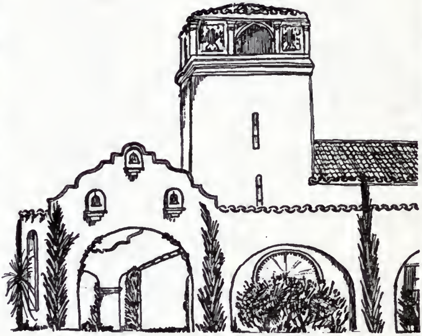

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THE ANATOMY

OF THE

CENTRAL NERVOUS SYSTEM OF MAN

AND OF

VERTEBRATES IN GENERAL.

BY

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TRANSLATED FROM THE FIFTH GERMAN EDITION

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TO HIS TEACHER,

PROFESSOR WILHELM WALDEYER,

THIS FIRST ATTEMPT

AT A

Comparative Anatomy of the Brain

IS

DEDICATED

IN

REVERENCE AND GRATITUDE.

THE AUTHOR.

AUTHOR'S PREFACE TO THE FIFTH GERMAN EDITION.

NOT without a certain hesitation does the author come with this edition before his circle of readers. Though the previously small book has now grown to larger proportions, still it presents a subject which has not previously been comprehensively treated: *the comparative morphology* of the *central nervous system.*

Three parts have arisen from the original little work: parts which are so far independent of each other that they who have less interest for the more general matters and for comparative anatomy, by turning past the first two parts will find in the third a somewhat enlarged and richly-illustrated edition of the old book. Grateful for the interest which the medical profession have manifested in the work, the third part, which deals exclusively with the mammalian, and especially with the human, brain, has been carefully rewritten and enlarged through the addition of numerous figures made from photographs of sections. In order to facilitate the study from sections a complete series of frontal sections through the entire brain has been added.

Part I is introductory, giving the *fundamental ideas* accepted at the present time. It takes into consideration also *function,* which was not considered in earlier editions.

The second part of the book realizes finally a plan which, since the beginning of my studies in brain-anatomy, I have never allowed to escape my eye. Resting almost completely upon my own investigations, it gives a review of that which may be said, with some certainty, of the structure and course of development of the central nervous system in the vertebrate series. Those who have worked in this field, still cultivated, will, considering the difficulties which tower up everywhere, leniently judge that which is proffered. The first attempt at a general presentation, the book shows everywhere the insufficiencies which such a work must present. No one knows that better than the author himself. If, as here, the plan of the whole forbids going into details, it will not be possible to always give a sufficient foundation for that which is presented. So far as it has been possible, this has been supplied in the numerous figures whose addition has been made possible through the liberality of the publishers. This edition contains 113 figures more than the Fourth, and of the new ones, 99 are devoted to comparative anatomy. The central nervous system has formerly been studied mostly by physicians. To them, naturally, the first task was to gain a better understanding of the human brain, only the mammalian brain being brought in for comparison. We possess, however, even of the lower vertebrate types, several excellent descriptions.

By comparing animals low down in the vertebrate series the attempt is here made to determine where particular structures appear, how they vary, and what functions they may perform at different stages of their development. It has also been attempted to determine what belongs to each separate part of the nervous system as essential and fundamental. It is an attempt in which the author believed himself justified, in view of the fact that he had been occupied ten years in studies in the realm of comparative neurology.

The preface to the second edition of this book closed with the following words: "There must be a number of anatomical mechanisms which are alike present in all vertebrates: those which make possible the simplest expressions of the activity of the central nervous system. It is only necessary to find that animal, or that stage of development of any animal, in which this or that mechanism appears in so simple a form that it may be completely understood. Once one has anywhere perfectly established the relation of such a mechanism—*e.g.*, a nerve-bundle or a cellular structure—he is usually able to readily find it again even where, through adventitious matter, it is made more or less obscure. The discovery of such fundamental features of brain-structure appears to be the next and most important task of brain-morphology. Once we know them, it will be easier to understand the complicated mechanisms with which the more highly organized brain performs its function."

This was, in a way, a programme which has, in part, been carried out in the new edition.

EDINGER.

FRANKFURT-AM-MAIN, JUNE, 1896.

TRANSLATOR'S PREFACE.

The hearty reception accorded by the medical students and practitioners of America to Professor Riggs's translations of the earlier German editions makes it unnecessary for the editor of the present translation to introduce the work to Professor Edinger's circle of American readers.

The additions which have been made to the original since the last English translation increases the range of its usefulness. Originally addressed particularly to the needs of the medical profession, it now contains matter which is practically indispensable to the general student of neurology or of physiological psychology in the biological departments of our universities.

In a few instances passages, in Part II of the original, which appear in fine print and serve to amplify or to further explain certain statements of the text, have been condensed or omitted, justification for this being urged in the somewhat different needs of the American readers of the work. The "lectures" of the original have been presented as *Chapters.* This necessitates an occasional departure from the diction of the original.

The translators take this opportunity to acknowledge the efficient assistance of Mr. J. C. Gordon, of the Wisconsin State University, in the preparation of the manuscript.

The fullness of the index prepared by Dr. Charles L. Mix, Instructor in Neurology in the Northwestern University Medical School, adds much to the value of the book, both in its use as a text-book and as a book for reference. The translators express herewith their appreciation of the work done by Dr. Mix in preparing the index, and also in making the final proofreading.

WINFIELD S. HALL.

CHICAGO, NOVEMBER, 1898.

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PART I.

INTRODUCTION TO THE ANATOMY OF THE CENTRAL NERVOUS SYSTEM.

CHAPTER I.

REVIEW OF THE HISTORY AND THE METHODS OF INVESTIGATION OF THE CENTRAL NERVOUS SYSTEM.

THE anatomy of the central nervous system, whose features these chapters are to present, has, since the *renaissance* of anatomy, engaged the lively interest of numerous investigators. Vesalius, Eustachio Aranzio, Variolo, and Fallopia laid the foundations upon which, in subsequent centuries, the superstructure could be built. Even in the seventeenth century there appeared extensive monographs, which, considering the technique at command at that time, must be recognized as practically exhaustive: *e.g.*, the books of Th. Willis and of Raim, Vieussens. Nevertheless Willis could still describe as new such structures as the corpus striatum, the anterior commissure, the pyramids, and the olivary bodies. Important contributions on brain-anatomy were made even at that time by Sylvius, Wepfer, and Van Leeuwenhoek, the last of whom was first to make a microscopic investigation of the brain. Malacarne, in Italy; von Soemmering, in Germany; Vicq d'Azyr and Rolando, in France, contributed much, in the latter part of the eighteenth century, to the extension of our knowledge of the brain.

As our century dawned there was scarcely anything of importance to be added to the gross anatomy of the organs of the central nervous system. Little progress had been made, however, in what we must now recognize as the most important part of the morphology of the central nervous system, namely: in the knowledge of the finer relations of the parts,—of the course of the fibers. Even investigations in the comparative anatomy which were made in the first decades of the nineteenth century made no advance in this field. What remained to be done by essentially macroscopic methods has been accomplished by Reil, Gall and Spurzheim, Arnold, Reichert, Foville, Burdach, *et al.*

Reil, in particular, who first brought into general recognition as a preparatory method the artificial hardening of the brain, had discovered a great many facts which do not appear upon the surface.

As his most important discovery one must designate the boundary of the corona radiata and the pedunculi cerebri, whose relation to the corpus callosum, which traverses them, he first recognized; the Tractus tecto-spinalis and its origin in the Corpora Quadrigemina, the Nucleus lentiformis, the insula, and many other structures were incorporated into anatomy only after his investigations.

As a landmark at the beginning of this earlier period stands Burdach's book,—"On the Structure and Life of the Brain,"—in which, appearing in 1819, the author had carefully collected everything which had been accomplished up to that time and added much explanatory matter.

Up to about the middle of this century the technique consisted, for the most part, of gross dissection with the knife and of the separation of the fibers of hardened pieces of brain-tissue with the forceps. Gall, Burdach, Reil, Arnold, and Foville discovered much with the use of such methods.

It is especially due to Tiedemann and Reichert that, through embryology, the general morphological relations came to be better understood.

But since Ehrenberg (1833) had demonstrated that the brain (*Seelenorgan*) is composed of innumerable very fine tubes, since Remak (1838) had described the ganglion-cells more exactly, and Hannover (1840) had demonstrated their connection with the nerve-fibers, it was clear that a simple dissection of the brain and cord was not sufficient to yield the desired insight into their structure and relations.

Stilling's great contribution was the introduction and use of a new method: the preparation of thin sections, or, rather, serial sections, which were made in different, but definite, directions through the organ.[1]

The preparations so made were carefully studied, their pictures combined, and thus the architecture of the central nervous system was reconstructed. Through these methods and through the studies which he made with their help, Stilling laid the foundations for the modern anatomy of the spinal cord, the medulla, the pons, and the cerebellum. On January 25, 1842, Stilling allowed a piece of cord to freeze in a temperature of —16° C. (3° F.), and then made, with a scalpel, a fairly-thin cross-section of the same. "When I brought this under the microscope," he writes, "and with 15-diameters' magnification beheld the transverse commissural fibers, I was conscious of having found a key which unlocked the secrets of the wonderful structure of the spinal cord. Archimedes did not more joyfully shout 'Eureka' than did I at that sight."

Stilling's method is the one still most used for the study of the central nervous system. Its application is much facilitated by the hardening of the nervous tissue through dilute chromic acid or solution of chrome-salts: a procedure introduced by Hannover and Eckhard. The sections are

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[1] Rolando had previously made thin sections of the central nervous system (1824), but the reconstruction of the organs through combinations of extended series of sections is due particularly to Stilling.

made mostly with the microtome, which makes possible exact sectioning and large sections of unvarying thickness. Faultless serial sections of an entire human brain can now be prepared less than $^1/_{20}$ millimetre in thickness.

The sections may be studied unstained. All that Stilling found was seen in such unstained preparations. It is advisable, however, to stain them. We are indebted to Gerlach (1858) for having first drawn attention to the advantage to be gained through a soaking of the preparation in carmin. Later times have produced many staining methods; especially have anilin stains (nigrosin, etc.) been used. But only recently have we, through Golgi (1883), found a method which accomplishes more than the old one of Gerlach. This method is based upon the action of chrome-silver: blackening the cells and their processes. To it we are indebted for an entirely new and unexpected insight into the finer structure of the central nervous system.

Nissl first made it possible, through careful hardening and after-treatment with anilin stains, to make preparations which furnished a glimpse into the structure of a ganglion-cell. The course of fibers is not made much plainer through carmin staining. On the other hand, it is possible, through Weigert's (1884) valuable method of hæmatoxylin staining, to stain even the finest fibers a deep blue-black, and so, following Stilling's method, trace their course more easily than was formerly possible. One may also get beautiful preparations through treatment of the tissue with osmic acid, following Exner and Bellonci.

Since the time of Clarke's recommendations on this point (1851), the stained sections are dehydrated in alcohol and then through an ethereal oil or through xylol made transparent ("cleared").

In 1886 Ehrlich showed that it is possible, with methyl-blue, to stain axis-cylinders and ganglion-cells of living animals. In the hands of Retzius and others this process has become of the greatest importance for the investigation of the finer structure of these portions of the central nervous system.

Most of the investigators who have worked upon the central nervous system during the second half of this century have followed Stilling's methods.

We are indebted to two men, Stilling and Meynert, for most that we know of the minute structure of the brain and cord. It is to be noted that all later investigators have proceeded from that which these men established.

Benedict Stilling laid the foundation of all our knowledge of the pons, the cerebellum, the medulla, and the spinal cord through a series of most important works bearing testimony to unapproached industry: works which are certain to make for the great Cassel physician a *monumentum ære perennius.*

Meynert, however, not only systematically worked through the whole field of brain- and cord- anatomy, discovering, through sections and dissections, more new facts than had any previous investigator, Stilling excepted; but, upon minute anatomy as a basis, he formulated a theory of brain-structure which has equally influenced anatomy and psychology, bearing fruit up to the present time and stimulating investigators to new discoveries.

From the nature of the Stilling method it follows that the tracing of a nerve-tract for considerable distances is made certain only so long as the elements which combine to form it are not interrupted by ganglion-cells or turn out of the plane of the section, so long as it does not pass into a fiber mesh-work or from one bundle split up into numerous diverged fibrillæ. Even in the spinal cord of the smallest animals it seldom occurs that the entire course of a fiber may be seen in the plane of one section.

It was, therefore, necessary, after getting one's bearings in this difficult field through Stilling's work, to seek for further methods which would permit the finding and tracing of nerve-tracts.

As is well known, Waller (1852) showed that *severed nerves degenerate in a definite direction.* Türck had already shown (1850) that even the interruption of conduction in the spinal cord leads to degeneration, which progresses upward in some tracts and downward in others.

Through his studies, as well as through those of Bouchard, Flechsig, Charcot, *et al*, it was successfully demonstrated that in definite tracts of the spinal cord and the brain lie fibers which, when degenerated, separate themselves from the normal tissues along their entire course, and may thus be easily followed. The study of these secondary degenerations has since become important for the advance of the science with which we are employed. For this reason let us for a moment discuss Waller's law somewhat more in detail.

It is now formulated as follows: *The axis-cylinder of a nerve-fiber remains intact only so long as it is in connection with its parent-cell. It degenerates along with its sheath beyond the point where its connection with the parent-cell is severed.* But Forel has shown that, in the newborn after simple severing of the nerve and in adults if the nerve is divided very near to the nucleus (ganglion-cell), degeneration may occur also in the nerve-segment which is connected with the cell. Bregmann has also, in an investigation especially planned with this point in view, confirmed the theory of the degeneration of the central stump. This apparent contradiction of Waller's law has been solved by the studies of Nissl. Nissl has shown that a harmful influence is exerted upon the central cell from the point where the nerve is severed, and that the cell may be temporarily much damaged, at any rate structurally modified. In such cases the degeneration of the central segment of the axis-cylinder also supervenes, simply because it is not in connection with a *normal* parent-cell. In the consideration of secondary degenerations one must, in future, give due weight to these facts, which are of especial importance pathologically.

The region through which such a degeneration is always propagated is called a *tract* (*Fasersystem*). A number of diseases of the spinal cord, either in their inception or throughout their course, affect particular tracts: *e.g.*, only the posterior tracts of the spinal cord. Such diseases are called "System-diseases." The study of such diseases can be utilized for the increase of our knowledge of the course of nerve-tracts (Flechsig, Westphal, Strümpell). Further, through an exact study of pathological changes Charcot and his pupils—especially Pitres, Féré, Bellet, Brissaud, *et al*—have added much to our knowledge of brain-anatomy.

Occasionally malformations make it possible to differentiate one tract from another more readily than in the normal brain. Thus Kaufmann and others were able to study cases of absence of the corpus callosum in which, just because of the absence of the commissure in question, other features of the brain came out into previously unknown prominence. These observations suggested the experimental severing of particular parts of the roots or of the spinal cord, and, through the intentionally induced secondary degeneration, to gain further knowledge of the structure. Numerous experiments of this kind were made, and for many important facts we have to thank those experimenters who proceeded in this way. For example, through the nerve-cutting experiments of Singer and of Schiefferdecker and later of Löwenthal, Sherrington, Mott, *et al*, our knowledge of the course of nerve-roots in the spinal cord has been much enriched.

Such degenerations may be studied according to one or the other of two methods: One may either wait for the complete destruction of the fibers and then follow the course of the atrophied tract, or one may, within a few weeks after the operation, treat a preparation with a solution of osmic acid, which blackens the products of degeneration (Marchi). The last method especially gives very clear pictures, showing the degenerated fibers in lines of black points upon a clear field.

If, in a newborn animal, peripheral or central nerve-substance be removed, fibers involved in the injury or operation do not further develop, but, in fact, gradually, yet completely, degenerate.

Gudden (1870) used this fact to furnish us with a new and fruitful method of investigation. For example, after extirpation of an eye he followed, through means of sections, the atrophy taking place in the brain, and so found the central ending of the optic nerve in question. On whatever part of the brain he experimented he brought new and important things to light. In addition to Gudden we are also indebted to Mayser, Ganser, Forel, Monakow, and Löwenthal for important facts regarding the course of fibers in the spinal cord, the method of origin of cranial nerves, the course of the Tractus tecto-bulbaris in the brain, etc.

Occasionally cases are observed when nature herself similarly performs a Gudden experiment upon man. The author was able, in one case, to follow far up the spinal cord atrophied nerve-tracts which had been arrested in development through intra-uterine amputation of an arm; at another time opportunity was offered to study the nervous system of a child which, soon after birth, suffered an extended softening of the cortex of the parietal lobes. In the spinal cord the crossed pyramidal tracts were completely lacking.

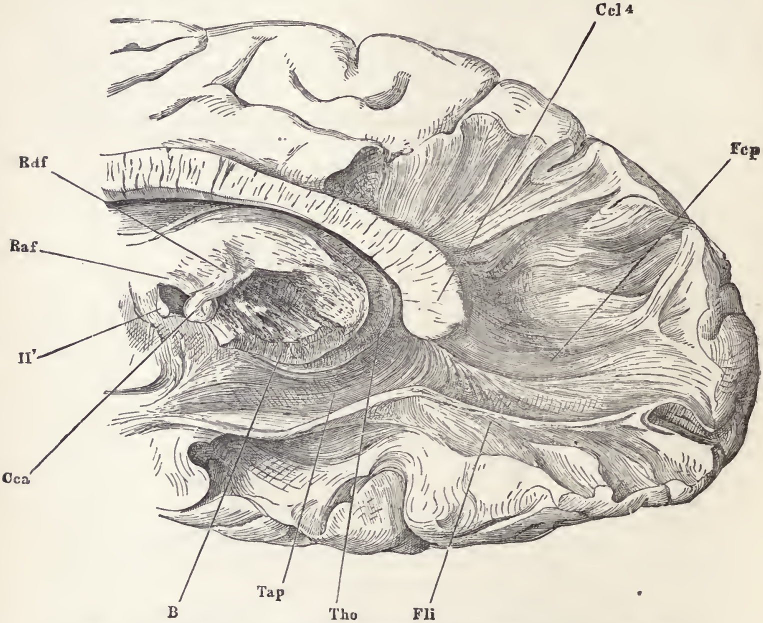

Fig. 1.—Showing the fibres of the corpus callosum prepared by teasing with forceps the hardened tissue. (After Henle.)

The knowledge of the course of nerve-tracts has made notable progress through the methods of secondary degeneration and of atrophy. But a still more fruitful source of knowledge is a new method based upon the study of the development of the nerve-sheath.

To Flechsig is due the merit of introducing and of exhaustively utilizing this new method. In a series of communications (1872-1881), and later in a larger work on the "Conducting Paths in the Brain and Spinal Cord" ("Leitungsbahnen im Gehirn u. Rückenmark," 1876), he showed that the different nerve-tracts, which, in sections of the central nervous system of an adult, appear so similar and uniform, differ essentially in the embryonic period and that they acquire their medullary sheath at different times. Whole "systems" in the cross-section of the spinal cord are still transparent at a time when others have already become white and medullated. The tracing of the white portions in cross-sections and longitudinal sections is much easier, and gives much more reliable results than does the tracing of fasciculi in fully-developed organs.

Fig. 2.—For description, see text.

A good idea of the peculiarities of the results of the methods thus far mentioned may be had from a study of the accompanying figures. Fig. 1 shows the result of a dissection, a separation of the fibers with forceps, and shows the course in the cerebrum of the fibers of the corpus callosum.

Fig. 2 is made from a frontal section through the cerebrum of a nine-months' still-born fœtus. The whole of this area is, in the adult, filled with nerve-fibers, which are difficult to follow because of their various directions and intersections. In the section in question, however, of all the numerous fibers of the cerebrum only the single tract designated the tegmental tract is medullated. In the figure the black lines locate it. At no other place in the cerebrum may medullated fibers be found. Hence Flechsig was able to discover, among the numerous little-known tracts of the cerebrum, the tegmental tract as a distinct one, and in part to trace its course.

Fig. 3 represents a section through the cervical portion of a spinal cord from a man who lost the left forearm before birth. Note that both gray and white substances—but particularly the former—are strongly atrophied on the left side. The exact determination of the extent of the atrophy justifies a conclusion as to the location of the central ends of the divided nerves.

Fig. 3.—For description, see text.

Knowledge of the general morphology of the central nervous system is gained through embryology. For our knowledge of the embryology of the organs we are now studying we are indebted especially to Kölliker, His, Tiedemann, Reichert, v. Mihalkovics, Götte, and Kupffer.

As early as the seventeenth century the first attempts were made to approach the brain in a comparative way; and the literature of the first half of this century contains a great number of monographs on the brain of the lower vertebrates. It was the fish-brain that was ever the subject of renewed study. The numerous studies of this time reached a climax in the work of Leuret and Gratiolet, on "The Vertebrate Brain"; also in such really great monographs as that of the Wolmar physician, Dr. Girgensohn, on "The Brain of Fishes" (1846). Naturally all of these works are concerned simply with the outer form of the brain. That is true, also, of several later ones, which, undertaken from the stand-point of general morphology, have given us exact knowledge regarding simply the external form. Among these may be mentioned the works of Gottsche, Viault, Valentin, Miclucho-Maklay, Baudelot, *et al*, who have given with exactness the anatomy of the selachian and teleostean brain. The brain of the amphibian and of the reptile has been much studied by comparative anatomists; there is, however, little of the older literature useful to the general morphologist except the works of Treviranus and of Carus.

But here was introduced the new technique of serial sections. Reissner and, later, Stieda were first to attempt to find their way through the difficult field by the aid of sections, and to the last-named author we are especially indebted for pioneer studies on the inner structure of the brain of the lower vertebrates. After Stieda had sectioned and figured the brains of representative fishes, amphibians, and birds, there rapidly followed other studies in the same field. Nearly all classes of animals were investigated. Fritsch devoted a beautiful monograph to the study of fishes. His statements, however, were later extended and in part much modified through a work by Mayser: a work which should be counted among the classics of brain-literature. Along with Mayser's monograph stands a work which may be especially recommended: "The Description of the Brain of Petromyzon," by Ahlborn. These works have laid the foundation for our present knowledge of the brain of the lowest vertebrates. Still, for want of good technique, they have been able to give but little relative to the minute structure.

The investigations of the Italian, Giuseppo Bellonci, alone showed what problems still resisted solution. Although Bellonci died young, the few short papers which he left belong to the very best that we possess in this field. Our knowledge of the brain of the lower vertebrates was given an especial impetus through the embryological and comparative anatomical studies of Rückhardt, to whom, next to Stieda, we owe the possibility of tracing the homology of single brain-structures of the lower vertebrates with the corresponding parts of the much better known mammalian brain. In America, where Mason had already published a comparative anatomical chart, we may mention Spitzka and his pupils; then Osborn, to whom we are indebted for important studies in commissures and on the amphibian brain; and Herrick, who with great industry studied representatives of every lower class. In England appeared the studies of Saunders. In Germany Wiedersheim, Köppen, Meyer, the author, and others were actively at work. From Australia we have received from Elliot Smith excellent studies on the brain of lower mammals. But for the most part the methods were yet quite insufficient; so that, despite much work, little reliable material was collected. The Amphibia and Reptilia have been, comparatively speaking, best worked, although certain parts of the fish-brain are at least fairly well known. The knowledge of the avian brain is most fragmentary. Its cerebral hemispheres have been studied quite insufficiently, though, through the studies of S. R. y Cajal, Van Gehuchten, and Brandis, something at least is known of the mesencephalon and of the origin of nerve-tracts. The most important study of the avian brain is that of Bumm.

The establishing of homologies has been more and more facilitated through Burkhardt's studies in comparative anatomy and through the embryological work of Kupffer and of His. Through these studies we first learned to recognize the importance in comparative studies of invaginations and evaginations observable upon the brain.

Comparative anatomy has not, up to the present time, increased our knowledge of the course of nerve-tracts as much as we were justified in expecting. The interest in the minute structure has been slight compared with that in the determination and description of the outer form, notwithstanding the fact that the former is the kernel, while the latter is but the outer shell. This may be attributed to the inadequacy of the methods which were at command. Only a few were able clearly to recognize, in the labyrinth of tracts,—present even in the lowest invertebrates,—single fasciculi, or to differentiate single ganglia and nerve-origins. Simple and clear as are the outer features of the lower vertebrate brain, the inner structure is, nevertheless, hardly less complicated, especially in those regions posterior to the Thalamencephalon, than in the mammals themselves. The cells and nerve-tracts which are involved in the simplest motor, sensory, or psychical apparatus must, indeed, be everywhere the same, and they are not altogether simple and clear even in so low a form as the larva of the cyclostomii.

That the solution of the problem might be more nearly reached, the author has endeavored to combine the comparative anatomical methods with the study of nerve-sheath development.

We are now able to stain and to trace every individual nerve-sheath. In fact, the comparative embryological method succeeded finally in finding in the embryos of the lower vertebrates the very simple relations sought for and to fix definitely upon a number of nerve-tracts as common to all vertebrates.

Of the very greatest importance for our general idea of the nervous system were the discoveries which followed upon the Golgi impregnation method and upon the Ehrlich method of vital staining with methyl-blue.

Through this amplification of the method we are finally in a position to reach a clearer understanding of the relations of the cells to each other and to obtain a more definite idea of the minute structure in general.

To these methods we are indebted for the most important discoveries made in recent years, for the insight into the previously-unknown nervous system of the invertebrates, and for Retzius' happy discovery: *that the entire nervous system of an invertebrate may, under certain circumstances, be seen in its complete connections.* Through the excellent work of this investigator we have become familiar with the peripheral and central nervous systems of representatives of numerous classes of invertebrates. The vital methyl-blue staining, which more than any other has made these results possible, is very perishable, and work with it is difficult, requiring exact estimation of the proper time, etc. So the process recently taught by Bethe for fixing, hardening, and cutting the tissue stained with methyl-blue was welcomed gladly.

It is to be expected that the method in its present perfection will make possible an especially rapid progress of knowledge.

The means to the end are many. For every single problem one must always ask the question: What method is to be applied that one will have to meet only the simplest relations? Seldom will the study of the organs of adult man lead to trustworthy results; it will usually be necessary to create artificially greater simplicity.

