. The undoubted automatism of the uterine muscle-fibres must, however, be taken into account, and the act should be regarded as composed of both automatic and reflex elements. We have here to deal with that variety of contractility peculiar to smooth muscle, in which central and peripheral influences work together to bring about the result. It is perhaps not going too far to regard all such actions, like that of the heart, as primarily automatic and called out by direct stimulation, but as modified and controlled by reflex influences. The parturitive contractions of the striated muscles of the abdominal walls are probably more generally reflex in nature, modified, however, by voluntary efforts.

Multiple Conceptions.—According to the records given by different statisticians, the frequency of twin births varies considerably in different countries. In 13,000,000 births in Prussia, G. Veit[1] found the number of twins to be 1.12 per cent., or 1 in 89 births. In the cities of New York and Philadelphia recent reports give the ratio of twins to single births as 1 : 120, or 0.83 per cent.

Observations of discharged Graafian follicles in cases of multiple conceptions show that twins may arise either from separate eggs or from a single egg. The presence at birth of a double chorion is commonly regarded as diagnostic of the former origin, that of a single chorion of the latter. In the former case the two ova may come from a single Graafian follicle, or from two follicles situated within one ovary, or from both ovaries, direct observation of the ovaries themselves being required to determine the origin in any particular case. The two ova are discharged and fertilized probably at approximately the same time. There are two distinct amnions. The two placentas may be either fused into one or wholly separated from each other, and accordingly the *decidua reflexa* may be single or double. The two offspring may be of separate sexes, and do not necessarily closely resemble each other. In cases where the two embryos come from a single ovum their origin is little under-

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[1] G. Veit: *Monatsschrift für Geburtskunde und Frauenkrankheiten*, 1855, vi.

stood. It is conceivable that it may arise from the presence of two nuclei within the one ovum. It is more probable, however, that it is due to a mechanical separation of the blastomeres after the first cleavage or later in segmentation.[1] Driesch,[2] Wilson,[3] Zoja,[4] and others have shown that in various invertebrates and the low vertebrate *Amphioxus*, single blastomeres, isolated from the rest by shaking or other unusual treatment, are capable of developing into small but otherwise normal and complete embryos. No reason is obvious why such an occurrence cannot take place in human development, if in any accidental manner within the Fallopian tube the blastomeres become separated. Driesch observed in the sea-urchins and Wilson in *Amphioxus* that incomplete separation of blastomeres produced two incomplete organisms more or less united together. It is not improbable that even in man cases like the Siamese Twins, and greater monstrosities, may be similarly accounted for. In cases of double pregnancy from a single ovum the two amnions are usually separate, in rare cases a breaking away of their partition wall throwing them into one; the two placentas usually fuse more or less into one, the blood-vessels of the two halves always anastomosing; and a single *decidua reflexa* covers both. The two offspring are uniformly of the same sex and their personal resemblance is always close.

In Veit's statistics of 13,000,000 births in Prussia, triplets occur with a frequency of 0.012 per cent., or 1 in 7910, and quadruplets 1 in 371,126 births. There are well-authenticated cases of quintuplets. In all of these cases a single ovum rarely, if ever, contributes more than two embryos, and these are characterized, as in the case of twins, by being of similar sex, by possessing a single chorion, and by close personal resemblance.

The Determination of Sex.—In most, if not all, civilized races more boys are born than girls. This is shown in the following table:[5]

Boys born to 1000 Girls born (1887–91).

Italy	1058	England	1036
Ireland	1055	Connecticut	1072
German Empire	1052	Rhode Island	1049
France	1046	Massachusetts	1046

The proportional birth-rate of the two sexes is usually fairly constant from year to year. This means that constant regulating factors are at work. What determines sex in any one individual is ill understood. The sexual organs in the human embryo are well differentiated at the eighth week of intra-uterine life, hence the sex of the child must be settled previously to this time. It is at present quite impossible to say whether it is settled in the germ-cells previous to their union, in the act of fertilization, or during the early uterine life. Many facts, both observational and experimental, and

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[1] *Cf.* Fr. Ahlfeld: *Archiv für Gynäkologie*, ix., 1876.

[2] H. Driesch: *Zeitschrift für wissenschaftliche Zoologie*, liii., 1892; lv., 1893; *Mittheilungen aus der Zoologischen Station zu Neapel*, xi., 1893.

[3] E. B. Wilson: *Journal of Morphology*, viii., 1893.

[4] R. Zoja: *Archiv für Entwickelungsmechanik der Organismen*, ii., 1895.

[5] *Bulletin de l'institut international de statistique*, vii.

more hypotheses, bearing upon the determination of sex, have been brought forward. The Hofacker-Sadler law (Hofacker, 1828; Sadler, 1830) is well known, as follows: If the father be older than the mother, more boys than girls will be born; if the parents be of equal age, slightly more girls than boys; if the mother be older than the father, the probability of girls is still greater. Since the promulgation of this so-called law facts for and against it have been brought forward, but the balance of evidence seems to be in favor of its truth. Thury in 1863 claimed that the degree of "ripeness" of the ovum is the determining factor—the female resulting from the less ripe ovum, hence the earlier after its liberation the egg is fertilized, the greater is the tendency to the production of a female; the later the fertilization, the greater the probability of a male. While it is not at all clear in what the "ripeness" or "unripeness" of an ovum consists, breeders have made use of this principle apparently with success—offspring conceived at the beginning of "heat" seem to be more usually females. Likewise, it is frequently believed that in human beings conceptions immediately after menstruation produce a larger proportion of females than later conceptions. Schenk[1] also bases his view on the condition of ripeness of the ovum. He regards the presence of sugar in the urine of the pregnant woman as evidence of incomplete metabolism in the body, thus of incomplete nutrition or unripeness of the ovum, and hence of tendency toward femaleness in the offspring. By means of a highly nitrogenous diet, which eliminates the sugar from the urine and increases the proportion of reducing substances, he claims to make the metabolism more complete, to insure a riper ovum, and hence to make it probable that the offspring will be a male. Schenk's reasoning is excessively hypothetical, and his present facts are too few to substantiate his claims. Düsing[2] accepts Thury's view and extends it to the male element—the younger the spermatozoon the greater the tendency toward the production of males. Hence among animals the scarcity of one sex leads to the more frequent exercise of its reproductive function, the employment of younger germ-cells, and therefore the relative increase of that sex. Further, the nearer a parent is to the height of his reproductive capacity the less will be the probability of transmitting his own sex to the offspring. Nutrition seems to have some obscure relation to the question of sex. Thus, by feeding tadpoles with highly nutritious flesh Yung[3] increased the percentage of females from 56 to 92. Mrs. Treat[4] showed that the butterflies of well-fed caterpillars became females, those of starved caterpillars males. Statistics among mammals and human beings indicate that the proportion of male to female offspring varies inversely with the nutrition of the parents, especially of the mother. Thus,

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[1] L. Schenk: *Einfluss auf das Geschlechtverhältniss*, Magdeburg, 1898. Authorized translation: *The Determination of Sex*, London, 1898.

[2] K. Düsing: *Jenaische Zeitschrift für Naturwissenschaft*, 1883, xvi., and 1884, xvii.; also published separately, *Die Regulierung des Geschlectverhältnisses bei der Vermehrung der Menschen, Tiere und Pflanzen*, Jena, 1884.

[3] E. Yung: *Comptes rendus de l'académie des sciences*, Paris, 1881, xcii.