From time to time it has been attempted to comprise in a schematic drawing what was known of the minute anatomy of the nervous system. The oldest schematic representation of the brain-tracts known to the author is that of Descartes, in "Tractatus de Homine," which appeared in 1662. Among the older representations belonging to this class may be enumerated: schemes of the spinal cord by Kölliker, by Ludwig, by Bidder, and by Leydig, and the renowned schema of Stilling. The diagrams of Meynert, of Aeby, and of Flechsig include a larger field,—from the spinal cord to the Corpora Quadrigemina,—while that of Jelgersma includes the entire nervous system.

In the following chapters the reader will often find in the figures and in the statements what is really only a sort of *schema*. Such a method serves the purpose of presenting in the clearest possible way the most important facts regarding the nerve-tracts of the central nervous system. Not only are lines drawn to represent facts won by purely anatomical methods, but also to represent those tracts which could be determined by well-observed pathological facts. A schema is not always a picture of nerve-tracts; it is often simply a graphic representation of the conclusions which may be drawn from numerous observations. A schema is a tottering structure. It must be repaired, sometimes here, sometimes there: or often in part torn down and reconstructed. It has been contended that one has no right to construct schemata in a field where there are so many deficiencies as in our knowledge of the central nervous system. But let us join with the venerable Burdach, who wrote in 1819: "It is not alone necessary to collect building material. In every period in which a new mass of material is collected we must start anew to erect an edifice. This giving of definite form to the knowledge will in no way retard the spirit of inquiry which leads to new discoveries; on the contrary, it is only when we get a comprehensive view and behold the imperfections of our knowledge that we know what direction future investigations must take. May the attempt at such structures ever be renewed, for no such attempt fails to advance knowledge!"

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The active work in this field is shown by the fact that between 1885-1894 not fewer than 1285 studies in the anatomy of the central nervous system were reviewed in this periodical.

CHAPTER II.

FUNDAMENTAL CONCEPTIONS: GANGLION-CELL AND NERVE.

THE significance and position of the central nervous system of the Vertebrates can only be understood when one takes into consideration its development, its relation to the peripheral nerve-endings, and to the organs of special sense.

The central apparatus stands in no wise so isolated or so separated, through morphological or physiological differences, from the peripheral apparatus as it was, until recently, supposed to be.

Among both vertebrates and invertebrates both systems are derived from the outer embryonic layer: from the epiblast. In vertebrates a part of this thin lamella forms a deep, longitudinal groove which, gradually closing in and separating from the remainder of the epiblast, becomes the tubular fundament of the central nervous system. Another part of the epiblast, lying close beside the groove on either side, forms the fundament of the spinal and cranial ganglia. Many widely-disseminated places produce cells which, even in the higher animals, either remain in the periphery and form cutaneous sense-organs or they sink more or less deeply and form the fundament of other sense-organs; for example, the olfactory or auditory apparatus or the apparatus of equilibration. This relatively simple picture becomes somewhat more complicated in that many fundaments, which among invertebrates remain completely peripheral, among the vertebrates lie close beside the central system, fusing with it. It is further complicated in that, when the neural groove is once closed, cell-groups wander out from it into the periphery, there later to become independent and scattered ganglia.

The longitudinal, laminated, epithelial plate which curved in to form the groove representing the fundament of the central nervous system is called the *medullary plate*. Very early there appear in it, in all classes of vertebrates, changes which lead to the formation of different kinds of cells. Among the epithelial cells, and formed from them, appear the *Germ-cells*: large, round, protoplasmic structures,—the fundaments of the future *ganglion-cells*. The axis-cylinders grow from them later, and still later numerous other processes arise from the cell-body, thus stamping the cell as a multipolar one.

Epithelial cells remain, in part, as the boundary of the central canal of the nervous system. Then in all vertebrates they send peripherally a process which persists until in adult life and which is usually somewhat branched and ends close beneath the pia. There one often meets curious enlargements of the cell-extremity, from which, as in the epithelial cells of the sense-organs, a delicate bristle-like projection rises. In man and the higher mammals the epithelial processes do not appear to reach the periphery in the post-embryonic period. The epithelium of the central canal is ciliated.

Fig. 4.—*A*, *B*, Ganglion-cells; *c*, Neuroglia-cells; *D*, Axis-cylinder; *p*, Protoplasmic processes. From the spinal cord. (After Ranvier.)

But not by any means are all epithelial cells employed in lining the central canal. Through cell-division there arise very many new structures, and one finds that these recede farther and farther from the central canal, with whose wall they often remain in connection through a fine fibre. The branching processes of these cells form a net-work which, in the adult, may permeate the whole substance of the central nervous system, being more dense in some locations than in others. His, their discoverer, called these cells, which form a part of the frame-work, the *Spongioblast*; he designated the incomplete ganglion-cells *Neuroblasts.*

When the central nervous system has once passed its first stage of development practically the same histological relations manifest themselves as one meets in the adult condition. Let us turn our attention briefly to these.

The whole central nervous system is constructed of connective tissue and nerve-tissue. The first is represented by the sheathes of the numerous vessels, which permeate the organs everywhere as a dense net-work, and by the neuroglia.

The neuroglia consists of an infinite number of fine fibrillæ, of very different caliber, which permeate the whole central system, and, because of the innumerable intersections, present the appearance of a fine mesh-work. At many of these points of intersection thin plate-cells lie upon the fibers, giving rise to the appearance of neuroglia-fibers (*Gliafasern*) arising from these cells,—Deiter's cells (see Fig. 4, *c*).

The neuroglia-net differs somewhat in different parts of the central nervous system, and forms here and there dense accumulations in parts quite devoid of nerve-substance. Thus, a thick layer of nearly pure connective tissue covers the whole surface of the brain and cord and extends a short distance along the nerve-roots in the form of a plug. In the same way there is found on the inner surface of the central nervous system just under the epithelium an especially rich development of neuroglia. The net-work in the gray substance is in some parts denser, in others less dense, than in the white substance. The larger nerve-cells are frequently so encircled that they appear to lie in a fine meshed basket.

The neuroglia is a peculiar tissue found, as yet, only in the central nervous system,—except that the optic nerve possesses glia. It may be absolutely differentiated from other kinds of tissue by its peculiar reaction to staining when in pathological conditions. Wherever in the central nervous system nerve-substance degenerates through disease, the glia (neuroglia) appropriates the empty space. The replacement with glia has a limit only where its elements are destroyed along with the nerve-substance and where its power of growth is not sufficient to fill up the large deficit.

It has already been mentioned that the epithelium of the central canal and the ventricles sends long processes into the surrounding nerve-substance. In man these reach the external surface only in a few places. These fibers, an instructive figure of which is here presented (Fig. 5), belong naturally to the supporting tissues.

In Fig. 6 is represented (*E*) a section through the neuroglia-net of the gray substance of an adult man as it appears after treatment with the Weigert method.

The real nerve-tissue which fills the meshes of the figured net-work consists of ganglion-cells and nerve-fibers. The form of the ganglion-cells is exceedingly varying. There are small, nearly-spherical forms with few processes, and there are multipolar cells with numerous processes and twenty times as large as the ones just described. In the lobes of the N. vagi of the Torpedo and in the Medulla of the Cyclostomii are ganglion-cells so enormous that one may easily see them with the unaided eye. Indeed, in the spinal cord of the electric eel—*Malapterurus*—are two isolated ganglion-cells of such size that the immense single nerve-fiber which each sends out

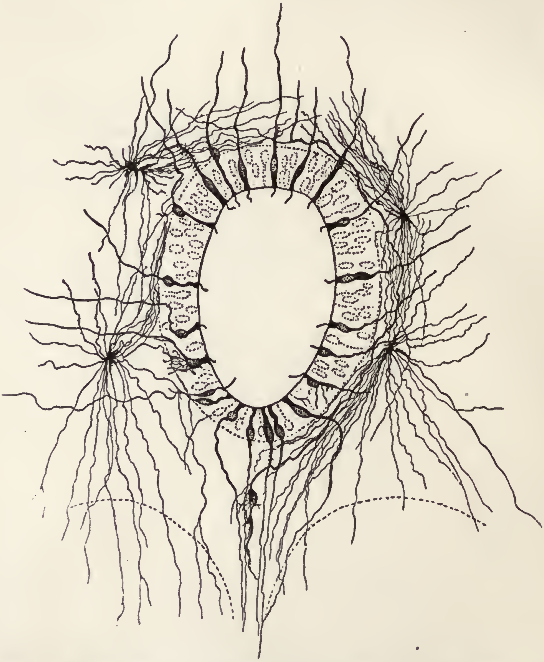

Fig. 5.—Epithelium and neuroglia surrounding the central canal. Section through the spinal cord of a human embryo of twenty-three centimeters' length. Prepared by the Golgi-Cajal method. Note that only a part of the cells have taken the silver precipitate,—a marked advantage mentioned above,—for only through this is it possible to recognize what belongs to any one cell. (After Lenhossek.)

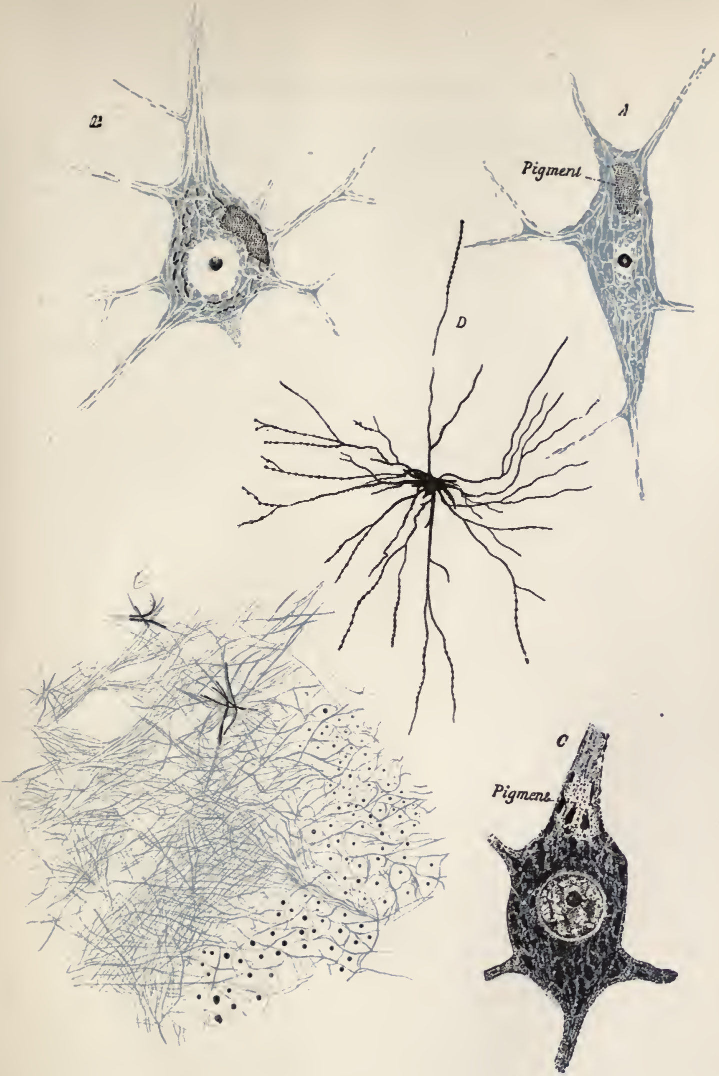

Fig. 6.—*A* and *B*, Cells from the anterior horn of a human spinal cord. Fixed with alcohol and stained with methyl-blue. *C*, Ganglion-cell fixed with alcohol and stained with hæmatoxylin. *D*, Ganglion-cell from anterior horn of fœtal dog. (After an original preparation by Ramón y Cajal.) Prepared with Golgi method. *E*, Neuroglia. (After an original preparation by Weigert.) Neuroglia-fibers blue; axis-cylinders black. (After an original preparation by Nissl.)

suffices to innervate the large electric organ. Quite different appearances are obtained according to the technique used in the preparation of the ganglion-cells. In Fig. 4 two ganglion-cells are represented as they appear after treatment with carmin and picrocarmin. Fig. 6 (*D*) shows a cell treated according to the Golgi method in which the silver precipitate shows the processes in a beautiful way before unequaled. Of the structure of the cell nothing can be seen. Structural figures, important in investigations in the realm of pathology, are only gotten in other ways. Fig. 6 (*A* and *B*) shows what microscopic technique has accomplished up to the present time. Many ganglion-cells bear pigment of yellowish-brown color. In the two cells figured the pigment is indicated in dotted black.

The nerve-fibers originate from the ganglion-cells. Wagner first showed that in many of these cells *only one* process may be followed directly into a nerve, and other investigators have confirmed it. This process is called a Neuraxon, an Axis-cylinder Process, or a Neurite. What became of those neuraxons which did not pass into nerve-trunks; what rôle was played by the other processes of the cell,—the protoplasmic processes, or Dendrites,—remained in complete obscurity until Gerlach stated in 1870 that all these form among themselves a net, and from this there arise nerve-fibers again.

In the course of the last few years our knowledge has undergone an unexpectedly extensive amplification, made possible by the progress of histological and of histo-physiological technique. First Bellonci, through osmium staining, then still more conclusively Golgi, through treatment of the cells with sublimate or even with silver precipitates, succeeded in demonstrating that from some cells the neuraxon passes directly into a nerve-fiber, but from other cells neuraxons arise which break up into a net-work. Lateral twigs coming from those neuraxons which arise from the first-described cells are said to take part also in the formation of this net-work. Golgi supposed that nerve-fibers pass out again from the net-work. There is then a twofold origin for nerve-fibers: one direct, the other indirect, through the means of the net-work. The dendritic processes, it is asserted, have nothing to do with the formation of nerve-fibers. Such were the results of Golgi's observations.

What Golgi inferred from the study of numerous, sometimes complicated, views of the brain-cortex and spinal cord of man and mammals, Haller was able to see directly in the ganglia of mollusks and worms, where the histological relations are very distinct. But, according to his view, the net-work arises from cell-processes which are essentially equivalent one to another. Through these studies, as well as those of Nansen and others, the proof seemed conclusive that there are two modes of origin of nerve-fibers: a direct one and one through the medium of a net-work.

But it soon became apparent that this valuable discovery had only opened the way to other much more significant ones: that it held only a part of the truth. A Spanish scholar, Ramón y Cajal, who worked with the Golgi silver method, published in close succession a series of studies whose results—confirmed and amplified by Kölliker, Gehuchten, Waldeyer, Lenhossek, and others—lead us to new views. We stand yet in the current of changing opinions, receiving daily new contributions to this interesting question. We can already picture to ourselves the minuter relations of the elements in the central nervous system. But this picture which is to be developed is not founded upon purely anatomical investigation. At the same time that histological preparations brought us to the new views, His, on the basis furnished by embryology; Forel and Monakow, from studies in the realm of pathology, came to a conception of the origin and end of nerve-tracts which nearly coincides with that reached by the anatomical method. Retzius finally succeeded, indeed, in demonstrating, through vital methyl-blue reactions on the living nerve-cells of many lower orders of animals, much which harmonizes well with conclusions from histological preparations.

The ganglion-cells usually send out two kinds of processes from their bodies: a moderately-fine process, the neuraxon, neurite, or axis-cylinder, which is first to spring from the cell; and the thicker dendrites or protoplasmic processes, which break up into fine twigs. The dendrites appear somewhat late in embryonic development. The neuraxons always end apparently by breaking up into branches. Two kinds of cells can be differentiated: (1) those in which the process is so short that the ramifications lie close by the cell (Fig. 152, *g*) and (2) those with long-extended neuraxons (Fig. 152, *d* and *f*). Along its course, which sometimes extends for many centimeters, such a process gives off more or less numerous lateral branches, or collaterals. These also end, like the main process, in fine subdivisions. We have long known that the neuraxon of a nerve-fiber is composed of numerous separate fibrillæ. So there is nothing striking in the statement that along the course of the nerve individual fibrillæ branch off from the main trunk. Naturally, one has very infrequent opportunity to follow a neuraxon with certainty from its origin to its end. But all that has been learned regarding the termination of this important cell-process,—what has been observed, and what has been inferred from prepared specimens,—indicates that it, in truth, branches out into fibrillæ at its termination. If it passes out from the central system to the periphery, as in the spinal nerve-roots, it ramifies in the muscle-tissue—motor end-plates—or between epithelial cells—plexuses of the sense-organs. But relatively few of the neuraxons pass to the peripheral organs. Very much the greater part of them, after a shorter or longer course, come into relation with another cell, grasping it or surrounding it with its terminal ramification (*Endpinselung*). If the cell-body is not very large, it has, nevertheless, abundant points of contact through its numerous dendrites; but, if it is very extended, as in the cells of the spinal ganglia, the dendrites are less needed.

The dendritic processes break up into a more or less abundant branching, whose surface may be further increased by the presence of innumerable, small, pedunculated knots (Fig. 152, *l*). A transformation of dendritic fibers into peripheral (efferent) nerves has not been demonstrated.[1]

On the physiological significance of the dendrites there are great differences of opinion. According to the author's investigations and from what may be learned from figures contributed by others, it seems most probable that the dendrites represent an *increase* of *surface* of the *ganglion-cell,* which is absolutely necessary to insure intimate relations with the surrounding fibers of neuraxons (from other cells). In Fig. 16 may be seen (*a*) the terminal process of a sensory cell of the olfactory epithelium passing as an olfactory nerve, or *fila olfactoria,* through the cribriform plate and breaking up into terminal fibrillæ in the olfactory lobe of the brain (see also Fig. 94). Their terminal ramifications intimately embrace the dense dendritic fibers from the ganglion-cells there located. Here one sees the relation between the olfactory tract of the first order and those cells from which are developed the olfactory tract of the second order, whose course lies within the olfactory lobe. The connection is here established only through the relation which the neuraxon of one cell bears to the dendrites of another.

Dendrites and neuraxons do not always pass off from the cell-body at different places. Among the vertebrates one may often notice that the cell sends out a process, that appears quite like a dendritic process, from near the origin of which a neuraxon branches off. Among many invertebrates this is, indeed, the rule. In the river cray-fish, for example, the pear-shaped ganglion-cells send out usually one thick branch from which the dendrites branch off laterally and the neuraxon develops farther on (Fig. 8). Here appears to be a condition which indicates that the two kinds of proc-

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[1] The most recent writings of American neurologists show a practical unanimity in the use of the term *dendrite* for the afferent cell-processes, and *Neuraxon, Axone,* or *Neurite* for the efferent cell-processes. In a vast majority of cases the dendrites are short, protoplasmic processes structurally, while the neuraxon is a long nerve-fiber having the structure described usually as an axis-cylinder. Figs. 15 and 16 make it evident that the afferent sensory nerve-fibers are dynamically to be classified with the dendrites; moreover, their development indicates a similar thing. These afferent sensory nerves are structurally axis-cylinders. In order to avoid ambiguity and confusion in this translation, the term *neuraxon* will be uniformly used for the efferent cell-processes. If the term axis-cylinder is used it will be understood to apply strictly to the structure of the fiber.—W. S. H.

esses of a ganglion-cell are not at all absolutely and fundamentally different from each other.

The developmental unit—which comprises ganglion-cell, neuraxon, dendrites, and their ramifications—is called a *neuron.* It is probable that the entire nervous system is composed of numerous neurons, built one upon another. The majority of these neurons appear to stand isolated, only connected to neighboring neurons through a contact so intimate as easily to make possible the transmission of physiological processes. Purely morphological studies here lead to no conclusions.

The labyrinth of fibers found in almost every part of the nervous system and the uncertainty of our present methods admit too easily of false conclusions; but the observations of experimental pathology and of pathological anatomy all teach that, if a ganglion-cell be diseased or injured, the changes will not be propagated farther than the processes of that cell reach. This is demonstrable on the axis-cylinder of a peripheral nerve, which can often be studied through many centimeters of its course. Its condition is absolutely dependent upon the condition of the cell from which it springs.

These circumstances also indicate that each ganglion-cell stands isolated,—not directly joined with any other. It must be mentioned, however, that conscientious observers have repeatedly described links of connection between different cells.

These are fundamental facts. They will be better comprehended after a review of what is known regarding the origin and course of a single, thoroughly studied tract.

Many motor nerves arise from large ganglion-cells which lie in the anterior horn of the spinal cord. From each of these cells there arises one neuraxon. It passes out of the spinal cord as a nerve-root, and then passes into a nerve-trunk, within which its course lies until in a muscle it branches off to the end-plate (Fig. 7).

That part of the system which reaches from the periphery to its first ending in the central system is designated as a *tract of the first order.* These tracts of the first order—in this case including anterior horn, motor nerve, and muscle-ending—have been, because of their peculiar relation in disease, for years classified together in pathology and separated from the tracts of a higher order.

The further transmission of the nervous impulse takes place in this manner among the mammals: to tracts of the first order connect tracts of the second order or even of the third and fourth in succession. All consist of these parts: ganglion-cell, neuraxon, and ramification. If we turn to the chosen example we find that, around the numerous dendrites which the ganglion-cell of the anterior horn sends out, there are many fine fibrillæ. These fibrillæ surround them without, so far as we know, coming into actual contact with them. These fibrillæ are in part collaterals from a tract which we know from observations in pathology passes from large cells in the brain-cortex downward through the brain and spinal cord. This tract —which consists again of brain-cell, descending nerve, collaterals, and ramifications—is adapted to the establishment of a connection between the brain and the end-plates in the muscles; it is the *central segment of the motor course of innervation*, or, at least, a part of it. This is the motor tract of the *second order*. How many of these units are involved in a complete motor process is as yet unknown. In Fig. 152 one observes that the ramified neuraxons of other cortical cells surround the dendrites of those large cortical cells from which the secondary motor tract originates. These represent tracts of higher order.

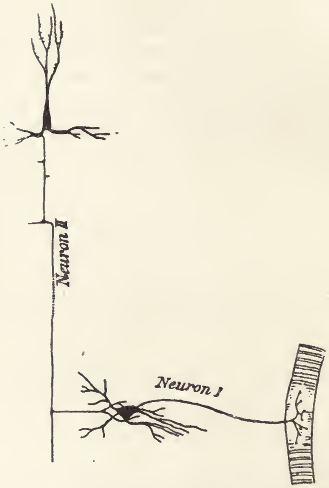


Fig. 7.—Schematic representation of the relation of ganglion-cell and nerve in a motor tract.

Work on the inner structure of ganglion-cells, for the revival of which we are especially indebted to Nissl, has not yet led to conclusive results, especially because the significance of the fine lines which appear after treatment with sublimate, alcohol, and basic anilin stains is not yet clear; also because it is not yet always certain how much these structural features may depend upon the influence of the reagents themselves. Nevertheless, the work of Nissl, who especially advised fixation with alcohol, has led to very important results already applicable. In the body of all ganglion-cells one finds, after fixation with alcohol, a substance which stains with basic stains and a substance which does not. The first appears in different cells, and probably in different conditions of the same cell, in variable structural forms. One meets granules, threads, and spindles, as well as many other regular and irregular forms, of which only a few are, through position or form, well characterized (*Kernkappen, Verzweigungskegel, u. s. w.*). This structural arrangement differs so greatly that Nissl has, within the *ganglion-cell* genus, separated out a great many different cell-species. According to this author, definite differences appear also within the nucleus, which he utilized with the other characters in differentiating cells. If the ganglion-cell suffers any injury—be it the influence of a poison, of unwonted activity, or of a divided axis-cylinder—changes always arise within the stainable substance. When the injury is intense the changes may lead to an almost complete disappearance of the stainable substance. But if the nucleus remains uninjured the integrity of the cell-substance may be restored.

The study of this cell-change is of the very greatest importance. It opens to us finally a glimpse into the inner changes which proceed during cell-activity.

Hodge, as well as Nissl, has done most creditable work in this field. Hodge studied cells fatigued by direct stimulation or by stimulation through the medium of the axis-cylinder; also cells in the condition of fatigue,—ganglion-cells of bees after the day's work,—comparing them with rested cells. He found that the stainable granules always decreased; that the fatigued cell became more translucent; further, that it even became vacuolated. At the same time the volume decreased. On the last point, however, there is no unanimity of statement.

These differences are conditioned upon the present state of the technique. Complete unanimity of statement exists on the relation of the nucleus to fatigue. This always decreases in size, becomes serrated, and takes a darker stain than the rested nucleus.

Within the unstained substance the latest investigations by Becker, Flemming, Dogiel, *et al*, have demonstrated a delicate fibrillated structure. The appearance is as if each of the larger cells studied were traversed in all directions by long, delicate threads, which pass in and out with the cell-branches. Further, such threads do not always traverse the entire cell, but pass out again into that branch located next to the one by which it entered. Becker demonstrated this in the cells of the anterior horn. Only the improved method made the presence of these fibrillæ certain. Possibly they will yield a foundation for a better knowledge of the function of the ganglion-cell. Max Schultze drew attention to them, however, many years ago.

One looks upon the ganglion-cells and their branches as elements which bear the function of the central nervous system. Even in very low-ranked animals they appear isolated or gathered into knots: ganglion-knots. According as these ganglia lie isolated peripherally or collected in a particular arrangement and joined with each other by nerve-trunks they are classified as *peripheral ganglia* or as *central nervous system.* In general, it is recognized that in the animal kingdom there is a tendency toward the gathering of many ganglia into a single nervous system. The higher the rank, the larger is this system; but until the vertebrate rank is reached there are important parts of the nervous system always more or less separated and functionally as well as anatomically more or less independent.

Physiology shows how not only the individual ganglia which lie in the intestines function with relative independence, but how even structures like the spinal ganglia, frequently reckoned in with the central system, still enjoy relative independence from it functionally.

What we know of the anatomical structure and of the functions of the central nervous system of vertebrates forces us more and more to the conclusions (1) that even individual parts of the central system are themselves in a position to function to a certain extent independently, and (2) that even the brain and spinal cord of vertebrates are composed of a series of centers. Whether the one or the other of these is more highly developed, whether they are in connection with deeper centers, and whether they have connections among themselves and with higher centers determine the measure of the higher or lower development of the central system. We will find later that, in the course of the development of a class, individual centers connected with the central nervous system have reached a high development, while others have arrived at a certain stage (or reached a certain type) where they remain stationary and throughout all subsequent posterity remain everywhere alike.

One can conceive that in its essentials every nervous system is composed of afferent tracts and efferent tracts and of tracts which form the connections of the elements among themselves.

A good insight into the complete structure of a single ganglion may be gained by a study of the opposite figure (Fig. 8). It represents the entire first abdominal ganglion of the ventral nerve-cord of a river cray-fish, and owing to the comparative simplicity of the relations permits an insight into the details. We have here a sort of schema of a central nervous system, and gain at once an outlook over an entire mechanism adapted for the exercise of the functions of a central organ.

The nervous system of a cray-fish, like that of all arthropoda, consists of a great number of separate ganglia, which are united together by longer or shorter commissures. From the various-sized nerve-cells (*d*, *e*, *f*) there

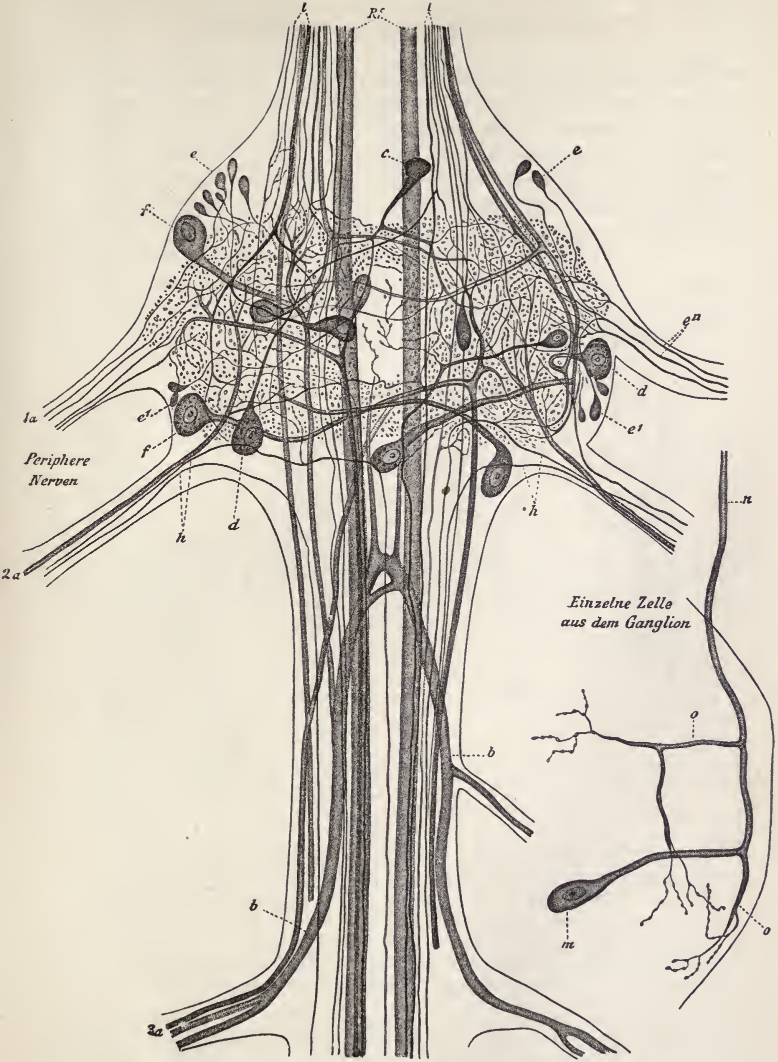


Fig. 8.—First abdominal ganglion of the ventral nerve-cord of *Astracus fluviatilis.* Living tissue stained with methyl-blue. Nervous tissue only is stained. Significance of large fibers *Rf* not understood. *m n o*, Single cell from the ganglion. *Periphere nerven,* Peripheral nerve. *Einzelne Zelle aus dem Ganglion,* a single cell from the ganglion. Further description in text. (After Retzius.)

arises always a single immense branch, which after a short course divides into one fiber, which, at the periphery of the ganglion, passes out as neuraxon, and one fiber, which remains within the ganglion, rapidly dividing into twigs. The neuraxon passes either direct (Fig. 8, *e*) into a nerve, in which case it is probably of motor nature, or it passes into a commissural nerve, which joins with the ganglion, with those located farther anterior or posterior, as is the case with all neuraxons from the very large cells (Fig. 8, *d* and *f*). The neuraxon may pass along the same side (*d*) or it may cross over to the opposite side (*f*). From the neuraxon the dendrites branch off and pass into the substance of the ganglion. In their finer ramifications they are well adapted to connect together the separate elements of the whole ganglion.

Fig. 9.—From the cornu Ammonis of the rabbit. *A*, Composite figure from preparations by S. R. y Cajal. *a, b, c,* Association-cells whose long neuraxons split up into moss-like twigs, which invade the layer of pyramidal cells (*A*). At the left is a completely-sketched pyramidal cell. Through its descending neuraxon it is in relation with the "brain-pith" and through its ascending dendrites it is in relation with other systems and cells not figured. Through the association-cells many pyramidal cells are brought into combination.

In the fine net-work which they form, appear nerve-fibers which come either from the peripheral-sensory nerves (2 *a*), or come from other ganglia (*l*, *i*). Note that the nerve-trunk (2 *a*) contains nerve-fibers which pass into the ganglion and those which come from other ganglia of the same side or the opposite side. How many possibilities of association are given in this simple ganglion!

Every cell and every fiber can, through the profuse terminal ramification, come into relation with innumerable other cells and fibers. Besides that, most cells stand in combination with tracts from distant centers and also from the periphery.

There are also cells—already demonstrated, at any rate, for all classes of vertebrates—which stand in no direct relation to the outer world and are adapted only for joining one central cell more intimately with that of another. These cells are called *Association-cells*. Such cells are very widely disseminated. Nowhere does their significance become more readily clear than in the *cornu Ammonis*: a portion of the olfactory cortex. Fig. 9 shows a section through this portion of the cortex.

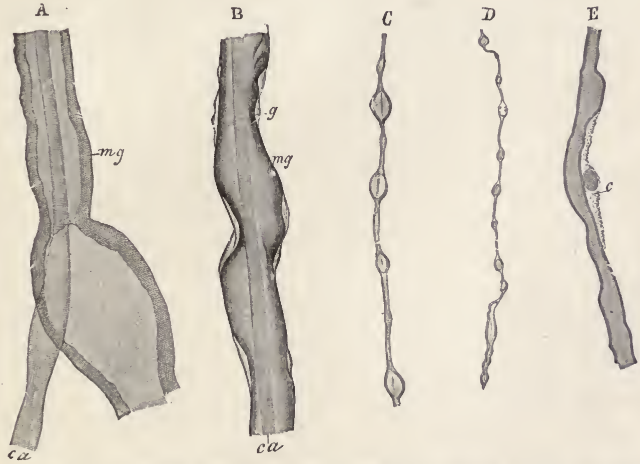


Fig. 10.—Isolated nerve-fibers from the spinal cord of a dog. *ca*, Axis-cylinder. *mg*, Medullary sheath. *g*, Outer sheath. *c*, Nucleus and protoplasm, to be seen occasionally on the surface of fibers. (After Ranvier.)

Below the layer of large pyramidal cells, which make up the principal cell-layer of this region, note the small cells which send their neuraxons near to the pyramidal cells or even through the layer, after which it divides into fine transverse branches, from which great terminal ramifications push in between the pyramidal cells from above and from below. These terminal bushes (*Endbäumchen*) are well adapted to join together the elements of the layer in which they terminate.

The nerve-fibers of the brain and spinal cord are of very varying width and in grown mammals probably all are provided with medullary sheaths.

Every nerve-fiber loses its sheath of Schwann where it enters the central system. Only a thin layer, present even in peripheral nerves and first seen by Ranvier, covers the axis-cylinder within the brain and spinal cord.

These are the elements from which the central nervous system is constructed.

In a general way, those parts which are composed principally of medullated nerves appear white (white substance); those in which ganglion-cells, axis-cylinders, and neuroglia predominate appear gray (gray substance). The gray substance is more vascular than the white.

CHAPTER III.

Central Organ and Peripheral Nerves (Physiological).

Next to a knowledge of the ganglion-cells, and of their grouping to form smaller or larger centers, the most important question is: What is known of these cells physiologically? And, first of all, we know that a motor nerve loses its function when separated from its cell of origin, and, too, that destruction of gray matter, in which sensory fibers end, destroys their function as well. We know, further, that, by irritation of the cells in which a nerve ends, we can produce all the phenomena which are ordinarily observed in the normal performance of its function. This fact alone has led to the deduction *that in the ganglion-cells and their inter-relationships we have the basis of nervous activity.*

Numerous experiments have demonstrated that a sensory impression, which, coming from the periphery, enters the nerve-center, may there excite cells of origin of motor fibers, and bring the end-organs of the latter, the muscles, into activity. This process is well known as reflex action. The examination of such reflexes led subsequently to the additional very interesting datum, that the sensory impulse does not always immediately excite a motor discharge, but rather that a certain intensity of the original irritation is necessary, although a feeble irritation, if continued for a time, may finally excite the motor apparatus. The theory is that *ganglion-cells have the property of storing up and retaining irritations coming to them until the accumulated irritation is too great or some new irritation arrives from some other direction, when they suddenly discharge.*

The small nerve-center of the crab, already mentioned in Chapter II, receives many fibers from the periphery, and sends out, from the large cells it contains, large fibers to the muscles. A glance at it and at the accompanying figure shows that a given irritation never affects one cell only, but rather that an impression, which is conducted from one point in the periphery by a single fiber to the nerve-center, may there "charge" a large collection of motor-cells. The subsequent discharge in like manner excites not just one motor fiber, but, according to the anatomical relations of the motor cells, brings an entire system of muscles into contraction. In this wise is explained (Exner) how a single sensory impression may lead to a complicated movement, in which many different muscles may take part. What kind of motor reaction occurs from a sensory impulse depends upon which of the sensory nerves are irritated, and especially upon the relationship between the cells which form the motor apparatus excited. There is much evidence in favor of the view that *such relationships, when once established in the course of evolution, are afterward inherited*; *so that the structure of a single nerve-center is practically the same for each individual, and that, through this inherited apparatus, numerous apparently complicated actions are made possible once for all.* But there are experiences which teach that *in certain portions of the nervous system constantly new associations are being formed by exercise.* The central nervous system would, then, consist of one part, which is congenital and arises from the primordial racial exercise

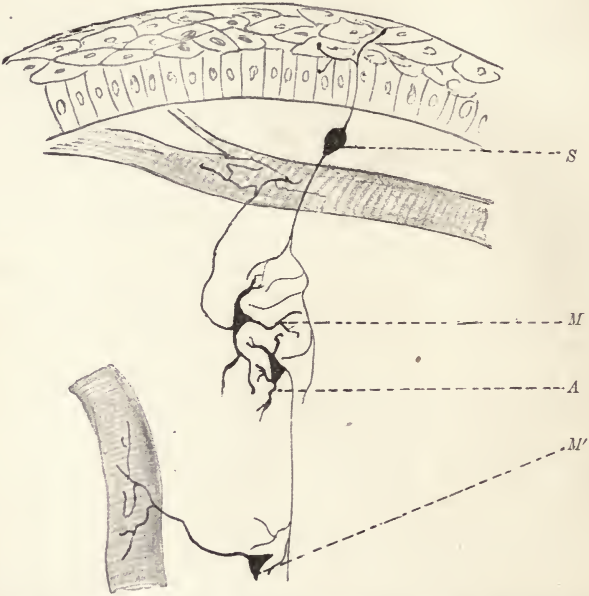


Fig. 11.—Schema of a very simply constructed nervous apparatus, comprising motor and sensory nerve and center; adapted for explaining the simplest reflexes. *S*, Sensory cell whose dendrite brings to it impressions from the skin, while its neurite, or neuraxon, passes to the nerve-center, where it influences *M* and *A*. *M*, Motor cell for the upper muscle. *A*, Association-cell which transmits stimuli received by *S* on to *M′*, where it takes effect either simultaneously or subsequently. *M′*, Motor cell for the lower muscle.

(phylogenetic), and of other parts which, only by use during the person's life, derive their relationships (ontogenetic).

Congenital mechanisms are found in all parts of the nervous system, but observation of movements of embryos and infants shows that, at least in respect to the nervous apparatus connected with the vegetative functions, as in the sympathetic and in the large territory of the spinal cord and the bulb, such mechanisms predominate. Probably to these may be added a large part of the midbrain and cerebellum. Comparative anatomy teaches that, up to the higher mammals, the apparatus lying anterior to these parts are capable of still greater variations; and observation of the cerebral cortex in its particular development specially shows that here, in cases of individuals, new paths may, by practice, become fixed.

In so far as motor phenomena are considered as the result of irritations, the necessary apparatus is called the movement-complex. This word was coined by Exner, to whom we are indebted for an excellent review of many of the related facts. One should not imagine, however, such collections of ganglion-cells as entirely simple. The majority of movements require some time for their execution, during which numerous other muscles may come into play besides those first concerned. There must, therefore, be paths leading from one collection of cells to another, the latter group being affected by the irritation only when the action of the former is ended.

Such processes are known (Exner) as successive movement-complexes. Exner determined from physiological observations that, when one searches carefully the nervous system of the invertebrates, one may easily find anatomical series, which, once meeting with an irritation, may discharge successive movements in perfect order. Especially the nervous system of annulata—for example, the earth-worm, which we understand well since the excellent researches of Retzius—shows how, from afferent sensory fibers, first a single motor cell-group is set in action, and then, through the processes of large association-cells, the impulse may be transmitted to the next ganglion (Fig. 12). Besides, every ganglion contains other motor cells whose neuraxons do not connect with the nerves of the corresponding metamere, but which end in muscles that are anterior or posterior to this. So an impression, which is received by an animal in any part of its body-surface, may bring into action first the muscles of that part, and then also those of metameres lying anterior or posterior to it. When such a successive movement has once begun, another element enters in to regulate it. With the changing position of the muscles and limbs, change also the sensory impressions received by them. Consider the above-mentioned earth-worm. The muscles of the first metamere contract from irritation of the apparatus of touch; perhaps, too, those of the second. But by reason of these contractions other portions of the integument come into contact with the ground; new impulses are excited, which pass to still other ganglia; and in this way the contractions may extend to include farther metameres; in short, an irritation affecting one portion of the worm's body, provided there is the necessary co-ordination of movements present, brings the whole animal, in a purely reflex way, into motion,—crawling. Indeed, this crawl-

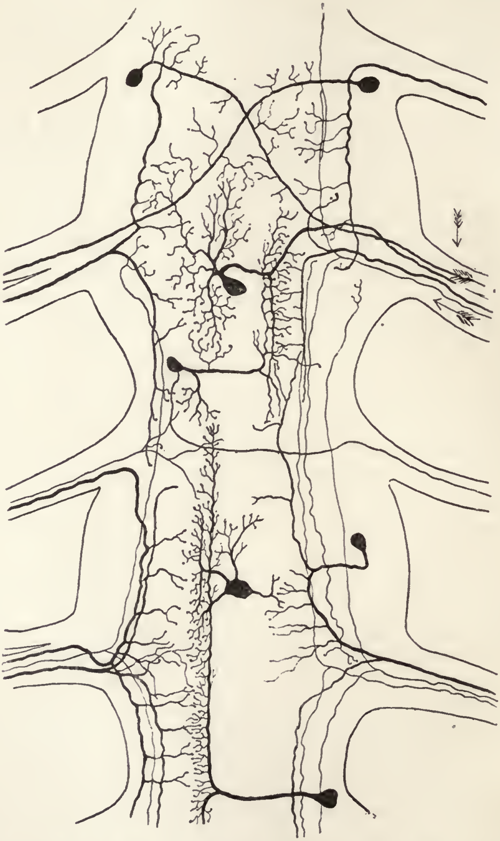


Fig. 12.—Several ganglia from the ventral cord of an earth-worm,—*Lumbricus terrestris*,—showing the elements for successive movement-combinations. (After Retzius.)

ing may give the impression of an extreme effect in proportion to the irritation. If one turns a sea-urchin on its back, it begins at once to lay hold of the ground with the long suckers which cover its whole body. Each arm, however, contracts instantly, when it touches the ground. The almost egg-shaped animal is thereby more closely drawn to the ground. Then a peculiar thing happens, as Romanes and Ewart have well described. At one place, no matter which, apparently, the arms are more strongly contracted. Immediately all the others lose their hold, and the animal turns toward that side where the stronger contraction occurred. As a result of this, other arms are brought into contact with the ground, and they contract in turn, and the process is repeated until the sea-urchin stands upon edge, and then new pedicels come into action and finally bring the animal into its normal position. Here we have a purposive movement, apparently practicable only through minute care and reflection, which may be explained by simple reflex processes: by the contraction in the muscles of the ambulacral feet following excitation of their sensory nerves. That the movement is a regulated one bespeaks a combination of the nerves of the ambulacral feet. But in this simple experiment appears a new faculty, which until now we have not mentioned among the properties of the central nervous apparatus: the cessation of motion when once the animal reaches a position of rest. There must here be introduced an inhibition from the center, otherwise one could not understand why the sea-urchin should not keep on turning until tired out, since even in the normal position new arms are always coming in contact with the ground. In fact, it is a property of nerve-centers, everywhere recognized, that they are not only able to excite movements, but also to prevent them. The mechanism is not yet clearly understood. Doubtless such inhibitions are propagated, as are the movements, from the ganglion first excited to the others.

It would be very alluring to follow from these first ideas further along the events in a given part of the nervous system, or to see what takes place in the internal nervous arrangement in the production of a given complicated action. However simple, though, may be the most primitive nervous apparatus, regarded anatomically, such views are misleading.

As the simplest central nervous arrangement, we can consider that which is made up of centripetal sensory and centrifugal motor fibers, in which it is agreed that the ends of the sensory nerve are in contact directly, or through the mediation of a second cell, with the cell of origin of the motor nerve. Such simple combinations are widely found in the invertebrates as well as in the vertebrates. They occur partly in the sympathetic ganglia, partly also as direct reflex-paths in the central nervous system. Absolutely isolated, simple reflex-centers are not yet known, but even the smallest are in connection with others similar to them. Such a center is seen in Fig. 11. But all the cells are only slightly dependent on each other, being, for a large part of their function, wholly independent. As an example of such isolated reflex action, we have the movements occurring in the musculature of a portion of the intestines removed from the body, which take place with entire regularity, when irritated on its mucous membrane. The influence on these short reflex-arcs, which larger and more extensive arcs have, is well known; such, for example, as those passing through the sympathetic ganglia and the spinal nerve-roots. These form new neurons, which are connected with those of the intestines, influencing, exciting, and restraining them.

THE PERIPHERAL NERVES.

All examinations of the vertebrates have shown that the *motor* nerve arises from a large ganglion-cell, which sends out its neuraxon to a muscle.

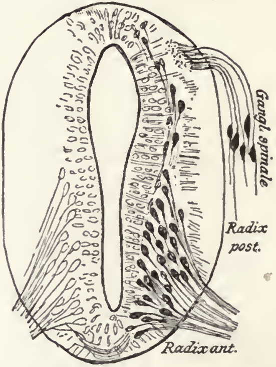


Fig. 13.—Section of the spinal cord of a human embryo of the fourth week. Note ventrally the anterior or motor root developing from cells of the cord. In the dorsal portion (four and one-half weeks) the sensory root grows in from cells of the spinal ganglion. (Combined from figures by His.)

where it ends by division. Everything that has been observed with invertebrates indicates that there, also, this is the case. On the other hand, with invertebrates the direct observation has been made of nerve-fibers originating in cells in the skin, sensory nerves, passing into the central organ, and there ending by free extremities. *His* has made valuable examinations along this line with vertebrates (Fig. 13).

In embryos of vertebrates the central nervous system, as is well known, presents, in the early stages of development, a canal. *His* determined that the fibers of the peripheral nerves have two quite-different origins. All motor fibers arise as axis-cylinder processes, or neuraxons, from the cells lying in the ventral portion of this canal. Each cell sends out a fibril toward the surface, and there the fibrils approximate each other to form ventral nerve-roots. The sensory root-fibers, which arise mainly dorsal, have an entirely different beginning. They proceed from the ganglia which lie near the cord throughout its length, and not from within the cord itself. From the cells of these ganglia (spinal ganglia and ganglia of the cranial nerves) fibers grow in two directions. One set enters the central organ, the other grows toward the periphery as sensory nerves.

In the vertebrates the cells of origin of most motor nerves, especially those supplying striated muscle, are in the central axis. They have already been considered as forming good examples of the superposition of different neurons. But not all of the motor nerves arise in this way. Scattered throughout the body we find ganglion-cells, whose axones end in the non-striated muscle-fibers of the blood-vessels, the intestines, the heart, and other viscera. These cells, usually classed as belonging to the sympathetic, must be regarded as motor cells, because on their normal supply depends the inherent power of contraction which these organs possess. They lie in many locations—for instance, in the intestinal walls and the heart—in relatively close contact with other axones which arise from other places, as from the spinal cord, etc. Here, too, then, in the sympathetic there are motor paths of different orders. We have seen that in mammals a large share of the secondary motor paths reach, in some way, to the organs of consciousness. That is not true of all these tracts. It is better to consider the motor centers, the central and peripheral sympathetic as capable of independent action, and to determine in each case how far higher nerve-tracts associate themselves to these, and how far higher nerve-centers can affect their action. With mammals all the striated muscles are innervated from the central organs, and only the smooth muscles, as well as those of the heart, are to some extent independent of them; but with the lower animals there are also, in the periphery, many ganglion-cells for voluntary muscles.

The sensory nerves in vertebrates are mainly outgrowths from the cells of the spinal ganglia. They also split up when they arrive at the periphery, and end either freely in the epithelium or in some modified end-apparatus, usually an epithelial structure. Aside from the ontogeny of the sensory nerves, much of interest is known of their phylogeny. As is well-known, the outer covering of slightly-developed animals, as the cœlenterates, among the ordinary epithelial cells, presents still others characterized by their arrangement in groups and by the possession of a long end-filament, which sinks into the nervous system. In the whole list of lower animals it is a frequent occurrence that cells lying in the

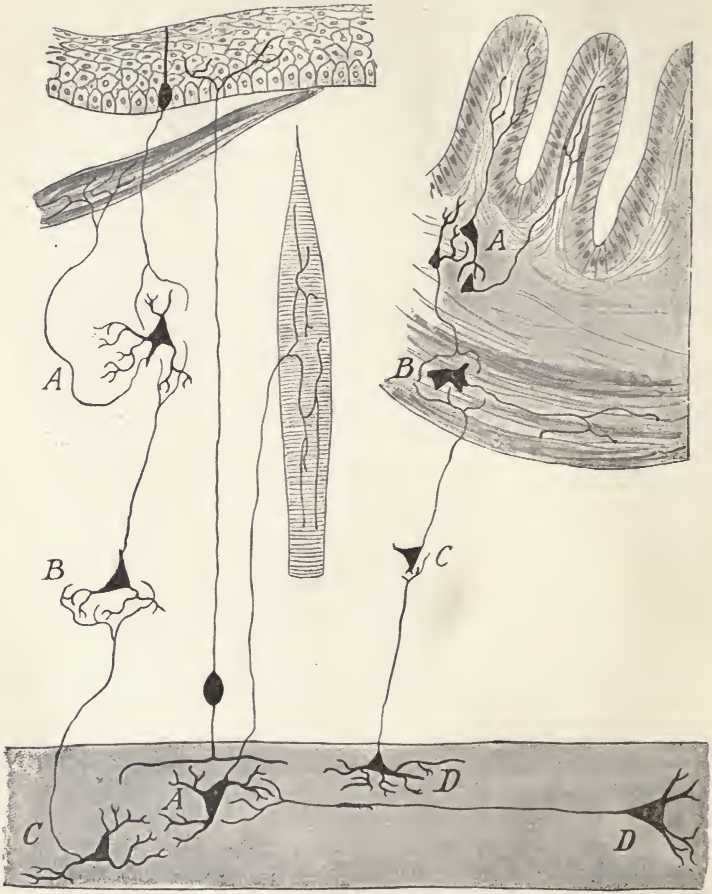


Fig. 14.—Schema of the peripheral and central nervous system. The relations shown do not exist in any particular animal, but represent rather the principles determined from a comparative study of many animals, and are introduced for the elucidation of the text. Note the motor and sensory nerves, peripherally and centrally located *centers*, and the connections represented. *A*, *B*, *C*, and *D* indicate that the tract is one of I, II, III, or IV order, respectively.

ectoderm are joined to the neighboring nerve-centers by such fibers. Their position in the epidermis indicates that this is a part of the sensory apparatus, and all doubts about this being true disappear when one recognizes how frequently these cells are in relation with structures adapted to the reception of special impressions. Long, stiff hairs, swinging brushes, projecting horns, seem easily able to communicate tactile impressions, while one may find analogous cells arranged to form the walls of a cavity, in which a pebble, an otolith swinging inside the cavity, represents the sensory apparatus for maintaining the equilibrium. Lentiform parts of the ectoderm lie in other places in front of such cells, and are well adapted to transmit rays of light or heat to these cells in a peculiar manner. It would scarcely be possible to describe all the manifold arrangements which function as sensory mechanisms in the invertebrates, but it must be emphasized that between the simple epithelial cell of the ectoderm and the highly differentiated apparatus are found all transitional forms, and that in the most highly developed this same type, the epithelial cell with a filament extending inward to the nervous system, reappears. There is one place where one may find a large number of intermediate forms in a limited space, ranging from a simple epithelial cell connected with the nerves up to the more complicated sense-hillocks. It is the skin of a transparent snail, the *pterotrachea*. The connection of epithelial cells with nerves leading to the central organ, in the angle-worm, has been well-described by Lenhossek during the last few years. Researches of my own and those of Retzius have fully confirmed his reports. From numerous cells of the integument are seen delicate fibrils arising, which extend to nerve-centers and there terminate by division. Lenhossek has formulated an hypothesis which has proved to be of great worth as a working-basis, and bids fair to simplify and extend our knowledge of the peripheral sensory nervous system. According to him, all sensory nerves, in the invertebrates as well as in vertebrates, arise from such cells that are originally in the integument. The cells recede deeper and deeper, leaving behind a long and often branched filament in the skin. In the vertebrates they extend as far as the vertebral column, forming the spinal ganglia. Whether the cells lie immediately in the surface-epithelium or are connected with it by their processes, the sensory nerves, they invariably send one filament back into the central organ. Retzius has described such transition cell-forms in mollusks, the peripheral filaments being of different lengths, where the ganglion-cells, corresponding to epithelial cells, are often found not in the skin itself, but under it at various levels. In Fig 15 is represented, after drawings of Retzius, a scheme aiding one to connect the foregoing with the development of the sensory nervous system.