[4] Mrs. Mary Treat: *The American Naturalist*, 1873, vii.

more boys are born in the country than in the city, and in poor than in prosperous families; the relative number of boys is said to vary even with the price of food. It is contended, moreover, and with some statistical support, that in the human race an epidemic or a war, either of which affects adversely the well-being of the people, is followed by a relative increase of male births. Statistics indicate also that the proportion of females is high in warm climates, that of males high in cold climates. Maupas[1] found that sex in the rotifer, *Hydatina senta*, could be controlled by altering the temperature of the medium surrounding the egg-laying females. In various experiments at a temperature of 26°–28° C. 81–100 per cent. of the eggs gave rise to males, the rest to females; at 14°–15° C. only 5–24 per cent. were males, the much larger majority females. Nussbaum[2] has brought Maupas's facts into harmony with the facts regarding nutrition by showing that the higher temperature carries with it a higher birth-rate and more rapid development, hence a greater need of food and relative lack of it for the individual; the result is poor nutrition and the production of an excess of males over females. It is claimed, further, that ethnic intermixture causes a decrease in the relative number of males born. This is strongly supported by a statistical study by Ripley[3] of the two races inhabiting Belgium, the Walloons, of the same origin as the Kelts in France, and the Flemish of German stock. Where these races are purest, the number of boys born to 1000 girls is 1064; along the region where the two races come into contact, however, the number may fall as low as 1043.

The above considerations are highly interesting and suggestive, but they have not yet been brought under general laws sufficiently to make their bearing upon the main problem wholly clear. It is probable that numerous factors are of influence in the determination of sex.[4] The general deduction from all the facts seems justified that unfavorable nutritive conditions surrounding the parents tend to the production of males, favorable conditions to the production of females. The experimental results indicate, moreover, that the conditions surrounding the parents or the developing embryo are largely responsible for the resulting sex. Watase[5] regards the embryo as neutral as regards sex from the time of fertilization up to a certain stage in its development; external conditions act as a stimulus to the sexless protoplasm, and the resulting response is a development in the direction of either maleness or femaleness according to the nature of the stimulus. How largely and in what manner this may be true of the human species is wholly unknown. Düsing[6] urges that the various factors determining sex have arisen through natural selection; they are conducive to the continuance of the species, and

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[1] E. Maupas: *Comptes rendus de l'académie des sciences*, Paris, 1891, cxiii.

[2] Nussbaum: *Archiv für mikroskopische Anatomie*, 1897, xlix. S. 227.

[3] W. Z. Ripley: *Quarterly Publications of the American Statistical Association*, March, 1896, v.

[4] For a critical review of the various theories see L. Cohn: *Die willkürliche Bestimmung des Geschlechts*, 2d ed., Würzburg, 1898.

[5] S. Watase: *Journal of Morphology*, 1892, vi.

[6] Düsing: *Loc. cit.*

they act in such a way that sex is in a certain sense self-regulating—the scarcity of one sex tends to the greater production of individuals of that sex; this is instanced by the fact mentioned above that after the destruction of males by war relatively more males are born than previously.

E. EPOCHS IN THE PHYSIOLOGICAL LIFE OF THE INDIVIDUAL.

Fertilization begins, somatic death ends, the physiological life of the individual. Between these two events the life-processes go on gradually, and, with the exception of birth, are marked by few abrupt changes. It is sometimes convenient to divide the individual life into a number of successive stages, as follows: the embryonic period, the fetal period, infancy, childhood, youth or adolescence, maturity, and old age or senescence. Such a division, however, is not physiologically exact, the stages are not sharply limited, and the terms are employed in very different senses by different writers. Between fertilization and birth the functions originate and are developed gradually. At birth the environment of the individual is abruptly changed, organic connection with the mother suddenly ceases, and profound physiological changes occur. At this time, or shortly after it, the individual is capable of performing all the functions of adult life with the exception of reproduction, the functions needing, however, to be exercised and improved before they are at their best. From birth to maturity, therefore, the physiological history is mainly a history of progressive modifications of function—modifications, indeed, of great importance, but secondary to the primary fact of function itself. The same may be said of the period of old age, with the difference that here the modifications of function are retrogressive. In the present book, devoted mainly to the physiology of the adult at the time of maturity, little can be said of the origin and development of function in the embryo; the modifications of function at different periods of life have been discussed in connection with the various functions themselves; certain topics of special physiological significance have, however, been left for brief treatment in this chapter.

Growth of the Cells, the Tissues, and the Organs.—All growth, whether of the cells, the tissues, or the organs, is the result of no more than three processes, viz. multiplication of cells, enlargement of cells, and deposition of intercellular substance, the first two processes being the most potent of all. Increase in the number of cells is largely, although not wholly, an embryonic phenomenon; increase in the size of cells and deposition of intercellular substance are especially important from the later embryonic period through the time of birth and up to the cessation of the body-growth. The periods of growth of the several tissues differ; in view of this it is quite impossible to designate any period except that of death at which the growth of the tissues wholly terminates. Detailed statistics of the growth of organs are wanting.

Growth of the Body before Birth.—The most obvious result of growth of the cells, the tissues, and the organs, is growth or increase in size of the body. Growth of the body continues actively from the beginning of the segmentation of the ovum up to about the age of twenty-five years, and results in an increase in all dimensions and in weight. In determining the extent of growth, the two most convenient and most commonly used measurements are those of length, or height, and weight. For the embryo the following table has been compiled by Hecker:[1]

Table showing the Average Length and Weight of the Human Embryo at Different Ages.

Month.	Length of embryo in centimeters.	Weight of embryo in grams.
Third	4 to 9	11
Fourth	10 to 17	57
Fifth	18 to 27	284
Sixth	28 to 34	634
Seventh	35 to 38	1218
Eighth	39 to 41	1569
Ninth	42 to 44	1971
Tenth	45 to 47	2334

The length and the weight at birth vary very greatly. The average measurements, as given for over 450 infants in Great Britain, are, for height, males 19.5 inches, females 19.3 inches; for weight, males 7.1 pounds, females, 6.9 pounds. The weight at birth is said to be greater the nearer the mother's age is to thirty-five years, the greater the weight of the mother, the greater the number of previous pregnancies, and the earlier the appearance of the first menstruation. Race and climate are also of influence. Minot[2] believes that all of these influences work principally through prolonging or abbreviating the period of gestation, and that the variations at birth depend partly upon the duration of gestation and partly upon individual differences of the rate of growth in the uterus.

Growth of the Body after Birth.—In studying the growth of the body after birth two methods have been employed, named the "generalizing" and the "individualizing" methods. The former consists in deducing the course of growth by averages or other central values from statistics taken from a large number of individuals at different ages. It is the method more commonly employed; it shows the course of growth of the typical child, but is inexact in enabling future growth to be predicted in individual cases. The individualizing method consists in measuring the actual growth of the same individual through successive years; it shows well the relation of the individual to the type throughout the period of growth. The course of growth of British boys and girls from birth up to the age of twenty-four is graphically shown in the accompanying diagram (Fig. 229). Growth is here seen to be rapid during the first five years of life, then slower up to the tenth or the twelfth year. From thence up to the fifteenth or the seventeenth year —that is, preceding and including puberty—marked acceleration occurs, which in turn is followed by slow increase up to the twentieth or the twenty-fifth year. For from five to ten years thereafter slight increase in

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[1] C. Hecker: *Monatsschrift für Geburtskunde und Frauenkrankheiten*, 1866, xxvii.

[2] C. S. Minot: *Human Embryology*, 1892.

height occurs, while from the accumulation of fat the weight usually rises markedly up to the fiftieth or the sixtieth year. One of the most interesting results revealed by statistics is the relative growth of the two sexes. From birth up to about the age of ten or twelve, boys show a slight and increasing preponderance over girls, but the two curves are nearly parallel. The prepubertal acceleration of growth in girls, however, precedes that of boys, and is even accompanied by some check in the male growth, with the result that between the ages of twelve and fifteen girls are actually heavier and taller than boys. This fact, first pointed out in 1872 by Bowditch[1] from observations on several thousand Boston school children, has been abundantly confirmed by Pagliani in Italy, Key in Sweden, Schmidt in Germany, Porter in St. Louis, and others. At about fifteen years boys again take the lead and maintain it throughout life. Boys grow most rapidly at sixteen, girls at thirteen or fourteen, years of age; the former attain their adult stature approximately at twenty-three to twenty-five, the latter at twenty to twenty-one years. The details of growth and the actual measurements vary considerably with race; thus the supremacy of the American girl over her brother appears to be less marked and to cover a shorter period than that of the English, German, Swedish, or Italian girl. Children of well-to-do families are superior to

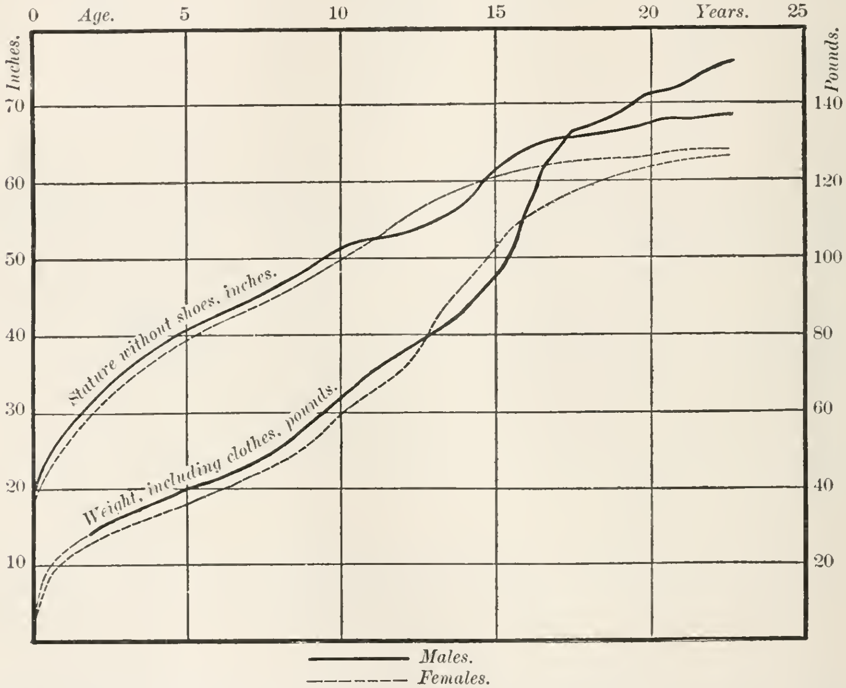

FIG. 229.—Diagram showing increase of stature and weight of both sexes, as determined by the Anthropometric Committee of the British Association.[2]

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[1] H. P. Bowditch: *Eighth Annual Report of the State Board of Health of Massachusetts*, 1877.
[2] Roberts: *Manual of Anthropometry*, 1878.

others in both weight and stature. Beyer[1] has shown that systematic exercise may markedly increase both height and weight. Disease may alter the form of the curve of growth. But the final result seems to depend less upon external conditions than upon race and sex. As an interesting accessory fact it was found by Porter[2] that well-developed children take a higher rank in school than less-developed children of the same age. If the percentage annual increase of the total weight be computed, it is found to diminish throughout life, very rapidly during the first two or three years, later more slowly and with minor variations of increase and decrease; that is, as growth proceeds and the powers of the individual mature, the power to grow becomes rapidly less. This is a peculiar and most interesting fact, and has not been explained. It would seem to signify that the sum of the vital powers declines from birth onward. Many facts indicate that the common conception, dating from the time of Aristotle, of human life as consisting of the three periods of rise, maturity, and decline, must give way to a more rational idea of a steady decline from birth.

Puberty.—By puberty is meant the period of sexual maturity, at which the individual becomes able to reproduce. In the male the exact time of its onset, characterized primarily by the appearance of fully ripe spermatozoa, is not well known, but is believed to be about one year later than in the female. In temperate climates, therefore, it usually appears in boys not before the age of fifteen; it is earlier in warmer regions. It is preceded and accompanied by acceleration in bodily growth, already spoken of. Other bodily changes, such as general maturation of the functions of the reproductive organs, alterations in the bodily proportions, increase of strength, and growth of the beard, all of which are elements of the transformation from boyhood to manhood, either occur at that time or follow soon after. One of the most obvious external changes is that of the voice. Its tone may fall permanently an octave, and for the time being become rough, broken, and uncontrollable. This is due to a rapid general enlargement of the laryngeal cartilages and a lengthening of the vocal cords.

In the girl the oncoming of puberty is marked more exactly than in the boy by the appearance of menstruation, in the majority of girls in temperate climates at the age of fourteen to seventeen. But other characteristic anatomical and physiological changes in the body occur. The uterus, the external reproductive organs, and the breasts become larger, while the pelvis widens. The prepubertal acceleration of growth has been mentioned. Nervous disorders are especially prone to make their appearance at this time. The subcutaneous layer of adipose tissue develops and confers upon the outlines the graceful curves characteristic of the woman's body. The mental faculties mature, and the girl becomes a woman earlier and more rapidly than the boy a man.

[1] H. G. Beyer: "The Influence of Exercise on Growth," *Journal of Experimental Medicine*, 1896, i. p. 546. See also "The Growth of U. S. Naval Cadets," *Proceedings of the United States Naval Institute*, 1895, xxi. p. 297.

[2] W. T. Porter: "The Physical Basis of Precocity and Dulness," *Transactions of the Academy of Science of St. Louis*, 1893, vi., No. 7. See also "The Growth of St. Louis Children," *Ibid.*, 1894, vi. No. 12.

Climacteric.—At the sixtieth year the power of producing spermatozoa, and, therefore, the reproductive power of man, begins to wane. It continues, however, in a diminishing degree, even to extreme old age, and there is no recognized period of ending of the male sexual life.

In woman, on the other hand, the sexual period continues for only thirty to thirty-five years, and the climacteric, menopause, or change of life, marks a definite ending of the power of reproduction. In temperate climates it occurs usually between the ages of forty-four and forty-seven; in warmer regions it comes early, in colder late. It is earlier in the laboring classes, and later where menstruation has first appeared early. Its most characteristic feature is the cessation of menstruation, which is a gradual process extending over a period of two or three years and characterized by irregularity in the oncoming and the quantity of the flow, and by gradual diminution. But the cessation of the menses is but one phenomenon in a long series of changes that profoundly affect the whole organism and endanger life. The reproductive organs and the breasts diminish in size, and ovulation ceases. The changes in the pelvic organs are in general the reverse of those occurring at puberty. The organic functions generally are rendered irregular; dyspepsia, cardiac palpitation, sweating, and vasomotor changes are frequent; vertigo, neuralgia, rheumatism, and gout are not rare; a tendency to obesity occurs, though sometimes the reverse; irritability, fear, hysteria, and melancholia may be present; the disposition may be temporarily altered; all of which changes indicate that the female organism at this time suffers a profound nervous shock. The loss of the weighty function of reproduction and the adaptation to the new order of events are not accomplished quietly.