It is not only in the lower animals that the sensory end-cells are met with in the periphery; they are similarly found in the vertebrates, and in many different forms, as is the case in the nerve-endings of the sense-organs. The epithelium of the nasal mucous membrane, like that of the angle-worm, sends only one process back into the brain; but in the ear there are no end-cells in this sense, the corresponding cells lying in the spinal ganglion of the cochlea, while their branched peripheral processes surround the hair-cells of the crista acustica, or of the organ of Corti, after the manner of the sensory nerve with the epidermis-cell (Fig. 16). So also with the taste-fibers has such a branching around cells been determined. In the retina, we know, there are nerve-fibers which come from the brain and arborize around their respective cells, while there are also ganglion-cells in it, whose axones pass backward into the brain.

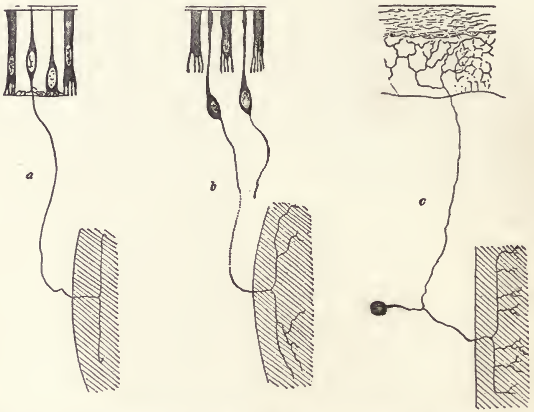


Fig. 15.—*a*, Sensory epithelium of the earth-worm. *b*, Sensory epithelium of the snail. *c*, Spinal ganglion-cells of a vertebrate. (After Retzius.)

[One process of the cell (*c*) extends to the skin as a sensory nerve-fiber; it is the homologue of the *dendrite*, but in this situation is structurally modified into a typical *axis-cylinder*. One process extends into the central nervous system, and is the efferent *neuraxon*, *axone*, or *neurite*, also here having the structure of a typical *axis-cylinder*. Such cells have been called bipolar, because they possess two axis-cylinders; inasmuch, however, as they possess but one neuraxon, the utility of the term *bipolar* might be called in question.—W. S. H.]

Sensory nerves are widely distributed over the entire body. They are located not only in those places usually known to be sensitive, but also in all other tissues and organs. Whether one examine the liver or the kidney, the lungs or the wall of a blood-vessel, one always finds delicate nerve-arborizations in unsuspected numbers. A large portion of them end probably in the peripherally placed sensory end-cells belonging to the reflex-arc of the sympathetic; another portion may very probably be traced to the spinal ganglia and even to the spinal cord itself. Especially the investigations of the last few years, making use of the silver and methyl-blue stains, have not only disclosed the wealth of nerves in the different organs, but have also shown that we have regarded the sensory innervation of the sensitive surfaces, as the skin and the gustatory mucous membrane, as much less fully supplied than they really are. One finds there enormous plexuses of nerve-fibers beneath and between the epithelial cells, and they send one, often many, fine fibrils to each cell. Fig. 17 indicates, for example, how surrounding every hair there lies a veritable crown of nerve-fibrils (*A* and *B*), how

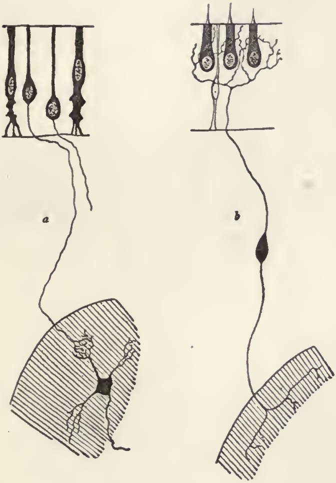


Fig. 16.—*a*, Sensory epithelium of the nose sending the neuraxon as fila olfactoria, or olfactory nerve, backward into the brain, where it breaks up into branches. The neuraxon is, in this situation, a non-medullated axis-cylinder. The dendrite is represented by the distal process of the specialized olfactory cell. *b*, Cell from the Ganglion spirale of the cochlea; the dendrite passes from its peripheral arborization around the bristled cells of the macula, or hair-cells of the organ of Corti direct to the ganglion-cell, whence the neuraxon passes as Ramus cochlearis Nervi acustici toward the brain. (After Retzius.)

to the epithelial cells of a frog's gum there pass end-fibers (*C*), and how the pigment-cells in the skin of fishes are densely surrounded by a regular net of fibers (*D*). In the liver, too, and the bladder, and in many other places, one can find numerous examples of the abundant peripheral innervation. We have always attached too great importance to the single end-apparatus, overlooking the fact that really the major portion of the body-tissues is supplied with nerves for every cell. One can hardly overestimate the wealth of nerve-fibers in the real end-organs themselves, as the taste-

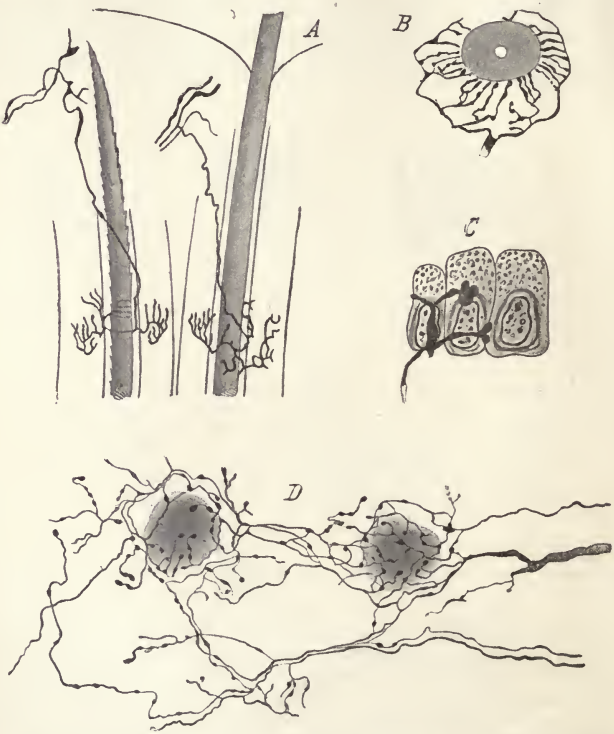


Fig. 17.—*A*, Hairs from a mouse. *B*, Cross-section of same. (V. Gehuchten.) *C*, Nerves to the epithelial cells of a frog's gums (*Gingiva*). Methyl-blue preparation by Berthi. *D*, Pigment-cells from the skin of *Alburnus*, showing the nerve-reticulum. (Berthi and Bunge.)

papillæ and the tactile papillæ. Good staining discloses with each of them plexuses of unsuspected density of arborization.

For what services may such an abundant sensory innervation be provided? It occurs immediately to one that there is a great number of reflexes, very necessary to the preservation of the individual, even though he be unaware of them. The regulation of the secretions, the blood-supply to the skin in relation to the caloric body-economy of the organism, the adjustment to varying illumination, the tension of the muscles and tendons through the respective tendon-reflexes, the different response by such varying tensions according to the intensity of the voluntary impulse, and many other phenomena could be cited. To all of them is necessary, besides the motor part of the reflex-arc, a sensory part. Indeed, Exner, to whom we are indebted for indicating the importance of these short reflex-arcs and the rôles they play in the organism, has pointed out how, in general, *for the production of any movement the sensory innervation must be intact.* The act of swallowing, for example, divides into a voluntary and a reflex act. Anæsthetize the pharynx with cocaine, and the ability to perform the voluntary part of swallowing is preserved; the bolus, however, on reaching the œsophagus, produces no impression on it, and the reflex part of the act is lost. Here, then, is the reason why the mucous membrane of the gullet possesses such an apparently superfluous sensory innervation, and why, beneath and in its epithelium, there lie such great plexuses of nerve-fibers. Another good example of the importance of sensory regulation of purely motor phenomena is offered by the movements of the fingers. These movements are much impaired—the "fingers are stiff"—when sensory disturbances alone are present in the hand. This can be brought about artificially. Let the hand become too cold, and it becomes stiff; *i.e.*, cannot move well, even in those movements depending upon the muscles lying in the protected forearm. These latter muscles cannot contract normally, it appears, when no regulating impressions arrive from the tendon and joint nerve-endings. The stiff fingers, which one experiences often on a winter's walk, are due to the presence of "Senso-mobility." Probably many motor disturbances of hysteria are of this category.

An abundant sensory innervation is, therefore, necessary, not only for countless reflex actions, but for the regulation of many seemingly purely voluntary movements, as well.

By "sensory innervation," however, one must not think only those processes are meant which enter into our consciousness, but rather all those by which from any place in the body impressions are conducted to the nearest ganglion or to the central axis. Whether they be conducted farther still, or whether they be recognized by the individual as they occur, does not affect their nature. Sensation and perception are not the same thing.

The most manifold tracts and centers serve sensibility, and in vertebrates, especially in man, who is able to give information in regard to the perception of certain impressions, we have found a multiplicity of sensations.

The sensory control required by apparently similar movements is not always the same. Particularly in the higher animals there seem to be more factors entering into this control than in the lower ones. But even mammals may, at times, through habit, etc., learn to dispense with one or another such factor; *i.e.*, may be successful in *performing* acts through the agency of elements which in lower stages of evolution were simply regulative in their action.

The importance of the single forms of this sensory regulation of entirely elementary motor mechanisms is well illustrated by the shrewd experiment of J. Richard Ewald. If one remove the labyrinth on both sides of a dog, the general muscular tone, and with it the power to maintain the vertical equilibrium, suffers so as to render walking and standing impossible. But this is gradually recovered from, the tracts for tactile and other impressions making up for the loss. Remove now both the cortical motor areas for the legs, and the severe motor disturbance reappears, the animal cannot produce co-ordinated, or, indeed, any regular movements. Still, here follows slowly a recovery. But the dog is in a serious state, being reduced to visual control for all his movements. When the room is darkened, or his eyes are bandaged, he falls helplessly to the ground.

Lower vertebrates—frogs, for example—cannot conceal the loss following removal of the labyrinths, because with them the possibility of substituting other forms of sensation from the cerebral cortex for those lost is very slight. They remain unable to jump after removal of the labyrinth.

The foregoing shows how complicated, even in the most ordinary act, the mechanism required for its performance is. By study and experimentation, one may, perhaps, recognize in the central organ at least enough of this mechanism to serve in explaining physiological and psychological processes.

PART II.

REVIEW OF THE EMBRYOLOGY AND THE COMPARATIVE ANATOMY OF THE VERTEBRATE BRAIN.

CHAPTER IV.

THE DEVELOPMENT OF THE BRAIN AND OF GANGLIA.

FROM the preceding chapters we learn that there are scattered ganglia with motor and sensory parts; but among the higher animals the greater part of the central nervous system is more or less concentrated into a definite location. Among vertebrates this concentrated nervous system includes a longitudinal cord—the spinal cord—into which the sensory nerves come from without, while from cells which lie in the cord itself the motor nerves arise. Those portions of the central system which receive or send out numerous large nerve-trunks in a relatively short space are much thickened. As examples, one may cite the cervical and lumbar portions of the spinal cord. This is especially the case in the cephalic parts of the animal. In consequence of this all of the craniata possess in this segment of the system an enlargement,—the *medulla oblongata.* From this arise the nerves for the branchial arches and for all the structures derived from them.

Another enlargement lies farther forward where in nearly all animals large optic nerves enter. Finally, one regularly finds at the extreme anterior end of the central nervous system a usually-large projection where the olfactory nerve takes origin.

In the spinal cord as well as anterior to it there exist connections of one level with another. These produce further enlargements of the central system.

Finally, with the system as just described there are associated other structures which are not in direct relation to the different nerves, but which may be, indeed, very important for certain functions of the animal. For example, one finds, dorsal to the medulla in all craniata, a more or less fully developed cerebellum. Ventral and anterior to the deep origin of the optics is an important apparatus,—the midbrain-base with the midbrain-ganglia,—which receives tracts from before and behind and which also sends out tracts. Finally, there is always developed anterior to the Thalamencephalon and dorsal to the deep origin of the olfactory nerve the basal ganglion of the forebrain,—the *corpus striatum,*—with which a brain-mantel may be associated.

As is well known, the spinal cord is alone sufficient to make the lower vertebrates capable of relatively complicated acts.

One is able to determine anatomically and even experimentally how the different brain-structures in the animal series were added to the spinal cord, essentially increasing the capability of the organism.

The amphioxus practically possesses only the spinal cord, corresponding to the metameres, which receives and gives off nerves. Whatever brain-structures it may have are so small that the investigations of our best men, covering several decades, have only recently—through Kupffer—succeeded in finding them. The brain-segments of the nervous system of amphioxus has as yet remained quite refractory to physiological experiments. A decapitated amphioxus conducts himself just like one which still possesses the pointed anterior end of the head (Steiner). However, all craniate vertebrates possess, anterior to the spinal cord, at least the brain-structures above mentioned. In the field of morphology one would hardly find anything more interesting or instructive than a glimpse of the development of the brain; of the progressive or retrogressive development of particular parts; of the development of higher structures from parts which in other animals still exist as simple cuticle. Let us now become acquainted with these processes step by step,—and see how the whole was gradually built up, how it came to be and how it is ever changing,—here increasing and there decreasing.

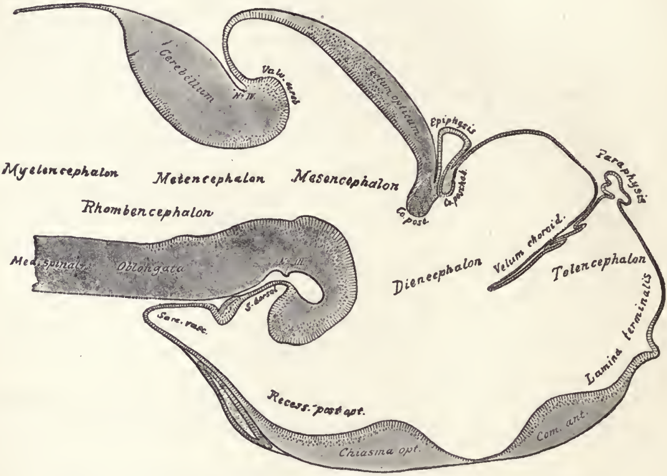


Fig. 18.—Sagittal section through the brain of a four-months' larval sturgeon. (After von Kupffer.)

Physiologically these things afford an especial interest, and it is to be hoped that they will some time afford also an especial interest psychologically. It is certainly to be regretted that these subjects are here still quite insufficiently recognized.

From the foregoing chapters we know that the entire fundament of the nervous system is furnished by the outer germ-layer,—epiblast,—that this fundament forms a plate which soon sinks in to form a groove. Very early the medullary groove becomes closed, forming a medullary canal. But even before this closure is complete one may recognize in all vertebrates, in the region where the brain is developing, three vesicular expansions: the (primitive) forebrain, midbrain, and hindbrain.

The wall which closes the forebrain anteriorly is called the embryonic *terminal lamina*; the closure of the original medullary plate results in a seam, or raphé.

Fig. 19.—Longitudinal section through the brain of a newborn kitten. The Thalamus (*Zwischenhirn*) and Corpora Quadrigemina (*Mittlehirn*) covered by the Cerebrum (*Vorherhirn*).

The section of the brain of a larval sturgeon (see Fig. 18) contains, as the description will show, the most varied fundaments for the further development of the separate brain-segments. Not all come to maturity; many remain in the stage here shown; but among the higher vertebrates the separate smaller segments of the brain-tube become metamorphosed into important structures, whose development may be very different for the different classes.

First note the small epithelial plate at the dorsal end of the lamina terminalis.

In most vertebrates there arises out of that part of the forebrain which lies dorsally and laterally from the lamina terminalis a new and important structure, the *Prosencephalon*: a large vesicle located anteriorly and dorsally, which is soon divided into right and left hemispheres by a longitudinal infolding from the dorsal surface. The hemispheres are not developed in the sturgeon; but, even if they were, they would not be shown in Fig. 18, because the section is median.

In mammals, the hemispheres, which are at first very insignificant appearing structures, soon grow enormously, bending posteriorly and thus covering gradually most of the other vesicles. Finally they rest like a mantle over the Thalamencephalon, the Mesencephalon (Corpora Quadrigemina), and the Metencephalon (Cerebellum and Pons).

Notwithstanding the turning back of the cerebral hemispheres, the cavities of the various brain-vesicles, later called ventricles, retain their communication with each other.

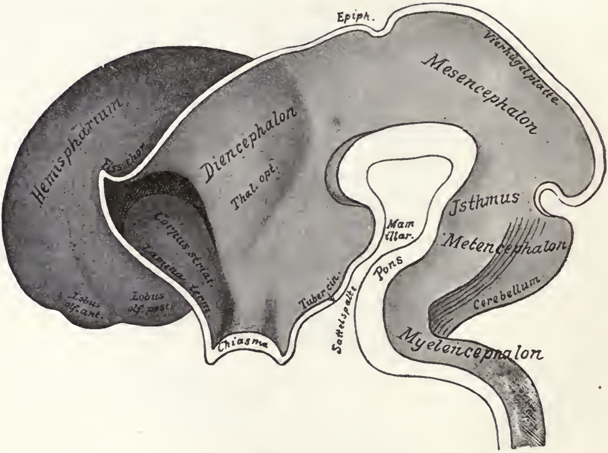


Fig. 20.—Median longitudinal section through the brain of a five-weeks' human embryo. (After His.)

Thus from the primitive forebrain-vesicle two structures are developed: *Prosencephalon*, or cerebrum (*Vorderhirn*), and, from that part of the primitive forebrain-vesicle which is not divided into hemispheres, the *Thalamencephalon* (*Zwischenhirn*).

In all mammals the walls of the hemispheres begin to grow thicker at this stage. But one soon discovers that that process is carried on by no means equally. Near the base are located the olfactory lobes as thick-walled masses and posterior to them, also basal, the great corpora striata. These masses are separated by a cleft from a more dorsal segment, the Pallium, or mantle, whose walls thicken relatively late. It is interesting to note the primitive relations which manifest themselves here. In all vertebrates the basal ganglia—corpora striata and olfactory lobes—are developed, but only among the higher vertebrates does the mantle reach a noteworthy development. In Petromyzon and in bony fishes the mantle remains a simple epithelial wall throughout life. But the Pallium is that portion of the brain which later bears the cortex cerebri, and is, therefore, the organ on whose development all higher psychical life depends. The Pallium of the sturgeon, for example, remains through life as thin as it is represented in the four months' embryo (Fig. 18).

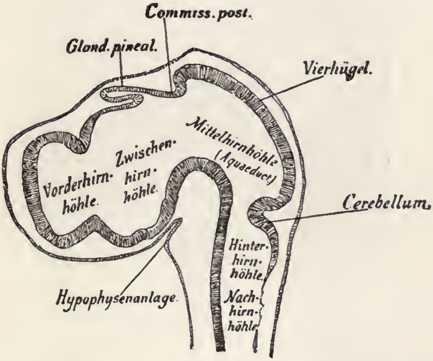


Fig. 21.—Longitudinal section of head of a four-and-a-half day chick. The five brain-vesicles are fairly well developed. *Vorderhirnhöhle,* Cerebral cavity. *Zwischenhirnhöhle,* Thalamencephalic cavity, or third ventricle. *Mittlehirnhöhle,* Aquæductus. *Hinterhirnhöhle,* Cerebellar cavity. *Nachhirnhöhle,* Cavity of medulla. The last two together form the fourth ventricle. *Hypophysenanlage,* Fundament of the hypophysis. *Vierhügle,* Corpora Quadrigemina. (After von Mihalkovics.)

The hemispheres are, in mammals, most highly developed, and are also here best studied. Their development should be, therefore, especially described at this point; while those parts of the brain which lie posterior to the cerebrum may better be described after we are acquainted with the brains of lower animals where the thalamus, and midbrain, and even the cerebellum show especial structural forms, which are either insignificant or quite lost in mammals. The roof of the Thalamencephalon remains through life for nearly its whole length as a simple epithelial layer. At the point of juncture with the Prosencephalon the epithelial plate is displaced downward by the encroachment of a highly-vascular growth from the cranial cavity: the *velum chorioideum.* From the relation of the hemispheres to the Thalamencephalon, their inner border must be continuous with the velum. In the frontal section through the cerebrum, shown in Fig. 22, this is made apparent. The figure also shows that the cerebral cavity is divided into one median and two lateral ventricles. The velum chorioideum sends expansions into the lateral ventricles: the *Plexus chorioidei laterales.* The place where the walls of the hemispheres pass into a simple epithelial layer (Fig. 22, *a*) is called the margin of the hemispheres. This margin is later marked by a fasciculus of white fibers throughout its whole length: *Fornix.*

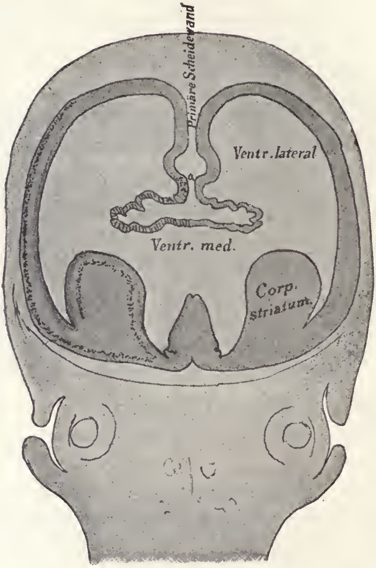


Fig. 22.—Frontal section through the head of a human embryo of two and a half months, showing the invagination of the cerebral cavity and the fundament of the corpus striatum.

When the most important parts of the cerebrum have once become well defined, it has the form shown in Fig. 23. It has grown out posteriorly and has also bent ventrally. Where, within the cerebral cavity, the corpus striatum is developing the outer wall is less expanded than in the other parts of the cerebrum.

In that place a relative retardation of the growth of the cerebral wall leaves a deep fissure, the *Fossa Sylvii.*

A *frontal lobe,* an *occipital lobe,* and a *parietal lobe* may now be easily distinguished upon the hemispheres. That part of the hemispheres below the Sylvian fossa is called the *temporal lobe.*

The hemispheres are still hollow within and the ventricular cavities conform naturally to the general cerebral form. Those parts of the ventricle which extend into the frontal, occipital, and temporal lobes have been called the *anterior, posterior,* and *inferior horns,* respectively. At this stage of development the median wall of the hemisphere demands our especial interest. As before mentioned, its ventral margin passes into the epithelium of the plexus chorioideus. This is the case also when the wall bends down with the temporal lobe. From the base of the lamina terminalis to the apex of the temporal lobe, the sickle-shaped fornix locates this margin. In the anterior part of the brain the *corpus callosum* is developed dorsal to the fornix. The commissural fibers of which the corpus callosum is composed determine a surface which forms an acute angle with the fornix (see Fig. 24).

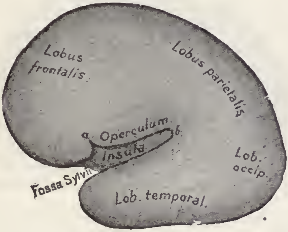


Fig. 23.—The brain of a human fœtus of the fourth month.

That portion remaining between corpus callosum and fornix, and which consists of the two thin laminæ of the primitive hemispherical division-wall (*primäre scheidewand,* Fig. 22) is called the *septum pellucidum.* These are important structures, which should be carefully studied in the accompanying figures.

Note carefully the anatomical relations shown in Fig. 22. In the base of the cerebrum is a thickening of the wall, which projects freely into the ventricle: the *corpus striatum.* From the corpus striatum as from the cerebral cortex nerve-fibers arise.

Many fibers which have their origin in the cerebrum must pass through the corpus striatum on their way to more distant parts of the central nervous system. The fibers thus passing through the corpus striatum lie in two masses: an outer and an inner one. The outer one is called the *nucleus lentiformis* and the inner one the *nucleus caudatus.* The mass of fibers between the two has received the name *internal capsule.* In the four months' human embryo the division of the corpus striatum is already clear, and the nucleus lentiformis and nucleus caudatus appear as independent gray masses.

The corpus striatum lies the whole length of the cerebral base. Posteriorly it is, indeed, very narrow and it is really only the median part which is always demonstrable. As tail of the caudate nucleus, it is always found in cross-sections through the cerebrum. The lateral part, the nucleus lentiformis, is much shorter. The nucleus caudatus projects freely into the ventricle. The same is true, anteriorly, of the nucleus lentiformis. In later embryonic life, however, the narrow cleft between it and the cerebral wall becomes so narrow as to be no longer demonstrable. But the cerebral wall may always, even in adults, be easily separated from the outer wall of the nucleus lentiformis, without the severing of fibers.

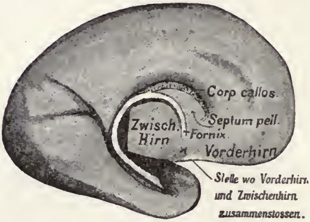


Fig. 24.—Showing median aspect of a hemisphere whose lateral or outer aspect is shown in Fig. 23. *Stelle wo Vorderhirn u. Zwischenhirn Zusammenstossen,* Place where cerebrum and Thalamencephalon come together. For further description, see text.

In the adult brain the position of the former cleft may become of great importance. At that place, for example, cerebral hemorrhages take place with especial ease, and the blood, even when it is small in quantity, fills the space between the cerebral wall and the outer side of the nucleus lentiformis.

The glimpse which has been presented of the developing brain has possibly already called forth the question: How does the brain grow? And the comparison with the richly convoluted brain of the adult may have suggested also the question: At about what time has the brain reached the form and size which it retains through the major part of life or until that time when advancing age induces senile decadence?