Senescence.—The progressive diminution in the power of growth from birth onward throughout life has been mentioned, and may be interpreted as indicating that the process of senescence begins with the beginning of life.[1] In the broadest sense this is true, and is confirmed by a study of various organic functions. In the more restricted sense senescence or old age comprises the period from about fifty years (in woman from the climacteric) onward, during which there is a noticeable progressive waning of the vital powers. The leading somatic changes accompanying old age are atrophic and degenerative, but detailed statistics of this period are almost wholly wanting. A marked cellular difference between the young and the old, which is shown by nearly if not quite all tissues, is the relatively large nucleus and small quantity of cytoplasm in the young, the proportions being reversed in the old. This has been pointed out as follows by Hodge[2] in the nerve-cells of the first cervical spinal ganglion:

	Volume of nucleus.	Nucleoli observable in nuclei.	Pigment much.	Pigment little.
Fetus (at birth)	100 per cent.	in 53 per cent.		
Old man (at ninety-two years)	64.2 "	in 5 "	67 per cent.	33 per cent.

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[1] *Cf.* C. S. Minot: *Journal of Physiology*, 1891, xii.

[2] C. F. Hodge: *Anatomischer Anzeiger*, 1894, ix.: *Journal of Physiology*, 1894, xvii.

Thus with the progress of age the nuclei become small and irregular in outline, and the cytoplasm pigmented, while the nucleoli are often wanting. The nuclear differences are even more marked in the cerebral ganglia of bees, where moreover, aged individuals possess a smaller number of nerve-cells than the young. The nuclear differences accord with the common belief that the nucleus is the formative centre of the cell. It has been shown that a decrease in the weight of the whole brain occurs in both men and women, beginning in the former at about fifty-five years, in the latter at about forty-five years. In eminent men the decrease begins later. The thickness of the cortex and the number of tangential fibres in it diminish especially after fifty years, and this probably signifies a loss of cells. There is a decrease in general brain-power, in power of origination, in the power to map out new paths of conduction and association in the central nervous system and thus to form habits. Reaction-time is lengthened. The delicacy of the sense-organs is noticeably less, and in the eye the hardening of the crystalline lens and the weakening of the ciliary muscle diminish the power of accommodation. The muscles atrophy and muscular strength is reduced. The pineal gland, ligaments, tendons, cartilage, and the walls of the arteries, show a tendency toward calcification, and the bones become more brittle. Subcutaneous adipose tissue disappears, but a fatty degeneration of cells is not uncommon, notably in all varieties of muscle-cells, in nerve-cells, and probably in gland-cells. The pigment of the hairs disappears. The size of the muscles, the liver, the spleen, the lymphatic and probably the digestive glands, decreases. The heart and the kidneys seem to retain their adult size. The vital capacity of the lungs, the amounts of carbonic acid and of urine excreted, diminish. The rate of respiration and of the heart-beat rises slightly. Ovulation is wanting, and the power of producing spermatozoa is lessened. The stature undergoes a slight and steady decrease. Boas[1] has shown that in the North American Indian this continues from about thirty years of age onward. All of these changes, the details of which should be carefully studied and reduced to anatomical and physiological exactness, demonstrate that senescence is characterized by a steady diminution of vitality.

Death.—Sooner or later vitality must cease and the change that is called death must come. The term "death" is used in two senses, according as it is applied to the whole organism or to the individual tissues of which the organism is composed. The former is distinguished as somatic death, or death simply, the latter as the death of the tissues.

Somatic death occurs when one or more of the organic functions is so disturbed that the harmonious exercise of all the functions becomes impossible. Thus, if the brain receives a severe concussion, the co-ordination of the organs may be interrupted; if the respiration ceases, the necessary oxygen is withheld; if the heart fails, the distribution of oxygen and food and the collection of wastes come to an end; if the kidneys are diseased, the poisonous urea is retained within the tissues. A continuation of any one of these profound abnormal conditions, which may be brought about by accident or disease, or a

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[1] F. Boas: *Verhandlungen der Berliner Anthropologischen Gesellschaft*, 1895.

simultaneous occurrence of several slight disturbances of function, such as is not infrequent in aged persons, may prevent the restoration of that concordance among the organs without which the individual cannot live. The most convenient and most certain sign by which somatic death may be recognized is the absence of the beat of the heart, and in nearly all cases this is the criterion employed. But it should be borne in mind that the failure of the heart to beat is but one of the causes, and frequently a very secondary one, the primary cause being then associated with other functions. It is at present in most cases quite impossible to trace the course of events by which the derangement of one function leads to the ultimate cessation of individual life.

Death of the tissues or of the living substance is neither necessarily nor usually simultaneous with somatic death. Constantly throughout life the molecules of living matter are being disintegrated, and whole cells die and are cast away; life and death are concomitants. With the cessation of the individual life the nervous system dies almost immediately. With the muscular tissue it is very different. The stopping of the beat of the heart is a gradual process, and, as Harvey long ago pointed out, the last portion to beat, the *ultimum moriens*, is the right auricle. For many minutes after death the heart, if exposed, will be found to be excitable and to respond by single contractions to single stimuli. Irritability is said to continue in the smooth muscle of the stomach and the intestines for forty-five minutes, and considerably later than this the striated muscles of the limbs can still be made to twitch by proper stimuli, in the cat and rabbit after twelve or fourteen hours.[1] Gland-cells die probably within a few minutes. As to the chemical changes undergone by the protoplasm in the process of dying, little can be said. The composition of dead protoplasm is comparatively well known, that of living protoplasm is at present largely a blank; and, although investigation has gone sufficiently far to offer a basis for several suggestive hypotheses, the latter are too abstruse for lucid discussion in the present space. Neither in somatic death nor in the death of the tissues does the body lose weight. Within fifteen or twenty hours it cools to the temperature of the surrounding medium. Rigor mortis, due to the coagulation of the muscle-plasma within the muscle-cells, begins within a time varying with the cause of death from a half hour to twenty or thirty hours, and continues upon an average twenty-four to thirty-six hours. Then the tissues soften, and soon putrefactive changes begin.

Theory of Death.—It has been intimated that all the tissues are destined to die. An exception must be made in the case of those germ-cells, both male and female, that are employed in the production of new individuals. They pass from one individual, the parent, to another, the offspring, and thus cannot be said to undergo death. This is the basis of Weismann's theory of the origin and significance of death in the organic world.[2] According to Weismann, primitive protoplasm was not endowed with the property of death. As found in the simplest individuals, like the *Amœba*, even at the present

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[1] Lee, Adler, and Bulkley: *American Journal of Physiology*, 1900, iii. p. xxix.

[2] A. Weismann: *Essays upon Heredity*, 1889, i.

day, with a continuance of the proper nutritive conditions protoplasm does not grow old and die; the single individual divides into two and life continues unceasing, unless accident or other untoward event interferes. With the progress of evolution, however, the cells of the individual body have become differentiated into germ-cells and somatic cells, the former subserving the reproduction of the species, the latter all the other bodily functions. Germ-cells are passed on from parent to offspring; they never die, they are immortal. Somatic cells, on the other hand, grow old, and at last perish. Death was, therefore, in the beginning, not a necessary adjunct to life; it is not inherent in primitive protoplasm, but has been acquired along with the differentiation of protoplasm into germ-plasm and somatoplasm, and the introduction of a sexual method of reproduction. It has been acquired because it is to the advantage of the species to possess it; in the simplest cases it should occur at the close of the reproductive period, and in fact it frequently does occur then. A superabundance of aged individuals, after they have ceased to be reproductive, would be detrimental to the race; it is to the advantage of the species that they be put out of the way. Death of the individual in order that the species may survive has, therefore, become an established principle of nature. But the higher animals are better able to protect themselves from destruction than the lower, and, moreover, they are needed to rear the young; hence in them the duration of life is frequently prolonged beyond the reproductive period.