If the brain is the organ upon the faultless performance of whose function the normal psychical processes depend, it is worth our while to know how long new tissue-elements may be formed and upon the increase of what part the growth of the whole depends. Investigations which might answer these important questions have made little advance. There is a complete lack of investigations on the multiplication of ganglion-cells in different parts of the brain in the post-embryonic period. Up to the present time karyokinesis of nuclei of central cells has been very infrequently found; so that it might appear as if the brain, which has approximately reached the form and weight of the adult organ at about the seventh year, had, by that time, established all of its ganglion-cells. Schiller's proof, that the slender oculomotorius of the newborn cat contains scarcely fewer fibers than the thick nerve of the adult, favors the theory of an early termination of cell-formation. There are, however, opposing statements. Thus, Kayser found in the cervical enlargement of the spinal cord of the newborn only about half as many ganglion-cells as in the same region of a 15-year-old boy, while the number found in the latter case was little different from that found in an adult man. Also enumerations which Birge and others have made on the spinal cord of the frog determined positively that in these animals the ganglion-cells continue to increase for a long time in adult life.

Probably the principal post-embryonal increase of nerve-tissue in man occurs in the growth of nerve-fibers and collaterals from ganglion-cells already present, and especially of the formation of medullary substance which continues throughout life. Donaldson, to whom we are indebted for an excellent work on "The Growth of the Brain," came to the same conclusion.

The human cerebrum having been an important object of your previous study, it has seemed profitable to describe its development somewhat in detail. But since we are not here concerned with the human brain alone, let us study in the brain of another vertebrate those first developmental processes which are common to all vertebrates. For this the brain of a reptile—the lizard—has been chosen. In this (see Fig. 25) one may readily recognize the typical parts of the vertebrate brain, because even in adult reptiles the relations are much simpler than in mammals.

The middle of the figure is occupied by the cavity of Thalamencephalon. Its roof is almost exclusively formed of epithelial plates whose numerous projections will claim our attention later. Even ventrally the wall, which is evaginated to form the sack-like *recessus infundibularis,* is only a thin one. The hypophysis lies close beside it. The lateral walls containing the optic thalami are not figured. The dorsal wall of the Thalamencephalon is directly continuous with the cerebral mantle, the Pallium, which is the dorsal wall of the Prosencephalon. The floor of the latter is occupied by the corpus striatum and the olfactory apparatus. Posteriorly the Thalamencephalon merges into the Mesencephalon, whose dorsal segment is called the *corpus opticum,* because here is the deep origin of the optic nerves.

The ventral segment of the midbrain, designated as Tegmental prominence (*Haubenwulst*) and Basis mesencephali, contains almost exclusively nerve-tracts, with, also, a few small nuclei. Turning at a sharp angle, the corpus opticum becomes continuous with the cerebellum. In this angle there are, in all vertebrates, two great nerve-decussations, the anterior one of which belongs to the nervus trochlearis. The cerebellum covers a part of the medulla even in the reptile. The greater part, however, is exposed and is covered by a thin choroid plexus: the *Plexus ventriculi quarti.* Then the cavity of the central system becomes narrower and narrower until it becomes a narrow canal which traverses the whole length of the spinal cord.

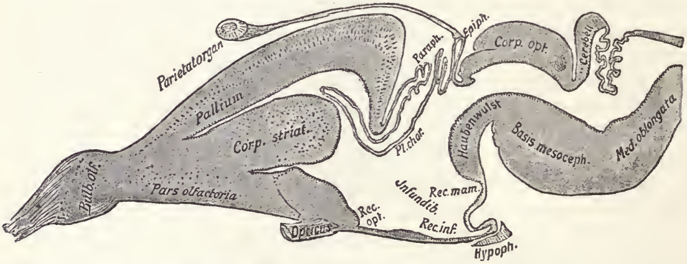


Fig. 25.—Reptilian brain. (A diagrammatic sagittal section.)

Something has been said of the development of the peripheral nerves in the previous chapters. If the central nervous system has progressed so far in its development that the principal parts are clearly distinguished one from another, then from the Thalamencephalon to the end of the spinal cord the central cavity (ventricle, or central canal) is inclosed with gray tissue: masses rich in ganglion-cells. Posterior to the midbrain the peripheral nerves arise from these ganglion-cells. *The motor nerves arise from cell-groups in the gray matter, and with few exceptions leave the spinal cord by the ventral side. Most of the sensory nerves arise from ganglia which lie close beside the central organ.*

From the ganglion every sensory nerve sends a number of root-fibers dorsally into the central nervous system. Most of the sensory root-fibers pass into the gray substance not far from the respective ganglia, but some of them run some distance, forward or backward, in the superficial layers before they reach their termination in the gray. These are designated as ascending and descending roots. The origin and arrangement of the ganglia afford much instruction and interest.

The earliest embryonic changes show that in these peripheral structures we have to deal with true derivatives of the central nervous system,—with parts which separated from it quite early. The ganglia arise from the margins (*Randstreifen*) of the medullary plate. When this plate rises on each side to form the medullary ridges which finally fuse along their marginal lips to form the medullary canal, leaving on each side a free edge, these margins come together and form an unpaired cell-rod, which, at first wedge-shaped, appears to sink more or less into the dorsal seam of the spinal cord. In consequence of an increase and a displacement of its cells it soon leaves this position, leaves the roof of the medullary tube completely, and is divided by splitting longitudinally into a left and right cord. Through segmental thickening the paired fundaments are divided into separate ganglia, which move more and more laterally along the medullary tube. When the segmentation is complete then the primary ganglia, so far as they are derived from elements of the central system, are complete.

While the spinal ganglia, from their above-described derivation, remain really a part of the central system, the ganglia of the cranial segment come into renewed contact with the ectoderm, or, more correctly, with the embryonic epidermis for a certain period of their development, and together with this form the *fundaments* of the *primitive sense-organs*. Every cranial nerve acquires two such contacts, or forms fundaments of two sense-organs, at two typical locations. These locations for the several cranial nerves occur in two longitudinal series: one more dorsally located, the *lateral*, or *Kupffer's, fundament*, and one more ventrally located, the *epibranchial*, or *Froriep's, fundament*. All of the Kupffer fundaments occur in a longitudinal line which begins anteriorly in the olfactory pit, passes through the oral pit, and in lower vertebrates is continued along the body as the *lateral line*. All of the Froriep fundaments lie in a longitudinal line which begins anteriorly in the lens-pit (*Linsengrube*) and thence runs along the dorsal ends of all the branchial slits. Of the Kupffer fundaments two persist and develop into permanent sense-organs: the *nasal pit* and the *auditory pit.*

The Froriep fundaments, on the other hand, have an exclusively embryonic existence, and were, therefore, regarded by their discoverers as ontogenetically persistent rudiments of lost ancestral sense-organs; and were called *branchial cleft organs* (*Kiemenspaltenorgane*). Definite traces of this embryonic connection with the epidermis are manifest in the adult in the Acustico-facialis, the Glosso-pharyngeus, and Vagus; the Kupffer series corresponds to the Ggl. acusticum, Ggl. jugulare of the IX and the Ggl. jugulare of the X; from the Froriep series arise the Ggl. geniculatum (VII), Ggl. petrosum (IX), and the pneumogastric ganglion (X).

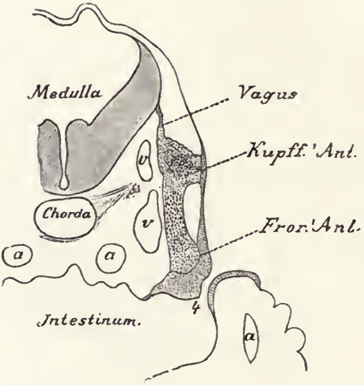


Fig. 26*a*.—Cross-section through the posterior part of the head of a shark embryo, of twelve millimeters' length. The section passes through the fourth visceral cleft (4) and through the vagus ganglion with its two epidermal contacts: the Kupffer fundament (Kupffer Anl.) and the Froriep fundament, respectively,—the lateral and the epibranchial fundaments. *a*, *a*, Arteries. *v*, Jugular vein. (After Froriep.)

The olfactory nerve occupies an exceptional position. At one time its primitive ganglion seemed to be quite absent. The *olfactory ganglion* of His arises independent of the nasal pit—the Kupffer fundament—as a purely lateral ganglion, migrates away from the nasal pit, approaches the brain, and fuses completely with the olfactory bulb. The nasal pit behaves also in a special way, in so far as it is the only one of the persistent fundaments which retains the character of the primitive sense-organs. Its cells remain *in situ* as peripheral nerve-cells which send their neuraxons into the olfactory bulb. In the case of other sense-organs—*e.g.*, the auditory pit—a separation takes place: the original peripheral nerve-cells migrate inward and become bipolar or pseudo-unipolar ganglion-cells, while the cells of the fundament which remain superficial become differentiated into "secondary sense-cells" of Retzius (Froriep).

While the relations in the trunk are quite simple,—since here a series of spinal ganglia lie beside the spinal cord,—those in the head will be found to present a much more complicated arrangement. It is exceedingly important here to obtain a clearer idea as to the number of fundaments or primitive elements which enter into these structures, because in all adult vertebrates of higher rank the relations presented by the cranial nerves are so complicated that the opinion has long been held that these nerves are not completely homologous to spinal nerves, but that all or nearly all of them are compounded from several elements into an apparently unified structure. Twelve pairs of cranial nerves are usually differentiated in mammals; even in birds the same thing may be true; but in amphibians and especially in fishes such an enumeration is quite arbitrary. In these lower vertebrates not only do the nerve-trunks receive other branches than those typical of the higher animals, but the sources of the roots are so manifold that it is not always possible to determine whether a particular root belongs to one nerve or another. For example, the Facialis consists essentially of motor fibers in the higher vertebrates, but in the aquatic lower vertebrates it receives a large reinforcement of sensory fibers which belong to the system of cutaneous sense-organs. Thus there exists no little confusion in differentiation of the Facialis and Trigeminus.

The cephalic end of the skeleton is phylogenetically compounded from a number of segments which have not yet with certainty been determined. It is probable that the number of ganglia and the nature of the nerve-roots may serve as guides in this problem. It thus becomes an important task to determine: (1) how many primitive pairs of cranial nerves there are, and (2) how these have been transformed and combined to form the cranial nerves which we find in the higher vertebrates. Incident to the transformation certain previously large and important nerves become superfluous and disappear, others change the direction of their course, and still others pass to organs which, during the racial or individual development, have had a function quite different from that which they have in the mature condition. For example, from the embryonic branchial fundaments important parts of the skull and of the middle ear develop; the branchial nerves are modified along with the other structures, and appear later in a rôle wholly different from that which they originally played (*e.g.*, N. petrosus superfic.). In fishes and aquatic amphibians the skin of the head is covered with a system of sensory end-organs which possibly serve for the perception of the changes of pressure in the surrounding medium. The sensory branches of the Facialis which in Amphibia innervate these organs are, in the metamorphosis to terrestrial amphibia, either lost or changed to quite insignificant twigs.

In the light of these facts it becomes evident that the formerly practical method of a simple morphological description of that which exists in the adult animal, and above all the simple transferring of mammalian relations

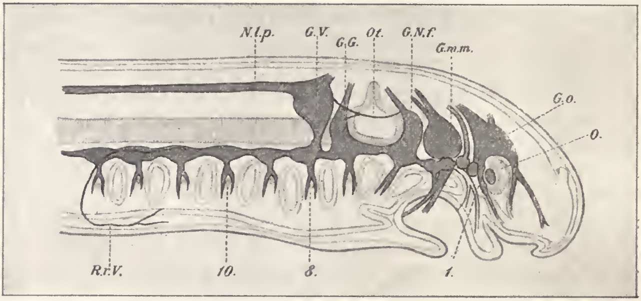


Fig. 26*b*.—Cranial ganglia and nerves of a four-millimeter *Ammocœtes*. (After Kupffer.)

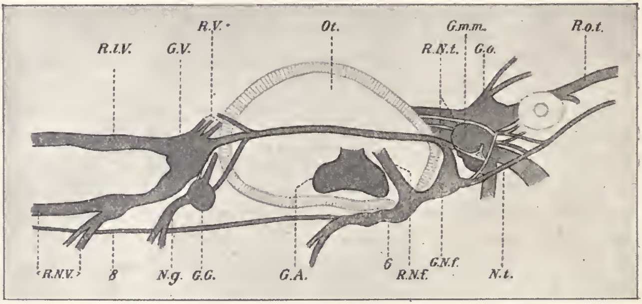


Fig. 26*c*.—Cranial ganglia and nerves of a twelve-centimeter *Ammocœtes*. (After Kupffer.)

Explanation of the figures: *G.o.*, Ganglion ophthalmicum. *R.o.t.*, Radix ophthal. N. trigem. *N.t.*, Nervus trigeminus. *R.N.t.*, Radices N. trigem. *G.m.m.*, Ggl. maxillo-mandibulare. *G.N.f.*, Ggl. N. facialis. *R.N.f.*, Radix N. facialis. *Ot.*, Otocyst. *G.G.*, Ggl. N. glosso-pharyngei. *G.V.*, Ggl. Vagi. *N.g.*, N. glosso-pharyngeus. *N.l.p.*, N. lateralis prof. *R.l.V.*, Ramus lat. Vagi. *R.V.*, Radices N. Vagi. *R.N.V.*, Rami N. Vagi. 1, 6, 8, 10, Epibranchial ganglia of these numbers, respectively.

to the lower vertebrates, can lead to no satisfactory results. The task of sufficiently describing the cranial nerves is to be accomplished in no other way than the following: (1) in gradually becoming acquainted with all of the separate nerves that correspond to a single segment of the head, and (2) in determining how these have been combined into larger trunks.

So far as we know at present, the simplest relations exist in the embryos of Cyclostomii. It is especially to Kupffer that we are indebted for the beginning of a somewhat clearer vision here. (See Figs. 26*b* and 26*c*.)

Note in the Ammocœtes of only four millimeters that the chain of epibranchial ganglia is connected dorsally with the five much larger dorsolateral ganglia. The most anterior one of the latter is the Ggl. ophthalmicum. From this most of the fibers which constitute the ophthalmic branch of the Trigeminus later develop. Posterior to this, and connected with the central system through two roots, lies the Ggl. maxillo-mandibulare. It will later be fused with the Ggl. ophthalmicum to form the Ganglion Gasseri and will give off the second and third branches of the Trigeminus. But in the meantime, fibers and ganglion-cells from the anterior epibranchial ganglia have become associated with the elements already enumerated. So the N. trigeminus is to be looked upon as already a most complicated structure, containing elements of most varied origin. Anterior to the otocyst lies the great ganglion of the Facialis, connected with the sixth and seventh epibranchial ganglia. When the animal becomes larger one recognizes that this ganglion is only an appendage of the great composite root of the Facialis; that in the composition of this nerve not only do fibers from the ganglion in question participate, but also numerous structures which arise from the now gradually disappearing epibranchial ganglia. Just posterior to the ganglion of the Facialis the previously continuous trunk of the epibranchial ganglia comes to an end (see Fig. 26*c* and compare Fig. 26*b*). Parts of this trunk are received anteriorly into a *Ramus buccalis,* and posteriorly into peripheral facial branches.

Here is an example of that which the author stated above regarding the value or significance of single nerves. The apparently single facial nerve contains elements of the most manifold origin and significance.

Posterior to the otocyst lie the Ggl. Glosso-pharyngei and the Ggl. Vagi; both intimately connected with the corresponding epibranchial ganglia. Later, when the epibranchial chain is broken, it remains intact posterior to the ganglion of the Vagus, where it appears like a nerve-trunk passing off from that ganglion and containing ganglionic nodes. It is the N. pneumogastricus, the Vagus, and it innervates the gills, heart, and other viscera.

CHAPTER V.

THE STRUCTURE OF THE SPINAL CORD.

IN the introductory chapters the fundamental elements of which the nervous system is composed were presented; also their arrangement in larger and smaller complexes, and the development of these and the principal divisions of the central system. In the following chapters will be presented the most important facts known regarding the structure of these principal divisions, beginning with the description of the best-known nervous systems: the mammalian and human.

First to be considered is the *spinal cord,* the lowest central nervous system, the one which is always present, and which forms the first place of *reception* and place of *origin* of nerves. On either side of it lie the *spinal ganglia* from whose cells the sensory nerves take their origin. They have been found in vertebrates of all classes. The ganglia are constructed of cells whose large bodies send out, in fishes, an axis-cylinder in each direction, the efferent one being the neuraxon, while the afferent one represents a modified dendrite (see Fig. 16, in Chapter II). The same is true in the embryos of other vertebrates; but in the latter the processes come to lie so close together that the first part of their course is represented by a single stalk, only dividing a little way beyond the point of origin. Fig. 27 shows several such cell-types from spinal ganglia. Wherever it has been investigated it has been found that one of the processes ran to the periphery as sensory nerve while the other passed to the central organ. All of these central processes taken together are called the *dorsal root* of the ganglion. The number of dorsal roots is very different in different animals; even among individuals of the same species there may be small variations. That depends upon the length of the animal and the number of the metameres which reach structural maturity. Ranged serially along the sides of the spinal cord these sensory roots enter the cord from the dorsal side. After their entrance they divide into ascending and descending branches, and also give off numerous collateral branches, which send twigs into the gray matter. This ascent and descent occurs in the dorsal segment of the spinal cord, and where many such nerves are present the whole bundle of longitudinally ranged nerves is called the *posterior tracts.*

Any section of the spinal cord shows that that organ is traversed centrally and longitudinally by a canal—*canalis centralis*—surrounded by epithelium, and that around this canal lies a very finely organized tissue, the *gray substance.* This is, in turn, surrounded by nerve-fibers, most of which run longitudinally. These longitudinal nerve-fibers represent the *tracts.*

The posterior root-fibers (dorsal roots) enter the gray substance after a longer or shorter course, usually in the posterior tracts, though in fishes in laterally located tracts as well. After entering the gray substance the fibers divide into fine terminal ramifications, which join a close net-work of fibrillæ, which fills the whole posterior segment of the gray matter. They probably come into contact there with the processes of smaller cells.

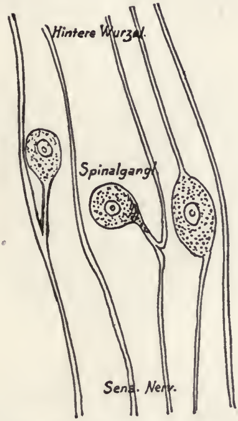


Fig. 27.—Several forms of spinal ganglion-cells, showing the cell-bodies, the afferent sensory nerves, and the dorsal roots (*Hintere Wurzel*).

The gray matter has been divided into posterior and anterior horns. A better expression would be: *dorsal* and *ventral columns,* because the projections are really columns which extend longitudinally throughout the whole length of the cord. The dorsal *columns* are formed from the fiber mesh-work of the posterior roots. The ventral columns are formed from the collection of ganglion-cells which give rise to the anterior roots.

The development of the dorsal and ventral columns depends naturally upon the number of nerve-fibers which are connected with them. The fishes furnish a good example of this. In this class of vertebrates a large part of the body-surface is supplied with sensory fibers, not from the spinal nerves, but from a branch of the Vagus. The spinal sensory nerves are, therefore, relatively small, and in consequence, also, the dorsal column of gray matter, as shown in Fig. 29.

But if, as in the case of *Trigla* (Fig. 29, *B*), many sensory nerves enter the spinal cord at any particular place, the dorsal column is much increased at that level. Fig. 29, *A*, shows a section of the spinal cord of the white-fish (*Leuciscus rutilus*). Note here the small dorsal columns which receive relatively small roots. Note, also, that between the dorsal columns the posterior tracts contain only a few fibers.

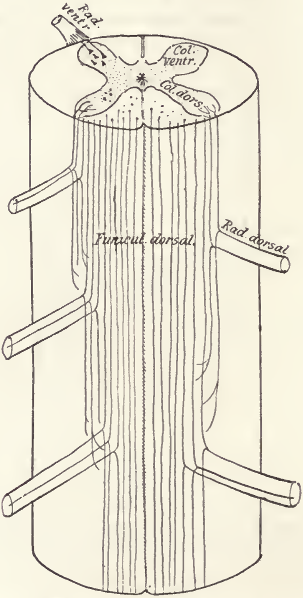
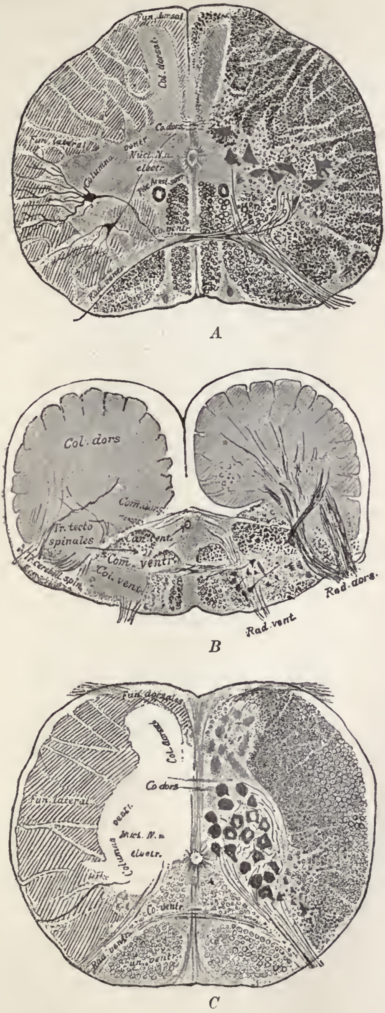


Fig. 28.—The diagram of the spinal cord as seen from behind. Showing the dorsal and ventral columns of the gray matter and the dorsal and ventral nerve-roots, illustrating also what was said about the posterior tracts.

The ventral columns from which the motor nerves arise are relatively small in *Trigla* in the cervical region, in the white-fish they are very much more strongly developed, but in the spinal cord of the electric eel (*Gymnotus*, Fig. 29, *C*) they reach a very unusual development. In the last case the



Figs. 29, 30, and 31.—Showing the different degrees of development of the gray matter. *A*, Spinal cord of *Leuciscus*; *B*, of *Trigla*; *C*, of *Gymnotus*; the last from a preparation by von Fritsch.

column in question contains, besides the small ganglion-cells which produce the motor nerves,—by chance not shown in the figure,—a mass of immense spherical ganglion-cells: the *Nucleus nervorum electricorum.* These cells certainly correspond to a group of motor cells in other animals; but, as you know, the electric organ of *Gymnotus* is shown by location and structure to be derived from muscular tissue.

After their entrance into the spinal cord most of the posterior root-fibers soon enter the gray matter; in part, however, they reach the gray matter only after a longer or shorter course in the posterior tracts. It has been found that a small number of the root-fibers actually pass through the gray matter, crossing over to the dorsal column of the other side to end immediately, or to end only after passing along the posterior tract of that side for a certain distance. These crossed sensory nerves pass from one side to the other in the *Commissura dorsalis medullæ spinalis.* They are very unequally developed in different animals, even in animals of related species. Besides that, the *commissura dorsalis* is unequally developed at different levels of the cord. The number of fibers in it depends upon the size of the posterior roots, and from the proximity of this to the point of section.

A certain portion of the posterior roots is not at once lost in the network of the gray matter, but proceeds farther ventrally to the region of the ventral column. This will be discussed later.

Finally it must be mentioned that in mammals a part of the sensory tract comes into connection with cells which stand in direct connection with the cerebellum through their axis-cylinders. These cells arranged in long columns—the column of Stilling-Clarke—have only been demonstrated in mammals. Their presence in fishes, reptiles, and birds is, however, at least probable, though their certain identification has not yet been successful.

Remember that the dorsal columns or posterior horns owe their existence to the entering roots, and that the posterior tracts are little more than the continuation of root-fibers. The same thing is true for a part of the lateral columns, varying with different orders of animals.

Such are the characteristics of the apparatus through which the impressions of the outer world are conducted to the central system. Before tracing the course of the afferent impulses within the central system, the *origin* of the *motor nerves* will be described. That may be readily done, since the essential facts have already been presented. Remember that in the ventral column (anterior horn) of the gray matter, lie long columns of ganglion-cells whose neuraxons for the greater part emerge from the anterior roots of the same side, while the smaller remaining parts cross over and emerge from the opposite root. As motor nerves, they proceed on their course. At quite regular intervals the ventral columns form ventrally projecting prominences of the spinal gray matter: the *anterior horns.* They also undergo an increase in size at places where many root-fibers leave the cord. Thus, in animals with legs there may be observed an enlargement of the spinal cord for both anterior and posterior extremities, the Intumescentia cervicalis and lumbalis, respectively. The difference in this respect between lizards and the snake-like "blind worms" is clearly visible. The enlargements are especially noticeable in a section of the spinal cord of the turtle, because these armored animals have very large nerves to supply the extremities, while the thoracic nerves are very small.

The columns of large ganglion-cells contain the centers of innervation

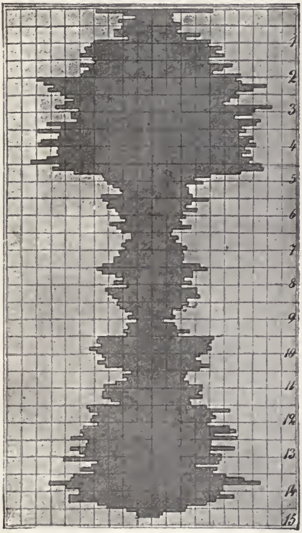


Fig. 32.—Projection upon a plane of the enumerated ganglion-cells of a frog's spinal cord. The figures at the right indicate the number of the corresponding spinal nerve. Note the enormous increase of the number of cells for arms and legs. (After Birge.)

for the individual muscles. These are arranged in groups. For the mammalian spinal cord the significance of a few of these groups is already known. It is known, for example, that the ganglion-cells which lie nearest the median line innervate the muscles of the back; and that a certain group of laterally located cells in the cervical cord provides innervation for the musculature of the thumb. This was found out by a careful study of the spinal cord of such animals as had suffered—through disease or experiment—paralysis of a particular group of muscles, comparing the microscopic appearances with those of the normal individual. How far such observations have been made in the human subject will be discussed later.

The cell-groups in the lower vertebrates appear so similar to those in the well-studied mammals that one is justified in assuming that there are also in the lower vertebrates definitely circumscribed *centers*.

The anterior gray horns do not, moreover, send all of their fibers through the anterior roots. It has been demonstrated for representatives of most classes of vertebrates that a very large bundle of fibres passes dorsally and leaves the cord by the posterior roots (see Fig. 33).

Since motor fibers reach the sympathetic nerve through the posterior root-fibers which innervate the musculature of the viscera, it is probable that in the above-mentioned fibers from the anterior horn we see the motor nerves of the viscera.

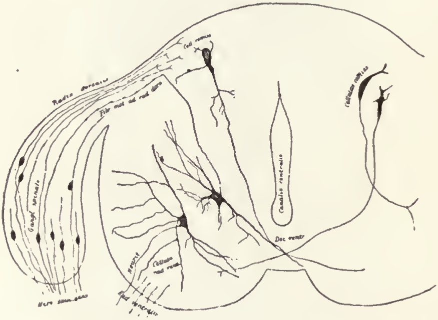


Fig. 33.—Section through spinal cord of a chick, showing motor fibers to the dorsal root (Fibr. mot. ad rad. dors.). (After Retzius.)

The two ventral cell-columns, belonging essentially to the motor system, and the two dorsal enlargements of the gray matter which receive the sensory roots produce upon a cross-section of the spinal cord of most vertebrates a gray figure similar to an H.

The central gray matter, in addition to the several elements already enumerated, contains such innumerable dendrites and collaterals of neuraxons from the root-cells that it presents a perfect labyrinth of meshes, into which enter the large tracts from the posterior roots, and these, passing through, ramify about the cells of the anterior horn. These sensory elements, which lie so close to the origin of the motor fibers, would be well adapted to bring about directly many short reflexes (see Fig. 34).

Not all of the cells in the spinal cord nor all of the fibers stand in direct relation to nerve-roots. There are very many cells which send their neurite, or axis-cylinder, out of the gray matter, either on the same or opposite side. Usually the neurite divides then into an ascending and a descending branch. Then, after a longer or shorter course, again, bending back into the gray matter, both branches end. On the way the main branches have sent numerous collaterals into the gray. Such cells are adapted to connect among themselves different levels of the spinal cord. Such neurons are called *cellulæ commissurales.* Many neurites from such commissural cells cross over ventrally to the opposite side, forming a decussation quite ventral to the gray: the *decussatio ventralis* of the spinal cord (Fig. 33, *Dec. vent.*). At just the same place there are still other decussating

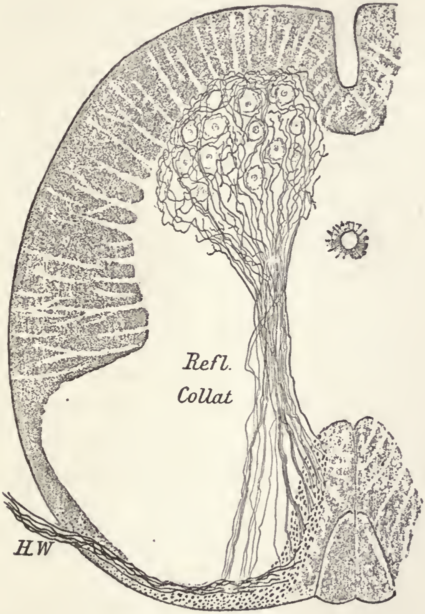


Fig. 34.—From the spinal cord of a newborn mouse. (After Lenhossek.)

fibers; namely, fibers from the anterior horn of one side to the anterior root of the opposite side; also in mammals more central tracts.

Among bony fishes and in part, also, among selachians, the individual elements of the commissura ventralis are so far divided that one may often recognize two quite distinct commissures. In the midst of the gray substance one may see everywhere long fascicles of medullated nerves passing upward and downward. In part these nerves are elongated fascicles from the roots, in part derivatives of the commissural cells, and in part fibers from other sources. Among cyclostomes and some of the bony fishes there are so many of these that it is not possible to trace a sharp line of division between the gray matter and the peripheral white matter.

But in most vertebrates we find the central gray matter of the spinal cord surrounded by white fibrous tracts. The spaces in the H (or X) which represent the outline of the gray may be named as follows: Dorsal or posterior tracts, ventral or anterior tracts, and lateral tracts. That the posterior tracts are mostly or entirely formed from ascending or descending fibers of the posterior roots has already been mentioned. In the lateral and anterior tracts we must look for those fascicles which arise from the *commissural cells* and which bring into association different levels of the cord. These are usually called, in brief, the *tracts of the cord.*

In most vertebrates, even as low as the fishes, there lie very long tracts in the anterior column. In fishes and larval amphibians one may find, close beside the gray matter, one or more very thick fibers: *Mauthner's Fibers.* Arising in the cranium, near the origin of the eighth nerve—the nerve of equilibration—from gigantic ganglion-cells, the axis-cylinder, surrounded by enormous medullary sheaths, may be traced as far as the caudal vertebræ, where they emerge with the last sacral nerves (Fritsch). When one recalls the importance of the caudal musculature in the maintenance of equilibrium in swimming animals, he will recognize that the musculature in question is in special relation with the nerves of the ampullæ. The apparent absence of these fibers from many eel-like fishes (Haller) depends upon the different method by which that form of body maintains its equilibrium. In Fig. 29 these fibers are designated as *Fibræ Acustico-sacrales.*

Thus far the spinal cord has been represented as an independent center. As is well known, it is able to function as such under many circumstances; all experiments on decapitated animals show this. They teach that in the spinal cord are not only tracts for the simpler reflexes, but that even very complicated movements may be innervated from the spinal centers and be brought into activity reflexly. When the decapitated snake winds itself about the proffered support; when the decapitated duck swims; or the decapitated rabbit is able to make several normal leaps, it is not to be otherwise accounted for than that there are in the spinal cord complete mechanisms for producing the movements which in life were repeated numberless times. In the experiments cited these mechanisms, once stimulated to activity, perform simple or successive combinations of movements in an exactly normal way.

The stimuli which reach the spinal cord from without—*i.e.*, those which reach it through the sensory nerves—are alone sufficient to produce much that was formerly supposed to be possible only through higher psychical processes.

The activity of the spinal cord can be influenced, regulated, inhibited, or stimulated by other parts of the central system. Let us consider, for a moment, those tracts which are adapted to exert the enumerated influences upon the activity of the cord.

The author's own investigations justify the statement that from the selachians and bony fishes to the mammals a few tracts are constant. In the first place, the spinal cord is always in communication with the cerebellum.

The *Tractus cerebello-spinalis* in mammals, probably also in birds and reptiles, lies in the periphery of the lateral column. In fishes the author has traced it posteriorly, but did not clearly make out its location in the columns of the spinal cord. There is, however, ground for the opinion that here, also, they lie in the lateral column and may be recognized again in the thick fibers which are to be seen in the lateral columns of the spinal cord of *Gymnotus* (Fig. 31).

Then there is always found a tract which arises from the depths of the Thalamencephalon and passes to the anterior columns. It has long since been known in the mammals, where it receives the name *Fasciculus longitudinalis posterior* (Fig. 44).

Finally it may be accepted as highly probable that a large tract which arises in the roof of the Mesencephalon, in the tectum opticum, passes into the *anterior lateral column*. In these fibers, which in fishes and birds are especially numerous at their place of origin, one has probably to deal with a central sensory tract. At its origin it is called *deep midbrain-marrow;* in its later course it is called the *fillet*, or *lemniscus*. In the spinal cord one may, with all certainty, recognize that fibers arise from this fillet where sensory nerves end. They arise from those cells around which the nerve-roots from the posterior ganglia ramify. It was possible, also, to demonstrate, regarding the spinal cord, that for those cells in the gray substance around which the dorsal roots ramify axis-cylinders arise which, after decussation in the ventral commissure, pass toward the brain in the anterior and lateral columns. These fibers arising from commissural cells are not yet with certainty to be differentiated. It is, however, probable, on clinical and experimental grounds, that there is a crossed sensory tract in the lateral columns, though the conclusive anatomical demonstration of it is not yet accomplished. The secondary sensory tract,—*i.e.*, tract of the second order,—which arises from the cells of the gray matter and passes toward the brain in the antero-lateral column, is, in all probability, a part of the fillet, ending in the roof of the midbrain. The complete system will, in future, be called the *Tractus tecto-spinalis* in the cord and *Tractus tecto-bulbaris* where it comes into relation with the medullar or bulbar nuclei.

In mammals there are, associated with those above mentioned, still other tracts. Of these the most important of all is the tract from the cerebral cortex: *Tractus cortico-spinalis.* This tract, as yet demonstrated only in mammals, has a different position in the cord in different species. It has been longest known in the human anatomy as the *pyramidal tract* of the *lateral column*, or *crossed pyramidal tract.* In the mouse and guinea-pig it lies in the posterior columns quite near the commissura dorsalis. In the dog and in all apes it lies in the dorsal segment of the lateral columns. In man a part of the tract passes also in the anterior columns. This part is, in man, more highly developed than in any other mammal; in the lower mammals, in fact, this part of the tract is represented by only a few fibers. This part is called the anterior or direct portion of the pyramidal tract, or the column of Türck.

Fig. 35.—*A*, Spinal cord of a dog whose Tr. cortico-spinalis has degenerated in consequence of removal of the cerebrum. *B*, Human spinal cord in which the anterior and lateral pyramidal tracts (Tr. cort.-spin. lat. et Tr. cort.-spin. ant.) have suffered degeneration in consequence of a hemorrhage in the left cerebral hemisphere.

One has the impression that these cortico-spinal tracts are developed in proportion to the measure in which the cerebral activity is called into play in those functions of the extremities which are in no way instinctive, but are learned and cultivated by the individual. Fig. 35 shows a human spinal cord in which these tracts are functionally destroyed through disease; also a dog's spinal cord which has suffered a loss of the corresponding tracts through removal of the hemispheres. The difference in the development of these tracts in man and in the dog is apparent.

It has already been stated that fibers pass from the white substance into the gray, and that fibers from cells in the gray matter join the white columns. But in amphibians and fishes there are other elements not yet mentioned. Numerous dendrites pass from the ganglion-cells out into the white substance and ramify there (see Fig. 29). The same is true in the embryo of birds and mammals, but in the adults of these classes one seldom finds such dendrites in the white matter.

Finally it is to be mentioned that in many lower vertebrates true ganglion-cells are found even in the midst of the white matter. There is a large group of such cells in the periphery of the dorsal column in Cyclostomes and in certain fishes,—the so-called *"Dorsal cells"*; and also near certain motor roots, large ganglion-cells which probably send their neurites into the motor nerves. A noteworthy condition which exists in birds is still to be described. Here in the lumbar segment of the cord a tissue-mass wedges itself in between the dorsal columns, pushing these so far asunder that it was formerly believed to be a true bifurcation: *Sinus rhomboidalis.*

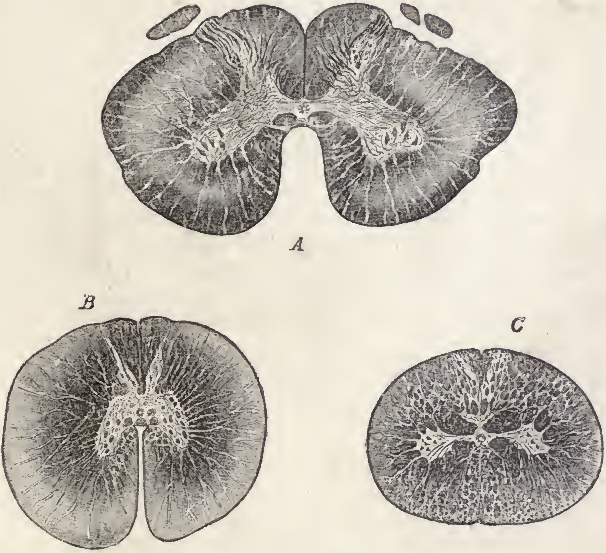


Fig. 36.—Sections of the spinal cord from large individuals of representative vertebrate classes. *A*, Section from the crocodile: *C. Africanus*. *B*, Section from the ostrich: *Struthio camelus*. *C*, Section from the shark: *Mustelus*.

It is evident that the elements which comprise the columns of the spinal cord are of very different origin. That cannot be inferred from a simple view of the cross-section. If one is to have even a general idea of the relations, it is at least necessary in every case to make a careful comparison of many cross-sections and longitudinal sections. But, to gain a clear concept of the relations, an extended study, aided by embryological and other methods, is necessary.

Those who are acquainted with the human spinal cord only are surprised at the great size of the spinal cord frequently observed in lower vertebrates. The spinal cord is, in these cases, a quite independent organ, whose size depends essentially upon the area which is to be supplied with spinal nerves and only in very small measure upon the development of the parts of the central nervous system. In the lower vertebrates it receives only a few fibers, and even in the higher vertebrates not many fibers from the more anteriorly located parts of the brain. If one would convince himself of this, let him compare in any large fish the small size of the brain with the relatively enormous size of the cord. The fish *Gadus æglefinus* especially possess a spinal cord which contains almost exclusively spinal elements and very few cerebral. The former are highly developed because the extensive body-musculature and surface require a rich innervation.

This striking relation may be readily followed even to the mammals. The brain of the horse or ox is much smaller than that of man, but their spinal cord is more than twice as thick as the human cord.

In this connection compare the accompanying sections (Figs. 35 and 36) of the spinal cord of representative vertebrates. All are drawn to the same scale of magnification.

CHAPTER VI.

THE OBLONGATA AND THE NUCLEI OF THE CRANIAL NERVES.

LET us now turn our attention to that part of the central nervous system which supplies the region of the head with nerves. Remember that the trunk portion of the nervous system—the spinal cord—represents a more or less independent center, joined to the cephalic segment through several tracts varying among different classes of animals; that an animal can live and can make approximately normal movements after the spinal cord has been completely severed from the cephalic part of the central nervous system. Indeed, if the cephalic portion, which contains important nerves for respiration and circulation, remains intact, and if the animal be protected from certain damaging conditions which manifest themselves under such circumstances, its existence will not be interrupted through the complete loss of the trunk portion. This is true even for mammals (Goltz); for lower vertebrates it is probable that even the cephalic portion also may remain functionless for a certain period without causing death.

We come now to the consideration of the complex of nerve-centers which are associated with those already described and which are not physiologically dependent upon them, though they may be influenced by them or may, in turn, influence them.

At the cephalic end of the spinal cord one may notice both macroscopically and microscopically marked changes of structure; the spinal cord merges into the *Medulla Oblongata.* These changes are with slight variations similar in all classes of vertebrates; but, among the lower vertebrates in which the branchial region is to be supplied with especially large nerves, the changes are much more apparent and clear than among mammals.

One always observes that the posterior columns diverge from each other and that the commissura dorsalis, just below them, and the adjacent gray substance about the central canal are visible. The dorsal closure of the central canal of the nervous system is effected by only a thin membrane. Passing anteriorly from the point of divergence of the posterior columns this membranous roof becomes wider and wider with the continued divergence of the columns. The widened central canal is the *fourth ventricle,* and the membranous roof—the *Tela chorioidea posterior*—merges anteriorly into the *Formatio cerebelli.*

Besides the changes above noted the nervous system is much greater in cross-section through the medulla than at any point posterior to that. This may be attributed to two circumstances: (1) the appearance of the *Formatio reticularis,* an "association-system" of short fibers, which is to be met at any point between the spinal cord and the base of the Thalamencephalon, but which is especially developed here; (2) the presence of nerve-centers. Within the skull there arise within a very short space three very large nerves: the Vagus, the Acusticus, and the Trigeminus. Where they take their origins—*i.e.,* at the location of the nuclei—the central organ is naturally much enlarged. The rich cerebral and cerebellar connections to such nerve-centers also add not a little to the volume of the medulla.

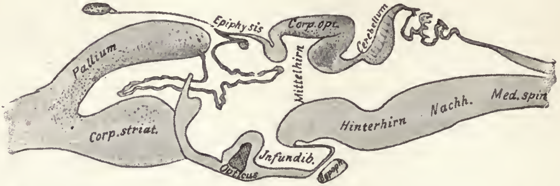


Fig. 37.—Sagittal section of an amphibian brain a little to one side of the median plane. Note the continuity of the Tela chorioidea posterior with the cerebellum. Note, also, the ample folds of the Tela, indicating that its surface is much greater than necessary to cover the fourth ventricle. *Med. spin.,* Spinal cord. *Nachh.,* Medulla oblongata. *Hinterhirn,* Floor of cerebellum (pons).

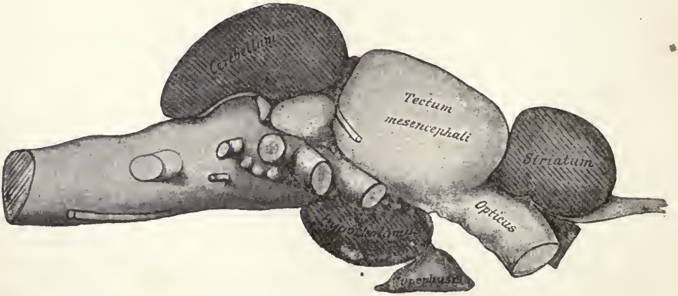


Fig. 38.—Brain of *Gadus æglefinus.* Those parts which do not belong directly to cranial nerves are shaded.

One usually has little conception of the great size of those parts of the central nervous system which are in connection with the cranial nerves among lower vertebrates. In the brain of the fish *Gadus æglefinus* (Fig. 38) the nerve-roots alone aggregate a much greater mass than that part of the brain not in relation to the nerves in question.

Sections through the medulla of fishes show that this is, for the most part, simply the origin of the great cranial nerves. All other systems of fibers are, compared with these, quite in the background. There exist also within the medulla several special centers which are in relation with the cerebellum and with the acusticus.

Finally, it is to be mentioned that this part of the nervous system is traversed by those tracts which pass to the spinal cord from the regions anterior to it, as well as fibers from the same source destined for the medulla itself.

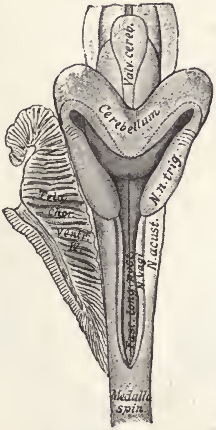


Fig. 39.—Dorsal view of the Oblongata and cerebellum of the sturgeon: *Acipenser ruthenus*. The Tela is dissected off and lies at the left. Note the large nuclei of the N. trigeminus, the N. acusticus, and the N. vagus. (After Goronowitsch.)

These notable changes which appear at the cephalic end of the spinal cord are still more apparent on cross-sections than in the outer form.

It may be best to choose as the first object for observation the medulla of the amphibian larva, because of its simple structure and its gradual differentiation from the cord (see Fig. 40).

Here the gray matter is constructed almost exclusively of that heaping-up of neuroblasts of which mention was made while discussing the embryonic development. In section *A* of the figure one recognizes the anterior and posterior columns of the spinal cord; but, since the section is from the cervical region, it is noticeable that the dorsal columns touch a much greater part of the periphery than is true at a lower level.

In section *B* the posterior horns diverge from each other and the dorsal epithelium of the central canal is used to form the Tela chorioidea.

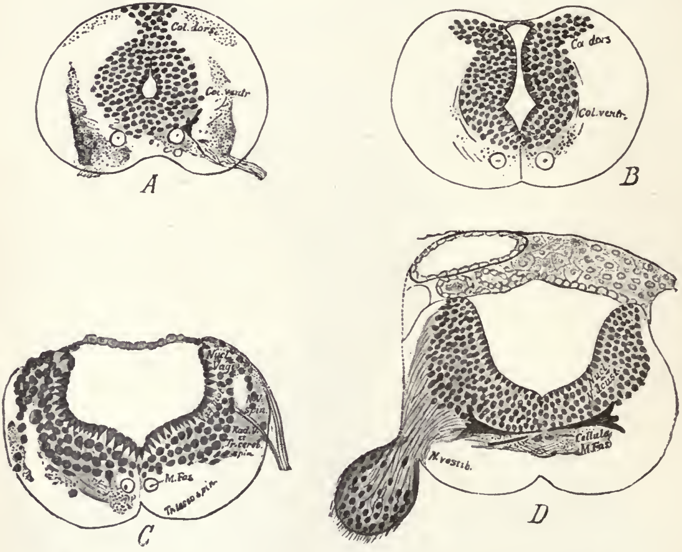


Fig. 40.—Four sections through the medulla of a four-centimeter larva of *Salamandra maculata*.

Now, on either side of the ventricle lie gray masses, destined, like the posterior horns (*col. dors.*), to receive sensory nerves. In figure *C* such a nerve—the Vagus, which enters here—is represented.

Note, at the same time, the increase of the posterior gray column (*col. dors.*) as the point of entrance of the Vagus. Still farther above, at *D*, the great Acusticus enters with one of its roots; and now one sees the relations of the spinal cord quite changed; but a single glance backward of the figures reveals to which portion of the gray matter the lateral margin of our preparation corresponds.

The anterior horns of the spinal cord are no longer clear in *B*; but here, and even better in *C*, note that fibers still arise from them. In section *A* they have given off the left cervical nerves functioning as *Hypoglossus*. In *C* they send, also, dorsal motor fibers, which turn to make the motor roots of the Vagus. The cell-column of the anterior horn remains intact for a greater distance; higher up the motor fibers of the Facialis arise; also those which join the Trigeminus. In the nucleus of the Facialis we have probably to do with another cell-group than that in the nucleus of the Vagus.

Let us now turn to a more complicated section on which may be demonstrated several of the especially important relations of the beginning of the medulla.

Fig. 41 presents a section through the lower end of the medulla of *Cephaloptera*, a large ray. Note the ventral columns, or anterior horns, from which arise nerves. The most anterior pair of cervical nerves, which supply about the same region that in higher animals is innervated by the twelfth pair of cranial nerves,—the Hypoglossus,—arises just like other spinal nerves.

The dorsal columns (posterior horns) are still to be seen, but it is already difficult to trace their resemblance to the typical ones previously described. They are much broader and changed to a looser, net-like, gray substance, upon which rests a striking crescent-shaped nucleus (Fig. 41, *Fun. post.*). The appearance of this long, trough-shaped structure, which reaches far up under the cerebellum, is characteristic for the upper spinal cord and the medulla. Higher magnification demonstrates that this noteworthy nucleus receives along its whole course fine fibers from the surrounding mass of fibers; and when one follows them upward one can trace them to the place where the Trigeminus courses from the Gasserian ganglion into the brain. Now, for the first time, one recognizes with what he is dealing: a great fascicle from the sensory nerve, which passes from the ganglion down into the cord to end in the above-described nucleus. This fascicle is called the *Radix spinalis Trigemini*; the nucleus at the end of the dorsal horn is its terminal nucleus: *Substantia gelatinosa Rolandi* (Fig. 41, *Nucl. N. V.*). On the median side of this nucleus lie fibers from the posterior columns (*Fun. post.*). They inclose, in turn, gray masses, located where in the cord the posterior columns lie, here called nuclei of the posterior columns (*nucl. fun. post.*). In birds and mammals the existence of nuclei into which a considerable part of the posterior columns enter is established beyond doubt, as will be shown later; but in fishes and amphibia it is not absolutely certain that a similar condition exists. In the *Cephaloptera* it is, therefore, with some hesitation that I designate this structure as the "nucleus of the posterior columns."

But the greatest difference between this section and one of a typical spinal cord is the fact that in the space between anterior and posterior horns innumerable commissural cells have made their appearance, cells whose large neuraxons, arranged in small fasciculi, pass upward through the medulla even into the Mesencephalon and Thalamencephalon. This is probably a great system of association-fibers which connect certain levels of the cranial segment of the central system to each other and with the anterior end of the spinal cord. This system, which is similarly located in all animals, is characteristic of the Medulla, and is well adapted to be the organ of those most intimately co-ordinated functions whose seat is in the Medulla. In the figure this region is designated as *Tractus brevis.*

Fig. 41.—Section through the medulla oblongata of a Ray: the *Cephaloptera lumpus.*

Without doubt we have to deal here with an increase of that structure already described with the spinal cord as the cellulæ commissurales and the tracts arising from them. As in the spinal cord, so here there exist fibers of short course, crossed and uncrossed. The ventral commissure, small in the spinal cord, naturally becomes much increased incident to the increase of the whole system. It is known from this point up to the Corpora Quadrigemina as the *raphé decussation.* Within this decussation, as in the spinal cord, are cross-fibers of other categories than those which arise from the cellulæ commissurales. But these will be described later.

The area of association-fibers—*i.e.,* the Tr. brevis of the oblongata—is just as well developed in the lowest vertebrates as in the highest representatives of that branch. In this connection compare Fig. 41 with Fig. 230 (*Processus reticularis*). It is evident that we have here to deal with the anatomical basis of very similar functions. Through this tract of association-fibers the fibers which pass from the spinal cord to the cerebellum, the Mesencephalon, and the Thalamencephalon are pushed laterally toward the periphery. Note in Fig. 41 the location of the Tr. cerebello-spinales and the Tr. tecto-thalamo-spinales.

The Tr. tecto-spinales contain, as was previously shown, crossed tracts from the terminal nuclei, into which the sensory fibers of spinal roots enter. They are, indeed, a secondary sensory tract from those nuclei to the roof of the Mesencephalon. In the medulla they are joined by the much larger bundle from the terminal nuclei of the cranial nerves and the now much enlarged bundle, which may be subdivided into numerous parts properly designated by the term *Tr. tecto-spinales et bulbares,* or more briefly the English name FILLET. The Fillet undergoes a further increase in the medulla. It comes from the nuclei of the spinal and cranial nerves of the opposite side. Bear in mind that in many vertebrates a large part of the posterior root-fibers does not end in the gray horns, but ascends to the medulla in the posterior columns. It enters the nucleus of the posterior column, which replaces the column at the lower end of the medulla. In birds and mammals in which the nucleus is very large one may determine with certainty that from this nucleus a system of arcuate fibers arise, which traverse the medulla to the raphé, cross to the other side, and join the Tr. tecto-spinales et tecto-bulbares, which pass toward the brim on either side of the median line.

The fibers in question—*Fibræ arcuatæ internæ medullæ*—are nothing else than a secondary tract from the points where the posterior root-fibers end. They are the last of the sensory nerves to cross to the opposite side of the central system and unite with those that crossed in the spinal cord.

The fillet, or *Lemniscus,* thus increased occupies a large field in the ventral and lateral part of the medulla.

So we have to deal here with tracts which, coming from the midbrain, reach the termination of the sensory spinal nerves by crossing to the opposite side of the medulla as arcuate fibers. Keep this in mind, for in the medulla, where the nerves have such large nuclei, we shall frequently find such arcuate fibers and be able to trace them into the fillet.