Weismann's theory has been the cause of much discussion, and the pros and cons have been set forth by eminent biological authorities. In its application to the human race it would seem that the factors of social evolution have brought it about that the aged are protected in the struggle for existence for long after their reproductive usefulness has ceased, and thus the working of a pitiless biological law has become modified.

F. HEREDITY.

Biologists are accustomed to recognize two factors as responsible for the character and actions of the living organism. These are heredity and the environment. Heredity includes whatever is transmitted, either as actual or as potential characteristics, by parents to offspring. The environment comprises both material and immaterial components, such as food, water, air, or other substances that surround the organism, and the forces of nature, such as light, heat, electricity, and gravity, that act as conditions of existence or as stimuli to action. The same principles apply to the character and actions of every cell of a many-celled organism, but here we must include in the environmental factor the mysterious influences that are exerted upon the cell by the other cells of the body. Of these two factors heredity acts from within, the environment from without the living substance. Among unicellular organisms the individual begins his career when the bit of protoplasm that constitutes his body is separated from the parent bit of protoplasm. Among higher forms, including man, the term individual may be applied to the fertilized ovum; the union of the ovum and the spermatozoon inaugurates the new being. From the inception to the death of the individual, life consists partly of manifestations of the powers conferred by the germ-cells and partly of reactions to environmental influences. In considering the details of vital action we are apt to overlook these fundamental facts and to evolve narrow and erroneous views as to the causes of vital phenomena. Biologists are seeking with increasing vigor to determine the relative importance of the parts played by these two principles in development and in daily life. It is needless to say that the problem is a difficult one and is still far from solution. In previous chapters of this book attention has been directed more especially to the external than to the hereditary factor. A work upon physiology would be incomplete, however, if it did not include an examination of the latter, especially since at the present time heredity is one of the leading subjects of biological research and discussion. It is proposed, therefore, in this section to present a brief outline of the facts, the principles, and the attempted explanations of the modes of working of heredity. It should be premised that, because of the present incomplete state of our knowledge of the facts, the highly speculative and involved character of most of the theories, and the constant, active shifting of ideas and points of view, such an outline must necessarily be incomplete and in many respects unsatisfactory.

Facts of Inheritance.—It is not proposed in this paragraph to enter into a discussion of the question as to whether a particular vital phenomenon is a fact of inheritance or a reaction to external influences. For our present purposes it is sufficient to record the common facts of resemblance to ancestors, and to assume that such resemblance, when present, has been inherited. Resemblances are strongest between child and parents, and appear in a diminishing ratio backward along the ancestral line. Galton[1] has computed that, of the total heritage of the child, each of the two parents contributes one-fourth, each of the four grandparents one-sixteenth, and the remaining one-fourth is handed down by more remote ancestors. The correctness of this estimate has been disputed by Weismann. The fact must not be overlooked that, in addition to and back of all the particular individual features that are inherited, a host of racial characteristics are transmitted—the progeny of a given species belongs to that species; the human being is the father of the human child, the child of Caucasian parents is a Caucasian, of negro parents a negro.

Congenital resemblances may be anatomical, physiological, or psychological, and in each of these classes they may be normal or pathological. Anatomical resemblances are the most commonly recognized of all: facial features, stature, color of eyes and of hair, supernumerary digits, excessive hairiness of body, cleft palate, monstrosities, and various defects of the eye, such as those that give rise to hypermetropia, myopia, cataract, color-blindness, and strabismus, are all known examples. Physiological peculiarities that may be transmitted include the tendency to characteristic gestures, locomotion and other muscular movements, longevity or short life, tendency to thinness or obesity, handwriting,

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[1] Francis Galton: *Natural Inheritance*, 1889, p. 134.

voice, hæmatophilia or tendency to profuse hemorrhage from slight wounds, gout, epilepsy, and asthma. Psychological inheritances comprise habits of mind, talent, artistic and moral qualities, tastes, traits of character, temperament, ambition, insanity and other mental diseases, and tendencies to crime and to suicide.

Latent Characters; Reversion.—Characters that never appear in the parent may yet be transmitted through him from grandparent to child; such characters are called *latent*. Among the most striking latent characters are those connected with sex. Darwin[1] says: "In every female all the secondary male characters, and in every male all the secondary female characters, apparently exist in a latent state, ready to be evolved under certain conditions." Thus, a girl may inherit female secondary sexual peculiarities of her paternal grandmother that are latent in her father, or a boy may inherit from his maternal grandfather characteristics that never show in his mother. An excellent example of such transmission, taken from the herbivora, is the common one of a bull conveying to his female descendants the good milking qualities of his female ancestors. In the human species hydrocele, necessarily a disease of the male, has been known to be inherited from the maternal grandfather, and hence must have been latent in the mother's organism. That in such cases the character is really potential, though latent in the intermediate ancestor, is rendered probable by such well-known facts as the appearance of female characteristics in castrated males, and of male characteristics in females with diseased ovaries or after the end of the normal sexual life.

Latency may be offered as the explanation of the numerous cases of *atavism*, or *reversion*, by which is meant the appearance in an individual of peculiarities that were formerly known only in the grandparents or more remote ancestors, but not in the parents of the individual. This subject is one of the most important in the whole field of heredity. Almost any character may reappear even after many generations. In the human species stronger likeness to grandparents than to parents is a frequent occurrence. The majority of the frequent anomalies of the dissecting-room are regarded as reversions toward the simian ancestors of the human race. The crossing of two strains develops a strong tendency to reversion, and because of this the principle of atavism must constantly be taken into account by breeders of animals and growers of plants. As an example of reversion after crossing may be mentioned the well-known one, studied by Darwin, of the frequent appearance of marked stripes upon the legs of the mule, the mule being a hybrid from the horse and the ass, both of which are comparatively unstriped but are undoubtedly descended from a striped zebra-like ancestor. Here the capacity of developing stripes is regarded as latent in both the horse and the ass, but as made evident in the mule by the mysterious influence of crossing. Darwin thinks likewise that the customary degraded state of half-castes may be due to reversion to a primitive savage condition which, usually latent in

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[1] Charles Darwin: *The Variation of Animals and Plants under Domestication*, 1892, vol. ii., 2d ed.

both civilized and savage races, is rendered manifest in the offspring that results from the union of the two. Reversionary characters are often more prominent during youth than during later life—a fact that has been quoted in favor of their explanation on the theory of latency.

Regeneration.—The facts of regeneration of lost parts must also be taken into account in a theory of heredity. Such regeneration may be either physiological or pathological. *Physiological* or *normal regeneration* has reference to the reproduction of parts that takes place during the normal life of the individual, such as the constant growth of the deeper layers of the epidermis to replace the outer layers that are as constantly being shed. *Pathological regeneration* refers to the replacement of parts lost by accident, and presents the more interesting and striking examples. The power of pathological regeneration in man and the higher mammals is limited. A denuded surface may be re-covered with epithelium; the central end of a cut nerve may grow anew to its termination; the parts of a broken bone may reunite; muscle may reappear; connective-tissue, blood-corpuscles, and blood-vessels may develop readily; and in the healing of every wound a regeneration of parts takes place. But in descending the scale of animal life the regenerative power becomes progressively stronger, and in many plants and low animals it is marvellous. Thus, the newt may replace a lost leg, the crab a lost claw, the snail an eyestalk and eye. If an earth-worm be cut in two, one half may regenerate a new half, complete in all respects. A hydra may be chopped into fragments and each fragment may re-grow into a complete hydra. From a small piece of the leaf of a begonia, planted in moist earth, a new plant with all its parts may arise. It is evident that the existing parts of an organism, if not too specialized, possess the power of restoring parts that are lost; under ordinary circumstances this power is latent. The growth of tumors is perhaps allied in nature to regeneration. A study of regeneration shows that in many cases the process of building anew follows the same course as the original embryonic growth. It is properly a phenomenon of heredity.

The Inheritance of Acquired Characters.—No topic in heredity has been more debated during the past twenty years than that of the possibility of the transmission to the offspring of characteristics that are acquired by the parents previous to the discharge of the germ-cells, or, in the case of the mammalian female, previous to parturition. Obviously, no one denies this possibility in the unicellular organisms, where reproduction by fission prevails, for there the protoplasm of the body of one parent becomes the substance of two offspring; in the transformation nothing is lost, and hence whatever peculiarities the ancestral protoplasm has acquired are transferred bodily to the descendants. But in multicellular forms, where sexual reproduction exists, the case is very different, for here whatever is transmitted is transmitted through germinal cells, or *germ-plasm*, as the hereditary substance contained in the germ-cells is now commonly called. The problem then resolves itself into that of the relation of the germ-plasm to the protoplasm of the rest of the body, the so-called *somatoplasm;* and the question to be answered is this: Are variations in the parental somatoplasm capable of inducing such changes in the germ-plasm that somatic peculiarities appear in the offspring similar to those possessed by the parent? Weismann classifies all somatic variations according to their origin into three groups—viz. injuries, functional variations, and variations, mainly climatic, that depend upon the environment. The problem of their inheritance is a far-reaching one, and upon its correct solution depend principles that are of much wider application than simply to matters of heredity; for if acquired characters can be inherited, there is revealed to us a most potent factor in the transformation of species, and the whole question of the possibility of use and disuse as factors of evolution is presented. The larger evolutionary problem need not here be considered.

Regarding the problem of the inheritance of acquired characteristics we may say at once that it is not yet solved. To the lay mind this may seem strange, for at first thought it appears self-evident that parents may transmit to their children peculiarities that they themselves have acquired. Affirmative evidence seems all about us, as witness the undoubted cases of inheritance of artistic tastes, of talent, of traits valuable in professional life, which seem to originate in the industry of the parent. But scientific analysis by Weismann and others of popular impressions, popular anecdotes and hearsay evidence, and accurate original observation, have revealed little that cannot as well be explained on other hypotheses. Anatomical and functional peculiarities of the body that are apparently new often reappear in successive generations, but to assume that they are acquired by the somatoplasm and have become congenital, rather than that they are germinal from the first, is unwarranted. Direct experiments by various investigators are almost as inconclusive. Weismann[1] has removed the tails of white mice for five successive generations, and yet of 901 young every individual was born with a tail normal in length and in other respects. Bos[2] has experimented similarly upon rats for ten generations without observing any diminution of the tails. The practice of circumcision for centuries has resulted in no reduction of the prepuce. The binding of the feet of Chinese girls has not resulted in any congenital malformation of the Chinese foot. Brown-Séquard,[3] and later Obersteiner,[4] have artificially produced epilepsy in guinea-pigs by various operations upon the central nervous system and the peripheral nerves, and the offspring of such parents have been epileptic. At first this would seem to amount to proof of the actual hereditary transmission of mutilations, yet in these cases the mutilation itself was not transmitted; the offspring were weak and sickly and exhibited a variety of abnormal nervous and nutritional symptoms, among which was a tendency toward epileptiform convulsions, the cause of which is still to be explained. Evidence from palæontology regarding the apparent gradual accumulation of the effects of use and disuse throughout a long-continued animal series seems to require the assumption of

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[1] A. Weismann: *Essays upon Heredity*, vol. i., 1889, p. 432.

[2] J. R. Bos: *Biologisches Centralblatt*, xi., 1891, S. 734.

[3] E. Brown-Séquard: *Researches on Epilepsy, etc.*, Boston, 1857; also various later papers.

[4] H. Obersteiner: *Medizinische Jahrbücher*, Wien 1875, S. 179.

such a principle as the inheritance of acquired characters, but even here the principle of natural selection may perhaps be equally explanatory.

The Inheritance of Diseases.—The question of the inheritance of diseases has also been much discussed. The same general principles apply here as in the inheritance of normal characteristics. The fact has been mentioned above that pathological characters, whether anatomical, physiological, or psychological, are capable of transmission. If, however, a pathological character has been acquired by the parent and is not inherent in his own germ-cells, it is extremely doubtful whether it can be passed on to the child. A diseased parent, on the other hand, may produce offspring that are constitutionally weak or that are even predisposed toward the parental disease, and such offspring may develop the parent's ailment. In such cases constitutional weakness or predisposition, and not actual disease, is inherited; the disease itself later attacks the weak or predisposed body. Proneness to mildness or severity of, and immunity toward, certain diseases seem to be transmissible. These subjects, however, are so little understood, and the real meaning of such terms as predisposition, inherited constitutional weakness, and inherited immunity, is so little known, that it is idle to discuss them here.

Considerable experimental work has been performed recently upon the transmissibility of infectious diseases. Undoubtedly infectious diseases cling to a particular family for generations. The transmitted factor is probably frequently, if not usually, simple predisposition. But in an increasing number of cases there appears to be transmission of a specific micro-organism. Such transmission is called *germinal* when the micro-organism is conveyed in the ovum or the semen, and *placental* or *intra-uterine* when the micro-organism reaches the fetus after uterine development has begun, and chiefly through the circulation. Of germinal infections syphilis seems undoubtedly capable of transmission within either the ovum or the semen. The possibility of germinal transmission of tuberculosis has been maintained, but is not fully proven. Of intra-uterine infections there have been observed in human beings apparently undoubted cases of typhoid fever, relapsing fever, scarlatina, endocarditis, small-pox, measles, croupous pneumonia, anthrax, syphilis, and possibly tuberculosis and Asiatic cholera. It is obvious that neither germinal nor placental inheritance, both taking place through the medium of a specific micro-organism, and not through the modification of germ-plasm, is comparable to inheritance in the customary sense.

Theories of Inheritance.—From early historical times theories of inheritance have not been wanting. Physical and metaphysical, materialistic and spiritualistic theories have had their day. Previous to the discovery of the spermatozoon (Hamm, Leeuwenhoek, 1677) all theories were necessarily fantastic, and for nearly two hundred years later they were crude. The theories that are now rife may be said to date from 1864, when Herbert Spencer published his *Principles of Biology*. Since that date they have become numerous. Even the modern theories are highly speculative; none can be regarded as being accepted to the exclusion of all others by a large majority of scientific workers, and the excuse for introducing them into a text-book of physiology is the hope that a brief discussion of them may prove suggestive, stimulating, and productive of investigation.

Germ-plasm.—Germinal substance, germ-plasm (Weismann), or, as it is sometimes called, *idioplasm* (Nägeli), must lie at the basis of all scientific theories of heredity. The father and the mother contribute to the child the spermatozoon and the ovum respectively, and within these two bits of protoplasm there must be contained potentially the qualities of the two parents. There is the strongest evidence in favor of the prevailing view that the nucleus alone of each germ-cell is essentially hereditary, or, more exactly, that the chromatic substance of the nucleus is the sole actual germinal substance. We have seen that the tail of the spermatozoon is a locomotive organ, and that the body of the ovum is nutritive matter. We have seen also that the essence of the whole process of fertilization is a fusion of the male and the female nuclei, or, more exactly, a mingling of male and female chromosomes. Hence most physiologists agree with Strasburger and Hertwig that the chromatic substance of the nuclei of the germ-cells transmits the hereditary qualities.