In the oblongata of the adult *Triton* (Fig. 42), which is chosen because it is closely related to the salamander larva shown above, you see the arcuate fibers from the region of the nucleus of the posterior columns well developed, and you recognize also, that they pass to an area on either side of the middle line, which is filled with severed fibers, while many of them cross to the opposite side in a ventral decussation. It is not usually possible to follow the whole course in a single section; thus the accompanying figure barely shows the relation between the arcuate fibers and the decussation.

With this survey of the more important constituents in the cross-section of the lower end of the medulla, it will be easy to understand the opposite figure (Fig. 43), which shows a similar section from the medulla of an alligator.

But what of the fibers of the anterior columns which were found in the spinal cord? In the section of the medulla of the ray (Fig. 41), they occupy exactly the same position as in the spinal cord. A part of these fibers pass, indeed, into the fillet, but most of them form a thick column, very striking in most sections, which maintains the same location through the oblongata, even increasing in volume. This tract—the *Fasciculus longitudinalis posterior*—may be followed to the base of the Thalamencephalon. It appears to receive fibers from all motor nuclei throughout its long course. Degeneration experiments on mammals teach that the fibers are, for the most part, short ones. In fishes, amphibia, and reptiles this fasciculus is one of the largest of the medulla. It occupies the whole floor of the fourth ventricle, as you see in the sturgeon (Fig. 39).

Fig. 42.—Cross-section through the Oblongata of a mature Triton.

In the midst of this tract in aquatic animals are the previously described thick fibers—*Fibræ acustico-spinales*—from the acusticus region to the caudal musculature. These fibers may be seen in Figs. 40 and 42, Fig. 40 *D* showing the decussation and the large terminal cell (*cellula M. Fas.*) from which on either side the fiber arises.

We have now located in the medulla most of the tracts previously known in the cord. One important tract remains yet to mention: the *Tr.*

cortico-spinalis. This tract is present only in mammals, and will, therefore, be specially treated later under the description of the mammalian brain. It may be stated here, however, that its fibers begin in the medulla, for the most part decussate, and then, as two large columns,—*the Pyramids,*—lie ventral to the anterior columns and the fillet, making there a simple addition to the picture which has already been presented. Frequently a child is born without a cerebrum, and it lacks, therefore, the pyramidal columns, and its medulla is similar to that of the other classes of vertebrates.

One meets these fiber-systems in all sections of the medulla farther toward the brain, until the cerebellar tract turns toward the cerebellum and the spinal portions of the cranial nerves pass out of their respective roots. Furthermore, bundle after bundle from the processus reticularis (*Associations-feld*) of the medulla ends, and bundle after bundle arises to end farther forward. However, the section, as a whole, varies little as to the parts already described.

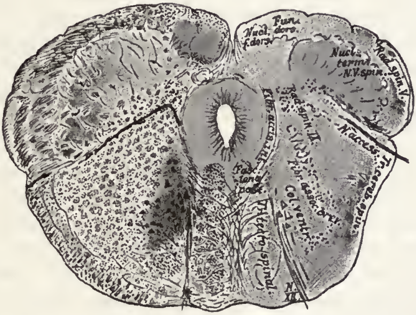


Fig. 43.—From the caudal end of the Oblongata of *Alligator lucius.* Note the origin of the Hypoglossus (*N. XII*) from the anterior horn (*col. ventr.*) and the terminal nucleus of the Trigeminus (*nucl. term. N.V. spin.*), dorso-lateral to which lies the Trigeminus root (*Rad. spin. V*). Note, also, the nucleus of the posterior columns (*nucl. f. dors.*), in which the fasciculus from the posterior root ends (*Fun. dors.*). Further study of the figure will reveal many features already discussed.

But another factor causes very marked changes in the structure of the medulla as one studies sections near the brain; namely, the nuclei of the cranial nerves and the arcuate fibers, which pass into these from the fillet and from the cerebellum.

The study of the nuclei of the cranial nerves in the medulla speaks conclusively for the position already taken that there is in the animal kingdom no such thing as a brain which is throughout of a higher or lower degree of development. Now here, now there, certain parts of the brain are more developed, and this development depends in no way upon the position of the animal in the phylogenetic series, but solely upon requirements: *i.e.*, upon the somatic characteristics which the animal has acquired in this or that region.

You will find that the bony fishes possess an exceedingly simple brain, which is not at all to be compared with that of man. But these animals possess not only much larger terminations for the optic nerves than does any mammal, but the nerve-nuclei in its medulla have such a development and such complicated relations that the same structures in reptiles, birds, and mammals seem, in comparison, very small and simple.

Thus the anatomical picture of the medullar nuclei of the cranial nerves varies much in the animal kingdom. I will, therefore, try to present a few facts which are common to all.

Let us divide the cranial nerves in question into two groups: a *posterior* group, including the Hypoglossus, the Accessorius, the Vagus, and the Glosso-pharyngeus; and an *anterior* group, including the Facialis, the Acusticus, and the Trigeminus.

If one views the cranial nerves only from the stand-point of the relations of their deep origin, one finds, throughout the whole animal kingdom, an astonishing similarity. For example, the terminal nuclei for the cranial nerves are, in fishes and mammals, located the same. They vary considerably, however, in the way in which the roots leave the central system. Subsequent to the origin of the nerves there takes place the most varying combinations of the root-fibers; so that the certain tracing of them to the surface of the brain is, in the lower vertebrates, a task on which comparative morphology is still at work. For example, the Facialis is sometimes so mixed with the fibers of the Trigeminus that it is only in the distribution at the periphery that it may be differentiated from that nerve.

The ventral columns of large ganglion-cells have been located as the origin of the motor nerves of the spinal cord. This cell-column may be demonstrated from the sacral region to the medulla. It consists of a series of nerve-nuclei between which lie commissural cells. It is advisable to separate this column into two series: a more ventral one (Anterior-horn zone of His) and a more lateral one ("Lateral-horn zone"). From the first arise the Hypoglossus and all of the anterior roots of the spinal cord for the trunk-musculature. From the latter arise principally fibers which are devoted to the motor innervation of the viscera, only in the medulla. These lateral-horn fibers become separated from the anterior-horn fibers and leave the medulla as motor fibers of the Vagus and Accessorius. Farther down the spinal cord they leave with other fibers of the anterior roots. According to Gaskell, the latter fibers enter a mixed spinal nerve, while the former enter the Sympatheticus. The most centrally located segment of the motor columns produce from their lateral divisions the N. facialis. The masseteric branch of the Trigeminus receives its fibers from cells which belong to both lateral and ventral divisions of the motor column.

The posterior horns of the gray matter are also continued through the medulla, where they are encroached upon by the Vagus, the Glossopharygeus, the Acusticus, and the Trigeminus after their origin from the nuclei. It was noted in *Trigla* (Fig. 30, *B*) that, in the trunk-segment, wherever the sensory nerves are especially strong the terminal nuclei are enormously hypertrophied. The same is quite generally the case with the terminal nuclei of the large medullar nerves. One of these—the longitudinally extended terminal nucleus of the spinal root of the Trigeminus—has already been described. We have now to do with a tract which, from its origin in the Gasserian ganglion, passes far back, ending in the cervical portion of the spinal cord. Such tracts are designated *descending tracts.* All sensory nerves of the medulla have such, but in no other case is the descending tract so large or so well known as in the Trigeminus. Knowing that all posterior nerve-roots after entering the cord give off a descending twig to a part of the gray horn lying farther posterior, one will not be surprised to find a similar thing true in the cranial nerve-roots of the medulla. The most posterior cranial nerve—the Hypoglossus—has already been described. It arises from a cell-group in the anterior horn (see Fig. 43).

From the same segment of gray matter, but from a somewhat laterally located cell-group, in reptiles, birds, and mammals, arise fibers which, passing laterally, leave the central system as the Accessorius (see Fig. 43).

In the lower vertebrates this nerve arises almost in the same manner, but its fibers usually pass higher and leave the medulla with the Vagus, joining the motor part of that nerve. In that case there is no reason why one should not compare the most posterior root of the motor Vagus with the Accessorius.

The Vagus itself passes to the dorsal margin of the medulla from the Ganglion jugulare. It penetrates the fiber-system that here lies in its way (*i.e.*, the Fibræ arcuatæ internæ arising from the nucleus of the posterior columns); also often the ascending spinal root of the Trigeminus, and ends there in a noticeable enlargement of the gray matter belonging to the posterior columns farther back. This may be readily seen in the accompanying figures from the medulla of a gold-fish.

In the figure one notes that the terminal nucleus of the Vagus is relatively very large: it has to receive a much larger nerve than in other vertebrates. A veritable tumor—the *Lobus nervi vagi*—results here.

In the brain of the sturgeon (Fig. 39) the nucleus of the Vagus is visible only as an elongated prominence, and in birds and mammals it forms only a slight prominence on the floor of the fourth ventricle (compare also Fig. 52).

From the ventral side fibers enter the vagus nucleus which cross over from the opposite side. The decussation is so striking in fishes that one may readily see its white fibers with the unaided eye. We have to deal here with a fascicle to the fillet. The nuclei of all cranial nerves possess such (Fig. 45, *Tr. vago-tect.*). Furthermore, the sensory nucleus of the Vagus receives an accretion (especially large in fishes) from the cerebellum where decussation takes place.

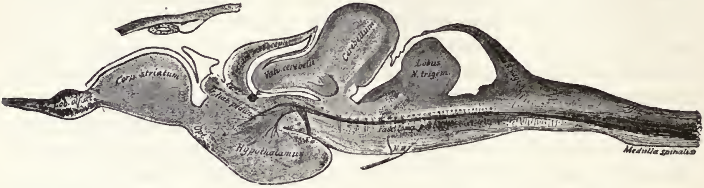


Fig. 44.—Sagittal section through brain, medulla, and upper cord of a young cyprinoid of four-centimeters' length, showing the course of the Fasciculus longitudinalis posterior.

In the higher vertebrates, also, there exists a vago-cerebellar tract, but in mammals at least it passes out with the root-fibers direct. In fishes and amphibians a part of the fibers of the Vagus innervate the skin just like sensory spinal nerves; but in the higher vertebrates the sensory part of the vagus contains only sensory nerves from the viscera. The Vagus contains

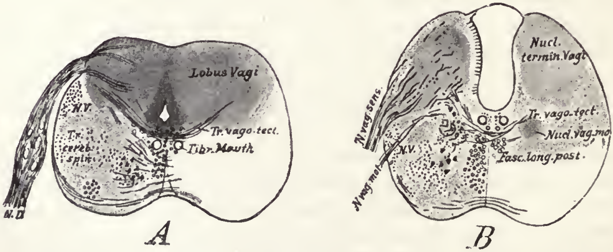


Fig. 45.—Two sections from the medulla of a young gold-fish—*Cyprinus auratus*—four centimeters long. Sec. *A* is the more posterior of the two.

also motor fibers. Recall that Fig. 34 shows fibers from the cells of the anterior horn to the sensory roots. When that figure was under discussion your attention was called to the fact that we probably have to deal here with motor elements to the visceral tracts. To Gaskell is due the credit of having shown how the motor tracts for the Vagus differ in no way from those already described for the spinal nerves. (Compare Fig. 34 with Fig. 46.)

Just as in the chicken the multipolar cell near the anterior horn sends its neuraxon out in the posterior root, so the similarly located motor nucleus of the vagus sends its neuraxons to the sensory vagus root, which is the homologue of a posterior root. The motor vagus fibers are essentially equivalent to the motor fibers in the posterior root. They arise from a nucleus which, in fishes, lies dorsal to the nucleus of the Hypoglossus, but

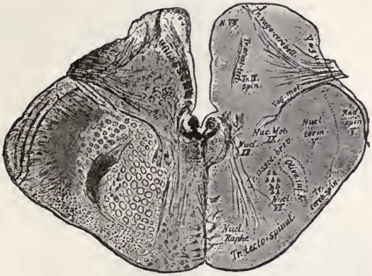


Fig. 46.—Motor and sensory vagus nucleus of *Alligator mississippiensis.*

in amphibians, reptiles, and birds lies ventrolateral to this. To be sure, the origin of the vagus fibers is frequently not sharply differentiated from that of the hypoglossus fibers. The nucleus is the *motor nucleus* of the *Vagus.* It sends root-fibers to the same and to the opposite sides. The decussation takes place very near the floor of the fourth ventricle.

That a part of the vagus root as a descending fascicle ends in the gray matter somewhat posterior to its entrance has been mentioned.

In the region of the Vagus a great number of root-fibers enter the medulla. It is not with certainty decided whether we are dealing here with a single nerve or with a fused combination. Only the most anterior of the sensory roots of the Vagus, always somewhat separated from the others at the surface of the medulla, has it been thought necessary to separate out as a distinct nerve: the *Glosso-pharyngeus.* This nerve, in all vertebrates, arises only in a small part direct from the gray matter of the spinal cord. A greater part becomes at once inclosed in a fascicle with several vagus roots and passes toward the spinal cord. Throughout the whole course as far as the first cervical nerve it is to be traced as a separate bundle.

The *Radix bulbo-spinalis Vagi et Glosso-pharyngei* gradually buries itself just like the bulbo-spinal root of the Trigeminus: in a thin column of gray matter which lies near it throughout its whole course. That is the bulbo-spinal terminal nucleus of this nerve. The fascicle is easy to find, ventral from the sensory nucleus of the Vagus.

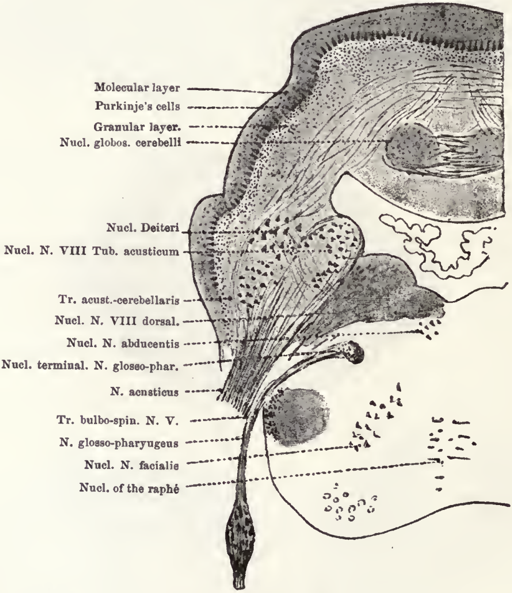


Fig. 47.—Region of the entrance of the Glosso-pharyngeus of a young sparrow, in which the development of the medullary nerve-sheaths is not yet complete.

The spinal cord offers, especially in fishes, numerous good examples of the fact (already cited in the description of the spinal cord) that from the small primitive fundaments are developed exceedingly important structures according to the various development of the peripheral organs. It is only with difficulty that the mature structures can be traced to their origin. The angler-fish—*Lophius piscatorius*—possesses, upon its head, lateral lines and tufts, innumerable delicate leaf-like appendages of the skin which completely mask the lazy ambushed fish, so that it appears like a flat stone overgrown with lichen and corals. Lying thus in the mud the angler lets its worm-like decoy float above it. The whole cutaneous region involved in these curious structures is, in fishes, supplied by the Vagus and Trigeminus. Fritsch, to whom we are indebted for much of our knowledge of the fish-brain, found that the nuclei of these nerves in *Lophius*—and in this fish alone—were supplemented by immense ganglion-cells which sent their neuraxons into the nerves. We have to deal here, evidently, with hypertrophy of the dorsal cells which lie near the periphery of the cord. These cells are so large in *Lophius* that they require for their nutrition separate little capillary loops, which lie among the cells.

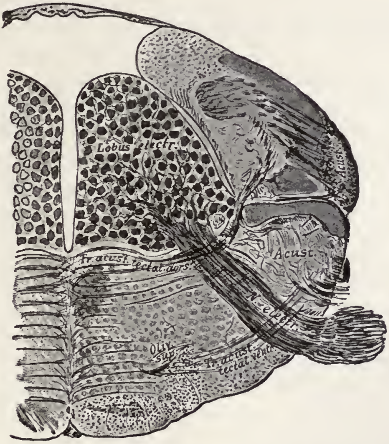


Fig. 48.—Medulla of the Torpedo. Section from the region of the vagus nucleus.

But still more interesting is the much-studied large nucleus which is found in the electric ray, far forward in the floor of the fourth ventricle, projecting into its cavity. This nucleus gives origin to the electric nerves, one on each side. This paired structure, frequently fused anteriorly, contains besides several small multipolar cells, a great number of gigantic ganglion-cells, which all send their neuraxons out into the electric nerves.

With our present knowledge of the nuclei of the selachian brain it is difficult to give these structures a positive interpretation, but the probabilities indicate strongly that we have to deal here with nothing else than an hypertrophy of a part of the motor vagus nucleus. The electric organ of the Torpedo is modified from a part of the head-musculature. Engleman has, in fact, been able recently to show how the electric plates of the electric organs develop directly from the muscle end-plates of the modified motor nerves.

CHAPTER VII.

THE MEDULLA (*Continued*).

AT the level where the Glosso-pharyngeus roots pass laterally to reach the surface of the medulla one may recognize, on the median side of them, a new nucleus: an *acusticus nucleus.*

This is the region of the origin of that cranial nerve whose relations are least known in the lower vertebrates. The investigations of recent years have finally made the Acusticus better understood in mammals. But even in birds and still more so in lower vertebrates we have to depend on what may be learned from sections. As yet, no one has attempted to study so extremely complicated a nerve by the degeneration-method or the development-method. But sections alone of this level of the medulla where the structure is so complicated give, only too easily, occasion for misinterpretations. I will at present, then, confine myself only to that which has been with certainty established.

The Acusticus always contains one portion which passes to the vestibule and one to the cochlea. The first, which supplies the labyrinth, is, as numerous experimenters have demonstrated, of especial importance for the maintenance of the equilibrium of the body. Ewald's experiments have shown how every fluctuation of the fluid of the lymph leads, through the agency of this nerve, to the disturbance of the equilibrium. They have also proved that the vestibule is especially important for the maintenance of muscle-tonus throughout the body. The cochlea is only slightly developed in fishes, but in birds it reaches a fair development. Corresponding to these observations the majority of the fibers of the auditory nerve go to the labyrinth and saccule. In mammals, for the first time, the portion of the nerve which supplies the cochlea becomes large.

In the brain one may recognize that in all lower vertebrates the major part of the auditory nerve ends in a striking knob-like nucleus, which is laterally located in the medulla where the peduncles of the cerebellum come down. Lodged in the angle between the medulla and cerebellum and as high up the vertebrate scale as to the birds, always covered with a formation similar to the cortex of the cerebellum, lies this great nucleus of the Acusticus, and receives on its ventral side the fibres of the auditory nerve. These fibers divide at once into ascending and descending branches and traverse the ganglion in dense fasciculi before they divide up and terminate. These fibers probably all arise from the ganglion-cells in the ear. (Compare Fig. 16 [*b*], Fig. 40 [*D*], and Fig. 47.).

A cross-section through the lateral part of the medulla in the region where the principal nucleus of the Acusticus is fully developed shows that under the cortex of this body lie very many sections of fibers. The nucleus has developed a special field, which has been designated by Ahlborn as the *acusticus field*. A large part of the fibers which lie here, all of which come from the Acusticus, turn upward toward the cerebellum and end in another nucleus, the *Nucleus acustico-cerebellaris*, which lies antero-dorsally adjacent to the principal nucleus of the Acusticus. Other fibers end in the principal nucleus, and a third portion proceeds backward as a posterior root.

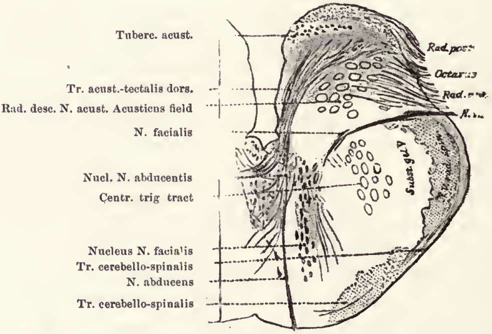


Fig. 49.—Most posterior portion of the acusticus nucleus of *Alligator lucius.*

The two mentioned acusticus nuclei are connected with the cerebellum through numerous fibers; especially with two spheroidal nuclei, which lie close to the roof of the ventricle,—the roof-nuclei of the cerebellum,—where a marked decussation takes place. But several cerebellar fibers pass direct to the auditory nerve itself: the *direct sensory cerebellar tract.*

From the reptiles upward through the vertebrate series one recognizes that, besides the two nuclei mentioned, new ones arise which, among the fishes and amphibians, are present in only a rudimentary form. These nuclei form a large mass located quite laterally from the principal nucleus, which consists essentially of large cells. One can easily differentiate them in birds and mammals. They are designated in the latter as *ventral nucleus* and *Tuberculum acusticum,* and are here larger than the principal nucleus. This last is called in mammals the *Nucleus dorsalis.* This homology, however, stands on very weak legs, as could be demonstrated if we could go more into the details of the acusticus nuclei of individual vertebrates.

The terminations of the auditory nerves are connected, not only with the cerebellum, but with numerous other parts of the brain. The whole lateral region of the medulla occupied by the auditory nerves is traversed by fibers and dotted with nuclei, which, either directly or indirectly through collaterals, maintain a connection with the Eighth. For mammals the relations are approximately known. For lower vertebrates the following may be advanced:—

On the median side there uniformly arise (observed in Selachia, Teleostei, Reptilia, and Aves) fibers which pass inward into the medulla and connect with a small ganglion there: *Oliva superior.* In mammals this body has long been known as the *Corpus trapezoides.* It has also been demonstrated that we have to deal here with a part of the *Tractus acustico-tectalis* (Fig. 49): the central connection with the roof of the midbrain. Doubtless there exists also another central connection in the lower vertebrates which does not take its way through the Corpus trapezoides. This is much the larger tract in all animals below the mammals. Note in Fig. 49 thick, easily visible fibers, arising from the principal nucleus in a strong tract, passing direct to the median line of the fourth ventricle near the floor, where it approaches the fasciculus longitudinalis posterior and even passes through this to the opposite side. It probably also reaches the tegmentum of the midbrain. Then we would have a *Tractus acustico-tectalis ventralis,* which passes through the olivary body into the fillet, and also a *Tractus acustico-tectalis dorsalis,* which would reach the same destination by another route (see Figs. 48 and 49).

Dorsal to the principal nucleus of the Acusticus lies (in all vertebrates above fishes), imbedded in the most ventral portion of the cerebellum, a large nucleus of multipolar ganglion-cells which, in close connection with the place of origin of the "tonus nerves," send their neuraxons through the territory of the Acusticus back toward the spinal cord. This nucleus is known in mammals as *Deiter's nucleus,* in general as *Nucleus tractus acustico-spinalis.* It is possibly a part of the apparatus which is necessary to transmit to the body-musculature the impressions received from the labyrinth (see Fig. 47). It is interesting to note in this connection that in Teleostei a branch from the region leaves the brain, not with the Acusticus, but (Stannius) in the nervous system of the *lateral line* supplied, for the most part, by vagus branches, with which they become associated. The significance of the lateral line and its associated structures as an organ of equilibration is made probable through this anatomical relation.

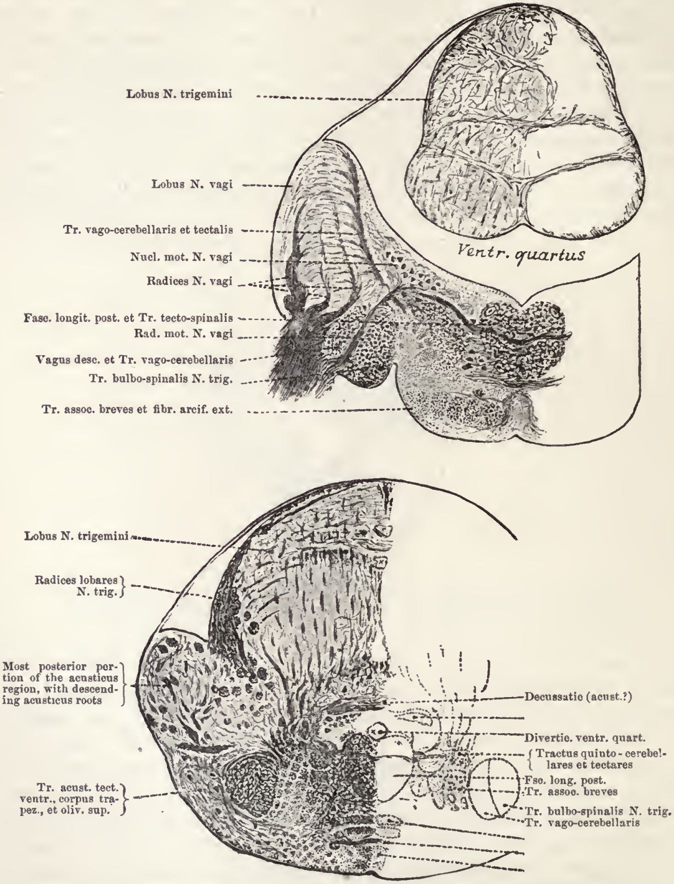
When you are reminded (1) that in the acusticus region of the medulla the long fibers of Manther arise,—fibers which end only in the posterior region and with which, in the spinal cord, we became acquainted as the *Tractus acustico-spinalis* (Figs. 29 and 40); (2) that the great terminal cells of these gigantic fibers ramify the acusticus region with their dendrites; then it will be clear to you what an important center of association for the most diverse regions lies in the middle of the medulla oblongata. The physiological experiments and the considerations which are involved in these anatomical relations lead to the conclusion that the part of the medulla just described represents an important center for the maintenance of *general equilibrium*.

Fig. 50.—Section of the medulla of *Alligator lucius* at the level of the motor nucleus of the Trigeminus. Simply the contour of the nerve is represented. Compare the thin Facialis in Fig. 49 with the large motor trunk of the Trigeminus shown.