As to the origin of the germ-plasm, two hypotheses have been suggested. Spencer, Darwin, Galton, and Brooks have argued in favor of a production of germ-plasm within each individual by a collocation within the reproductive organs of minute elementary vital particles—"physiological units" (Spencer), "gemmules" (Darwin)—which come from all parts of the body; hence each part of the body has its representative within every germ-cell. This hypothesis affords a ready explanation of numerous facts, but its highly speculative character, the entire absence of direct observational or experimental proof of its truth, and the demand that its conception makes upon human credulity, militate against its general acceptance. Weismann, the promulgator of the second hypothesis, denies altogether the formation of the germ-plasm from the body-tissues of the individual, and maintains its sole origin from the germ-plasm of the parent of the individual. Through the parent it comes from the grandparent, thence from the great-grandparent, and so may be traced backward through families and tribes and races to its origin in simple unicellular organisms. According to Weismann, therefore, germ-plasm is very ancient and is directly continuous from one individual to another; the parts of an individual body are derivatives of it, but they do not return to it their representatives in the form of minute particles. The general truth of Weismann's conception can hardly be denied.

As to the morphological nature of germ-plasm, two views likewise are held. One school, led by His and Weismann, holds that germ-plasm possesses a complicated architecture; that the fertilized ovum contains within its structure the rudiments or primary constituents of the various cells, tissues, and organs of which the body is destined to be composed; and that growth is a development of these already existing germs and largely independent of surrounding influences. In accordance with this idea, segmentation of the ovum is specifically a qualitative process, one blastomere representing one portion of the future adult, another blastomere another portion, and so on. This theory recalls in a refined form the crude theory of *Preformation* that was advocated during the seventeenth and eighteenth centuries by Haller, Bonnet, and many others, according to which the germ-cell was believed to contain a minute but perfectly formed model of the adult, which needed only to be enlarged and unfolded in growth. The other modern school, in which Oscar Hertwig is prominent, maintains that the fertilized egg is isotropous—that is, that one part is essentially like another part—that the architecture of the egg is relatively simple, and that growth is largely a reaction of the living substance to external influences. The idea of isotropy is based largely upon the experimental results of Pflüger, Chabry, Driesch, Wilson, Boveri, and the brothers Hertwig, who by various methods and in various animals have found that single blastomeres of a segmenting ovum, when separated from the others, will develop into normal but dwarfed larvæ; that is, a portion of the original germ-plasm is capable of giving rise to all parts of the animal. These results are interpreted to signify that segmentation, instead of being qualitative, is quantitative, each blastomere being like all the others. The second theory, like the first, resembles in some degree a theory of the past two centuries, advocated by Wolff and Harvey, and known as the theory of *Epigenesis*. According to this there was no preformation in the germ-cells, but rather a lack of organization which during growth, under guidance of a mysterious power supposed to be resident in the living substance, gave place to differentiation and the appearance of definite parts.

Modern microscopes have revealed no miniature of the adult in the egg, nor has modern physiology found necessary an assumption of extra-physical forces within living matter. With the increase of knowledge the old and crude preformation of Haller and Bonnet and the speculative epigenesis of Wolff and Harvey have given place to the new preformation and epigenesis of the present time, and all modern theories of heredity may be classed in the one or the other category or as intermediate between them. The modern advocates of preformation explain hereditary resemblance by the supposed similarity of all germ-plasm in any one line of descent. The modern advocates of epigenesis, while allowing the necessity of a material basis of germ-plasm, ascribe hereditary resemblance to similarity of environment during development.

Variation.—It is a commonplace in observation that, however close hereditary resemblance may be, it is never absolute; the child is never the exact image of the parent either physically or mentally. Variations from the parental type may be either *acquired* by the offspring subsequent to fertilization or to birth, and hence are to be traced to the action of the environment; or they may be *congenital*, that is, inherent in the germ-plasm. Although it is not always easy in the case of any one variation to determine to which class it belongs, yet the fact remains that the two classes exist; and a complete theory of heredity must recognize and explain congenital variation as fully as congenital resemblance. It is unnecessary to say that the origin of congenital variation is one of the much discussed and still unsettled questions. At least two causes of congenital variations are commonly recognized, although opinions differ as to the relative importance of the rôle played by each. These causes are differences in the nutrition of the germ-plasm, and sexual reproduction. As to the former, it is evident that the germ-plasm in no two individuals, even father and son, has exactly identical nutritional opportunities. Since the life of one individual is not the exact counterpart of the life of another, the germ-plasm of one individual has a different nutrition from that of another. It would hence be strange, even although we regard the germ-plasm as relatively stable, if with succeeding generations there did not appear variations that are sufficient to give rise to unlikeness in relatives. Differences in the nutrition of the germ-plasm in different individuals are, therefore, a true cause of variations. As regards sexual reproduction, it must be remembered that a new individual is the product of two individuals, that the two individuals have descended along different genealogical lines, and hence that the two conjugating masses of germ-plasm are different in nature. It is only to be expected, therefore, that the resulting individual shall be different from the two contributing parents. Thus sexual reproduction is a true cause of variations.

Having outlined the main facts and principles of heredity, let us now review a few of the specific theories that have been of value in clearing the clouded atmosphere.

Darwin's Theory of Pangenesis.—Darwin's "Provisional Hypothesis of Pangenesis" was published in 1868 as chapter xxvii. of his work on *The Variations of Animals and Plants under Domestication.* It was the first of the modern theories to attempt to cover the whole ground of heredity; it was accompanied by a most exhaustive presentation and analysis of facts, and it stimulated abundant discussion and investigation. In Darwin's own words the hypothesis was formulated as follows: "It is universally admitted that the cells or units of the body increase by cell-division or proliferation, retaining the same nature, and that they ultimately become converted into the various tissues and substances of the body. But besides this means of increase I assume that the units [cells] throw off minute granules which are dispersed throughout the whole system; that these, when supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived. These granules may be called gemmules. They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being; but they are likewise capable of transmission in a dormant state to future generations, and may then be developed. Their development depends on their union with other partially developed or nascent cells which precede them in the regular course of growth. . . . Gemmules are supposed to be thrown off by every unit, not only during the adult state, but during each stage of development of every organism; but not necessarily during the continued existence of the same unit. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation into buds or into the sexual elements. Hence, it is not the reproductive organs or buds which generate new organisms, but the units of which each individual is composed. These assumptions constitute the provisional hypothesis which I have called Pangenesis."

Since the cells of the body are represented by gemmules within the germ-cells, Darwin's theory is a theory of Preformation. It explains the facts of the regeneration of lost parts by the assumption that the gemmules of the part in question are disseminated throughout the body and have only to unite with the nascent cells at the point of new growth. Pangenesis explains reversion, since gemmules may lie dormant in one generation and develop in the next. It explains congenital variation, since the mixture of maternal and paternal gemmules is plainly different from the two kinds taken separately. It explains how acquired variations may become congenital, since an altered part throws off altered gemmules, and by the collocation of these in the germ-cells the alteration may be transmitted. It thus allows the transmission of acquired characters.

Darwin's assumptions of gemmules and their behavior are pure assumptions, for which subsequent investigation has not provided a basis of facts. As we have seen, also, the inheritance of acquired characters is greatly in doubt, and, if they are heritable at all, they can be so only comparatively feebly. Besides these objections it was early found that, with the increase of knowledge of the facts of heredity, it was necessary to modify very materially the theory of Pangenesis. This has been ably done successively by Galton,[1] Brooks,[2] and de Vries.[3] But neither the original theory nor its modifications have been generally accepted.

Weismann's Theory.—Since 1880, Professor Weismann[4] of Freiburg has published numerous essays upon heredity and allied subjects, in which, besides reviewing the views of others, he has developed in detail a new and elaborate theory of his own, that is the most ambitious attempt yet made to solve the problem of inheritance. In the course of their development Weismann's ideas have undergone some modification. Their leading features are as follows:

The essential hereditary substance, or germ-plasm, is the chromatin of the nucleus of the germ-cells. One of the fundamental tenets of Weismann's system is expressed by his own phrase, "the continuity of germ-plasm." By this is meant that the germ-plasm of one individual, instead of arising *de novo* in the individual by the collocation of multitudinous "gemmules" derived from the body-cells, originates directly from the germ-plasm of the parent, thence from that of the grandparent, and so on backward through all generations to the origin of all germ-plasms that took place simultaneously with the

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[1] Francis Galton: "A Theory of Heredity," *Journal of the Anthropological Institute*, 1875.

[2] W. K. Brooks: *The Laws of Heredity*, 1883.

[3] H. de Vries: *Die Intracelluläre Pangenesis*, 1889.

[4] August Weismann: *Essays upon Heredity and Kindred Biological Problems*, authorized translation, vol. i., 1889; vol. ii., 1892; *The Germ-plasm*, authorized translation, 1893; *The Effect of External Influences upon Development*, the Romanes Lecture, 1894.

origin of sex—germ-plasm is continuous from individual to individual along any one line of descent. Weismann draws a sharp line between *germ-plasm* and *somatoplasm*, or body-plasm, which latter comprises all protoplasm that the body contains except the germ-plasm. Germ-plasm once originated continues from generation to generation; somatoplasm develops anew in each generation from germ-plasm by growth and differentiation, resulting in a loss of its specific germinal character. Germ-plasm is stable in composition; somatoplasm is variable. Germ-plasm, being passed on from parent to offspring, is immortal; somatoplasm dies when the individual dies. Weismann believes that "the germ-plasm possesses a fixed architecture, which has been transmitted historically" and which represents the parts of the future organism. It consists of material particles or hereditary units called *determinants*, each of which has a definite localized position within the germ-plasm. The determinants are suggestive of Darwin's gemmules, yet they are not the same, for, while gemmules were supposed to represent individual cells, determinants are representatives of cells or groups of cells that are variable from the germ onward. Determinants consist of definite combinations of simpler units, or *biophors*, which are the smallest particles that can exhibit vital phenomena. Below biophors there come in order of simplicity of material structure the molecules and the atoms of the physicist. Above biophors and determinants Weismann finds it necessary to assume the existence of higher units, named in order *ids* and *idants*, the former being groups of determinants, and actually visible as granules of chromatin, the latter being the chromosomes of the nucleus. Each one of these various units is possessed of the fundamental vital properties of growth and multiplication by division. Such a complex system is Preformation in an extreme form. In fertilization idants of the sperm join with idants of the ovum, and the resulting segmentation nucleus consists of a mixture of paternal and maternal determinants. Within this mixture there exist in a potential state the primary constituents of a considerable number of forms which the future individual may assume. In ontogeny, or development of the individual, these primary constituents take two paths: some of the ids remain inactive and enter the germ-cells of the embryo for the production of future generations; other ids disintegrate into determinants, the determinants enter the embryonic cells that result from segmentation, and there themselves disintegrate and set free into the cytoplasm their constituent biophors; thus they determine the future character of the cells of the organism. The division of primary constituents into those that shall remain latent and those that shall become active is effected largely by the stimulation of external influences; hence, given several potential formations in the germ, external influences decide which one shall become the actual structure in the adult organism. Once set free and having become somatoplasm, neither the biophors nor the determinants are able to return to the germ-cells. In the adult, germ-plasm is never capable of reflecting in any way the characteristics of the somatoplasm which surrounds it on all sides. With its ancient ancestry it leads a charmed existence, largely independent of environmental changes. It follows that characters acquired by the adult are incapable of acquisition by the germ-plasm, and hence may not be transmitted. The *non-inheritance of acquired characters* is thus another of the fundamental tenets of Weismann's theory, and one about which he is most positive.

If these two principles of continuity of stable germ-plasm and non-inheritance of acquired characters be true, why are not all individuals in any one line of descent exactly like one another? How is congenital variation possible? In the first place, Weismann allows that germ-plasm, while eminently stable, is not absolutely so; it is subject to slight continual changes of composition resulting from inequalities in nutrition; and "these very minute fluctuations, which are imperceptible to us, are the primary cause of the greater deviations in the determinants which we finally observe in the form of individual variations." The accumulation of minute deviations may be aided greatly by sexual reproduction, or, to use Weismann's more exact term, which is equally applicable to the combination of sexual elements in sexual organisms and to the process of conjugation in the asexual forms, *amphimixis.* Given the infinitesimal beginning of a variation, the mingling of two lines of descent, with different past surroundings, may be a most powerful factor in strengthening the deviation and bringing it into recognition as a new character. Moreover, natural selection becomes here also potent as soon as the variation has assumed sufficient proportions to be seized upon by this important factor of evolution. In cases of reversion Weismann supposes the determinants to remain inactive in the germ-plasm for one or more generations and later to develop. The theory accounts for the regeneration of lost parts by the assumption that the cells in the vicinity of the wound, by the proliferation of which the new part grows, contain, besides the active determinants that have given them their specific character, other determinants that are latent until the opportunity for regeneration arrives. Some cells do not possess such latent determinants, and hence some parts of a body are incapable of reproducing lost parts.

Such are the main features of Weismann's theory—a germ-plasm of highly complex architecture and independent of somatoplasm; continuity of germ-plasm and non-inheritance of acquired somatic characters tending to preserve the uniformity of the species; slight nutritional variation of germ-plasm and sexual reproduction tending to destroy that uniformity; the result is inherited resemblance and congenital variation. The theory is now being most actively discussed.

Theory of Epigenesis.—Among epigenesists no one theory may be said to be pre-eminent. The main features of the epigenetic conception, already referred to, may be summarized as follows: The fertilized ovum is isotropous, *i. e.* all parts are essentially alike; germ-plasm probably consists of minute particles, but these particles do not represent definite cells or groups of cells of the adult; segmentation is a quantitative process; the early blastomeres are essentially alike, and any one of them, if isolated from the rest, may give rise to a whole organism, although under ordinary circumstances they react upon each other in bringing about the resultant individual; there is no predetermination, either in the germ-cells or in the segmenting ovum, of the ultimate form or function of the various constituent parts; morphological differentiation and physiological specialization are phenomena of comparatively late embryonic life, and the prospective character of any one cell, whether it is to be a muscle-cell, gland-cell, nerve-cell, or germ-cell, is determined by the influence of the surrounding cells and the surrounding physical and chemical conditions—"the prospective character of each cell is a function of its location." Extreme epigenetic views are not so numerous as those of preformation.[1]

The more moderate thinkers of the present time recognize truth in both preformation and epigenesis, and are endeavoring by experimental methods to determine how much share in the production of the characteristics of the offspring is to be ascribed to the original qualities of the germ-plasm and how much to the physical, chemical, and physiological phenomena of the immediate environment of the developing embryo. Such experimental work is performed at present upon the simpler and lower animals, mostly marine invertebrates, and has reference to the effect of changes in the composition of the water surrounding the embryo, the effects of various salts, of changes in temperature, of pressure, of electricity, etc., etc. Such work is now in its infancy, but it is doubtless destined to yield results of the highest value in an understanding of the true nature of heredity.

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[1] The best statement of a moderate epigenetic theory is to be found in O. Hertwig: *The Biological Problem of To-day; Preformation or Epigenesis?* Authorized translation.

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