At the level of the acusticus nucleus the motor columns, which reach toward the brain from the spinal cord, are not yet exhausted. They may be best imagined as a thin plate which bends greatly toward the sagittal plane, although somewhat removed from it, in the oblongata. From the dorsal part of this plate near the spinal cord the Hypoglossus arose. In the acusticus level there arises the Abducens: a part of the plate whose course may be easily recognized on Fig. 49. The ventral portion does not send its fibers out direct, but collects them from some distance into little fasciculi, which then all turn dorsally in order to bend laterally when they approach the gray matter of the floor. This curious knee-like course has already been met in the Accessorius (Fig. 43): a nerve which left the same cell-column farther posterior; also a part of the motor vagus root (Fig. 46) presents a similar thing. We now come to the two nerves which arise from the major part of the cell-column under consideration: viz., the *Facialis* and the motor *Trigeminus*. Both are not always sharply differentiated from each other in the region of the roots. In the lower vertebrates the motor Facialis is usually much smaller than the masseteric branch of the Trigeminus, probably because the face-musculature is less developed. Fig. 49 shows the position of the Facialis and of the nucleus of the Abducens in the alligator and in Fig. 50 is presented a section which cuts the motor column at a higher level when it dilates in the dorsal portion for the nucleus of the Trigeminus. The nucleus of the Facialis is not a single structure. In the longitudinal as well as in the antero-posterior direction it shows interruptions. For that reason one might easily designate in different animals different cell-groups as the origin of the nerve. But all of these cell-groups belong to the same mass of great multipolar cells, whose neuraxons pass into motor nerves.

Fig. 51.—***Lacerta agilis.*** **Region of exit of the Trigeminus (*N.V.*).**

At the anterior end of the medulla the gray mass which received the sensory nerves on the latero-dorsal aspect becomes again very much enlarged. At this point the Trigeminus nerve enters it. In this *frontal sensory nucleus of this nerve* only a part of the fibers from the Gasserian Ganglion end, while a greater part turn toward the spinal cord, there to gradually enter the gray matter, which we see in all sections from the upper end of the spinal cord to the entrance of the Trigeminus into the medulla. This descending portion has been described as the *bulbo-spinal root* of the *Trigeminus*. In such aquatic animals as fishes, dipnoi, and larval amphibia there exists over the whole head a system of canals bearing a sensory epithelium: an apparatus which probably serves for the detection of changes of pressure in the surrounding medium. It at least appears to be well adapted to such a purpose. In amphibia it disappears when terrestrial life is entered



Figs. 52 and 53.—From the Medulla of the barbel, *Barbus fluviatilis*; vagus and trigeminus roots.

upon. On the innervation of this apparatus, as well as on the sensory nerves of the head in general, we have been enlightened only in recent years through studies of *Pincus,* of *Cole,* and especially of *Oliver S. Strong.* It has been demonstrated that all of these animals possess a sensory portion of the Nervus facialis which innervates this canal-system of the head. Similar apparatus on the trunk receive principally branches from the Vagus. From what part of the brain the sensory portion of the Facialis arises is uncertain. Further investigation is necessary. *Strong* maintains that the Tuberculum acusticum comes into consideration. To the author it seems more probable that we have to do here with parts which have been previously attributed to the terminal apparatus of the Trigeminus. In all teleosts there is, in connection with the terminal nucleus of the Trigeminus, a large lobe which, in cyprinoids and other fishes, is connected with that of the opposite side, and is located transversely over the ventricle. Powerful bundles of fibres—designated in the figures as *"Rad. lobares N. trigem."*—pass out of the Lobus trigemini. Should further investigation substantiate the author's supposition that we are dealing here with the terminal nucleus of the sensory Facialis, then the names in the Lobus Nervi facialis will have to be changed. What is designated (Fig. 54) as *Tractus Nervi trigemini ex lobo* probably represents the sensory Facialis. But, without doubt, the origin of the nucleus requires, in lower vertebrates, to be most carefully studied anew.

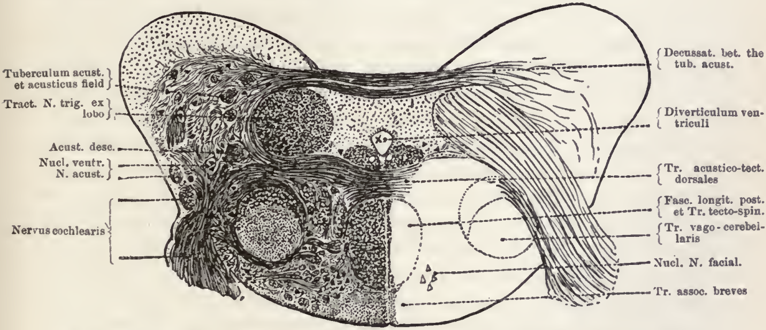


Fig. 54.—From the medulla of *Barbus fluviatilis*; Vagus and Trigeminus roots.

Figs. 52, 53, and 54 will elucidate the point better than a description.

In birds and, especially, in the armored reptiles the frontal nucleus of the Trigeminus is much less developed than in other animals. With each Nervus trigeminus there passes a fasciculus from the brain, which originates from the roof of the midbrain. This *Radix mesencephalica trigemini* arises from large, pear-shaped cells, which lie near the aqueduct in mammals.

It is probable that this nucleus is identical with one consisting of exactly-similar cells, which one finds in amphibians and reptiles quite near the median line of the *Tectum opticum,* or roof-nucleus, of the midbrain, which is especially large in turtles.

All trigeminus nuclei receive important afferent bundles from the fillet. These approach the nuclei *after decussation,* as is the case with other nerve-nuclei. Besides this they receive from the cerebellum a contribution regarding which it is uncertain whether it ends in the nucleus or leaves the brain direct with the nerve. This accretion from the cerebellum to the lobus trigemini is very large.

Up to the present we have, for the sake of clearness, let it be understood that the medulla contains nothing but the nuclei of the cranial nerves, with their associated tracts and connections. But there are still other fibers which enter the medulla on their way from the spinal cord to the cerebellum, as well as some which pass from the cerebellum into the nuclei of the medulla itself. Moreover, the medulla contains, besides the cells and fibers of the association-system, a number of special ganglia. Only one of these—the Oliva superior—has been mentioned in connection with the description of the Acusticus. But in all vertebrates there are still other groups of nuclei. In mammals the largest of these is the group designated *Oliva inferior,* which stands in close relation to the cerebellum, by which fact it is characterized. Up to the present time (if one stands by this characteristic) an oliva inferior has not been discovered in any vertebrate except in the mammal. We may, indeed, find, in reptiles, birds, and even in amphibians, nuclei which are similarly located in the medulla and which, in reptiles, are of similar structure (see Fig. 46); but a positive interpretation of this group is, as yet, lacking. The same is true of nuclei which are everywhere demonstrable at the ventral margin of the medulla, and especially toward the posterior end. At this point one finds, in mammals, the *nuclei arciformes.* Of all the details given, or possible still to give, remember especially that *the numerous longitudinal bundles whose cross-sections one sees in the ventral and lateral regions of all cross-sections of the medulla contain, besides the fasciculi of the association-system, connecting-fibers to the mesencephalon* and *thalamencephalon.* We have already met the tracts from the thalamencephalon to the spinal cord when considering the lateral columns. Even in the medulla this tract, especially well-marked in fishes, lies in the lateral region. It is much larger than in the spinal cord and gradually decreases posteriorly.

There are two fiber-systems of the medulla which we must now consider somewhat in detail, because they are of especial importance physiologically.

The first one of these is the *fascicle from the nuclei of the posterior columns* to the fillet, the most anterior fasciculi of the *Tractus tecto-spinalis.*

They have already been presented as *Fibræ arcuatæ internæ* (Figs. 42 and 43). This tract, which reaches full development only in the mammals, is probably already present among fishes. It is a portion of the great central fiber-system from the sensory terminal nuclei. After decussation it passes toward the brain in the fillet, and with it are gradually associated all of the crossed bundles from the nuclei of the cranial nerves,—the Tractus tecto-nucleares,—together forming the *fillet.*

The second important fiber-system belongs to the lateral margin of the medulla. Here lies the *Tractus cerebello-spinalis,* ventral from the spinal root of the Trigeminus. It arises, also, from the termini of the sensory nerves in the spinal cord. It does not turn toward the fillet, however, but passes anteriorly to the exit of the Acusticus, where it turns dorsally to the cerebellum. On the way it has received reinforcements from the posterior columns,—the *Fibræ arcuatæ externæ,*—demonstrated in fishes, amphibians, and birds. The united bundle is called the *Corpus restiforme*: inferior peduncle of the cerebellum. It has been carefully studied only in mammals; in this class it contains still other elements. Only a few of them are found also in birds and reptiles: *e.g.,* the acusticus-cerebellar tract and the bundle from the Deiter nucleus to the spinal cord.

Where an olivary body is demonstrable the fibers run from it to the cerebellum through the inferior peduncle restiforme.

At the frontal end of the medulla the Tractus tecto-bulbares et spinales turns dorsally to reach the roof of the midbrain. At this point a nucleus is always located within it (Fig. 50),—the *tegmental nucleus,*—which is much subdivided. The tracts to the cerebellum have, at this point, already turned upward; those which pass to and from the cranial nerves are present only in small measure. What remains of the features mentioned is confined to tracts which pass downward from the cerebellum and then to tracts which pass toward the medulla from the mesencephalon and the thalamencephalon. They lie in the ventral divisions, and are not yet, with certainty, to be differentiated from the fillet in the lower vertebrates. Besides this, the Fasciculus longitudinalis posterior lies dorsally and distributed over the whole breadth of the lateral areas,—the system of commissure cells with short bundles joining the different levels of the medulla with the floor of the midbrain.

In mammals—but, so far as I know, only in these—still another tract descends from the *cerebrum,* which remains in part in the frontal ganglia to be described later and in part ends in the nuclei of the cranial nerves with their final processes even in the spinal cord, where we have already learned to know it as Tractus cortico-spinalis.

We may now close our survey of the structure of the Medulla Oblongata. Now that it is shown what important nuclei of origin and termination lie here; what great association-systems occupy the whole, connecting all of its levels among themselves and with higher and lower centers; what important connections run from the oblongata to other parts of the brain, it becomes evident that just this part of the brain is the most important for the maintenance of life. On the one hand, one may, in a lower vertebrate, remove everything anterior to the medulla without so disturbing the vital functions that death supervenes, and may, on the other hand, remove the whole spinal cord without inducing anything more than complete motor and sensory paralysis. But no vertebrate can survive the removal of the Medulla Oblongata, that general origin for the most important nerves, that great center of co-ordination.

The importance of the Medulla Oblongata for the existence of the animal corresponds to the fact that this part of the brain reaches a high development earlier than any other part. This is true, both in the phylogeny and in the ontogeny of the central nervous system.

CHAPTER VIII.

THE CEREBELLUM.

DORSAL to the Medulla Oblongata and connected with it through several tracts, lies the Cerebellum. It is continuous posteriorly with the *Plexus chorioidei ventriculi quarti* and anteriorly with a thin sheet,—the *Velum anticum,*—which passes to the roof of the mesencephalon.

A study of Fig. 55 will make it evident that no part of the brain,—the cerebrum probably excepted,—manifests so many variations in its degree of development as does the cerebellum. The cerebellum is not more highly developed in the higher animals than in the lower, as is the case, however, with the cerebrum. On the other hand, we meet, even between closely related animals, very striking differences. The simplest form in which we find the cerebellum is presented by the Cyclostomes and Amphibia. That portion of the cerebellar roof which is turned toward the midbrain is thickened into a narrow plate or ridge, which lies transverse to the anterior end of the fourth ventricle. Even the reptiles do not possess a cerebellum which is essentially higher than this, except that those reptiles which swim (alligators, crocodiles, etc.) possess a cerebellum of twice the relative size and extent. Those great swimmers—the teleostei and the selachia—possess a cerebellum which is so enormously developed that it must lie in large transverse folds (Fig. 55, *A*); indeed, in the teleosts the cerebellum pushes forward under the roof of the midbrain into the aqueduct (Fig. 55, *C*). But that sluggish mud-fish,—the *Dipnoi,*—which, on the basis of other structures has been accorded the highest place among the fishes, *has a small cerebellum.*

A glance at Fig. 55 shows that, through the dorsal evagination of the cerebellar plate, there is produced a continuation into the cerebellum of the fourth ventricle. This *Ventriculus cerebelli* is still demonstrable when the size of the cerebellum has greatly increased, as in birds and mammals, except that it is then very narrow, and in the peripheral portions the narrow clefts usually completely disappear.

Into the cerebellum of fishes, amphibians, and reptiles there pass tracts, not only from the spinal cord, but also from the thalamencephalon and mesencephalon. The same tracts are found also in birds and mammals. But in the latter very large tracts pass also from the cerebrum to the cerebellum. These last-named tracts pass into new and special structures, which appear on either side of the median portion,—the *Hemisphæria cerebelli.* In mammals they are developed synchronously with the appearance of the Pons to proportions which greatly exceed those of the middle part,—which latter is now called the *Vermis.* But the median segment of the cerebellum retains even in man the characteristic worm-like transverse folding acquired by the cerebellar plate in the selachians. Immediately posterior to the cerebellum we meet in the roof of the medulla ganglionic masses which send out fibers of the Trigeminus and Acusticus. Usually fused with the cerebellum these form, in the higher vertebrates, unimportant nuclei; in fishes, however, well-marked lobes (see Fig. 55 *A* and *C*).

Nowhere else in the animal kingdom does the Vermis cerebelli reach

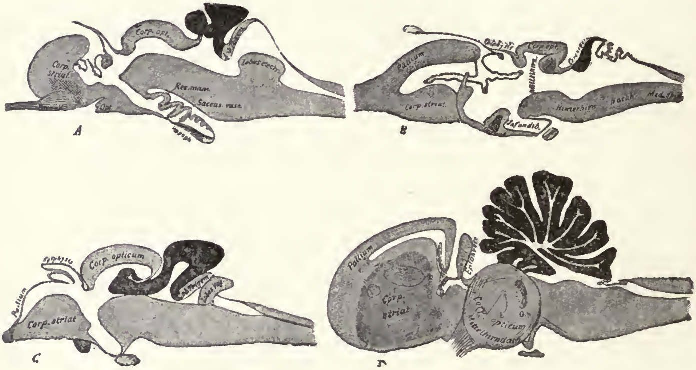


Fig. 55.—Semidiagrammatic sagittal sections through the vertebrate brain. The cerebellum appears in black, to show its relative size. *A*, Brain of Ray; *B*, of an Amphibian; *C*, of a Trout-embryo; *D*, of a Bird.

such enormous development as in the great swimmers and the birds. This circumstance, together with the fact that in the same animals there are especially large connections with the tonus nerves of the labyrinth and with the Trigeminus, makes it most probable that in some way or other the cerebellum must be involved in the maintenance of equilibrium. This is, in fact, indicated in its general development. The results of physiological experiments indicate the same thing.

Phylogenetically the cerebellum is one of the oldest portions of the brain. Experiments upon the supra-œsophageal ganglion in arthropoda indicate that it fulfills functions equivalent or similar to those of the cerebellum in higher animals.

The cerebellum is, without doubt, then, one of the most important parts of the brain, for a study of which one is well repaid.

Its structure is remarkably simple, and similar in all animals, the whole organ being a repetition of a simple histological type.

As previously shown, the cerebellum is ontogenetically developed from a simple cell-plate; and the figures just presented make it evident that the same is true of its phylogenetic development. All of the manifold forms of the cerebellum arise through a folding of the primitive cerebellar plate, the object of the folding being evidently an *increase of surface.* Whether the plate extends upward or downward, whether it remains small or progresses to a high development, it is always built on the same type. Let us take, as our starting-point, the further study of the reptilian cerebellum, because it is a simple thin plate which, lying transverse to the ventricle and transverse to the long axis of the brain, extends toward the crown. One may differentiate a frontal face, turned toward the midbrain, and a posterior face. A section shows at once that these two laminæ have a different structure. The posterior (internal) one is rich in ganglion-cells, while the

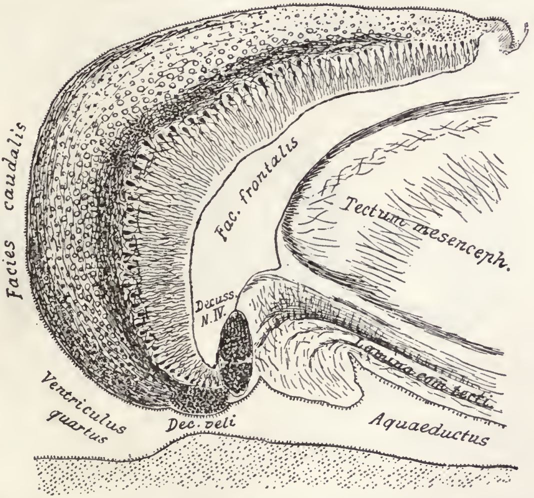


Fig. 56.—Sagittal section through the cerebellum of the lizard, *Varanus griseus,* showing the external lamina (*fac. front.*) and the internal lamina (*fac. caud.*).

anterior (external) lodges principally the dendrites from the posterior lamina.

Just at the boundary of the two laminæ lies a layer of large cells extraordinarily similar in all vertebrates,—the layer of Cells of Purkinje, and partly in the posterior or internal cerebellar lamina (granular layer).

The small multipolar ganglion-cells which fill the internal lamina seem all to send up their neuraxons into the molecular or external lamina.

There are, however, in this layer, and close to the cells of Purkinje, several other types of cells which, though known in birds and fishes, have been closely studied in mammals, and will, therefore, be described later.

The mass of fibers which pass into the cerebellum in amphibians and reptiles is so small that they scarcely make a separate layer on the epithelium of the ventricle, but break up at once and pass into the fine net-work of the latter. In teleosts, selachians, and higher vertebrates the condition is different. Here such a mass of medullated fibers pass into the cerebellum that one may always observe, between the epithelium of the ventricle and the internal or posterior lamina, a separate and sometimes very important layer composed solely of these afferent fibers. This is the medullary layer, or center of the cerebellum. The figure of *Varanus* (Fig. 56) shows the medullary center only in traces. Into this layer pass tracts from the midbrain and the thalamus, which are highly developed in fishes, but which are also demonstrable in other animals. For the lower vertebrates the material is, at present, insufficient. What is known, however (Teleosts, Schaper; Birds, R. y Cajal, Kölliker, and Edinger), shows that even in the more detailed relations the lower vertebrates are similar to the mammals.

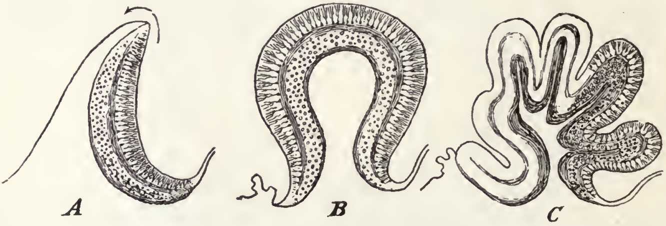


Fig. 57.—Somewhat diagrammatic sagittal sections through: (*A*) Cerebellum of a lizard; (*B*) Type of cerebellum of an alligator, crocodile, or turtle; (*C*) Type of cerebellum of a bird or mammal. To illustrate the increase of the cerebellum through folding of the cerebellar plate in the direction of the arrow over *A*.

It may be thus briefly summarized: *In the cerebellum fibers end and* *fibers begin; and through the branches of the cells located there is furnished a wide range of possibilities in the co-ordination of the processes which go on there.*

From the simple type—that of *Varanus,* for example—we may readily derive most of the other types of cerebellum. We have to deal with only two factors: with the development of the cortex and of the medullary center. If the cortex increases in size it presents folds. Fig. 57 shows how the simple lizard type is doubled in the swimming alligator and turtle, and how, through a farther folding of the same cerebellar plate, the avian or mammalian type may be derived. In teleosts the surface is relatively greater than in amphibians and reptiles and it arises from the facts (1) that the molecular, or inner, layer is thicker; and (2) that an unusual number of afferent bundles pass into the cerebellum, much increasing the medullary center over the ventricle. Thus arises an apparently massive body (see Fig. 44), in which the part that lies under the roof of the midbrain is designated the *Valvula cerebelli.* It has already been mentioned above that at the posterior end of the cerebellum there are associated parts which stand in special relation to the nuclei of the Acusticus and the Trigeminus. The separation of this region from the cerebellum is not yet to be sharply made in most vertebrates, but in selachians they are separately marked transverse folds; so that one may speak of a *Lobus cerebellaris Acustici* and a *Lobus cerebellaris Trigemini* (see Fig. 58).

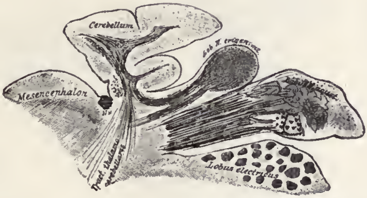


Fig. 58.—Sagittal section a little to one side of the median line through the cerebellum of a small ray.

In teleosts and even in selachians the cerebellum cortex extends some distance posteriorly and beyond these accessory structures. In birds and mammals they are completely included in the formation of the cerebellum, where they lie in the median portion,—in the Vermis.

Certain cell-groups easily demonstrable in mammals and birds, as yet hardly known in reptiles and amphibians, and easily found—to the extent of one cell-group—in fishes, may be called the special *cerebellar* nuclei. The last-named cell-group consists of two large spherical nuclei lying rather far to the posterior aspect,—the nuclei globosi cerebelli (see Fig. 47). They lie so direct in the plane of the nucleo-cerebellar tract and are so completely surrounded by the bundles of this tract, that they are probably to be counted in with this tract. In birds, and probably also in reptiles, small masses of cells lie laterally from these: the *Nuclei laterales Vermis.* In mammals one finds in the same region not only several small nuclei, but quite lateral from this, in the cerebellar hemispheres, a large much-folded nucleus: the *Oliva cerebelli* or the *Nucleus dentatus* (*Nuc. dentatus Olivæ*). It occupies the superior peduncle of the cerebellum. It has not yet been recognized in the lower vertebrates, but it is probable that it exists, because in these animals the superior peduncle enters the cerebellum.

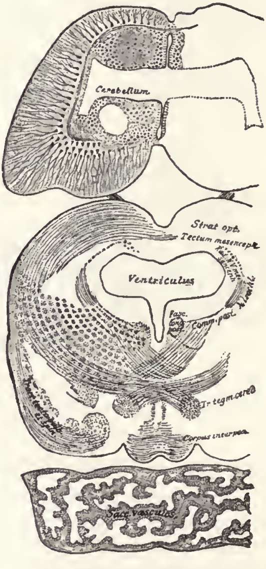


Fig. 59.—Frontal section through the midbrain of a shark: *Scyllium canicula.* Length of body, thirty centimeters. Showing the decussation of the Tractus tegmento-cerebellares.

Of the connections and the definite course of the fibers of the cerebellum there is, as yet, little known.

To be sure, we possess minute descriptions for several different vertebrate classes; but sufficient work has not yet been done with developmental or degeneration methods. Accept what is here presented as simply that which may be with some certainty now expressed.

The cerebellum stands in connection with other parts of the brain through its *peduncles.* The fiber constituents of the peduncles are, for the most part, constant, except that in the lower vertebrates appear certain tracts not yet found in mammals and birds, while in mammals there is a cerebral connection which is peculiar to this class.

Least known as to their real origin are several frontal tracts. In teleosts, whose large cerebellum contains easily recognizable afferent tracts, two tracts pass from the thalamencephalon: a fine-fibered posterior one and a coarse-fibered frontal one, the first into the cerebellum and the second into the Valvula cerebelli, the portion which lies under the roof of the midbrain. These are called *Tractus thalamencephalo-cerebellares.* These bundles have not, with certainty, been found in other animals. The *Brachium conjunctivum anterius* or superior cerebellar peduncle, is always present as the *Tractus tegmento-cerebellaris.* This is a bundle from a ganglion, which lies at the posterior end of the base of the thalamencephalon. Not far from its origin it decussates with its fellow. This decussation, which always lies at the level of the Oculo-motorius near the base, is a good point of orientation in investigations in brain-anatomy. Thence the fibers pass dorsally into the cerebellum (see Figs. 59, 61, 71, 83, 84, and 85).

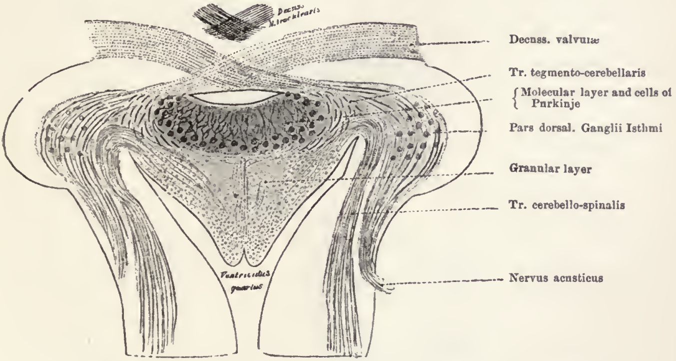


Fig. 60.—Section through the velum and cerebellum of a large lizard: *Lacerto muralis.*

Besides the tract named, still other fairly large bundles enter the anterior end of the cerebellum in fishes, amphibians and reptiles, but decussate just before sinking into the substance of the cerebellum. This decussation does not lie ventrally, as that just described, but dorsally in the velum, just posterior to the decussation of the Trochlearis, easily visible in reptiles (see Fig. 60).

The fibers of this *Decussatio veli* arise, in part, from the midbrain, but in larger part from the trigeminus nucleus. The detailed relations of this Decussatio veli are yet to be determined.

The connection between the cerebellum and the spinal cord is extraordinarily similar in all vertebrates, and is accomplished through the *inferior peduncles of the cerebellum.* Here one always meets that tract from the lateral columns, which, arising from a terminal nucleus of the sensory roots, is known to you as the *Tractus cerebello-spinalis.* Associated with it is the bundle from the Nucleus of Deiter in the acusticus region, which bundle probably also ends in the lateral columns. At any rate, Monakow could observe in mammals, and Bandis in birds, a descending degeneration from this nucleus when they severed an inferior cerebellar peduncle. The fibers of the Tractus cerebello-spinalis probably end in crossed and uncrossed ramifications in the dorsal plane of the cerebellum without the molecular or inner lamina.

In teleosts, selachians, reptiles, and birds the author has observed that within the medulla there are associated with the mentioned tracts still other afferent tracts from the nuclei of the posterior columns and from the posterior columns direct. The latter pass around the medulla ventrally, near its periphery,—Fibræ arcuatæ externæ,—till the tract is reached, when they fuse with it. In mammals the relations are the same; but here the inferior cerebellar peduncle contains yet other connections, especially the large afferent tract to the Oliva,—*Tractus cerebello-olivaris,* which has not yet been found in other classes.

Where the inferior cerebellar peduncle enters the cerebellum is the least understood portion of the whole nervous system. Here lies the acusticus nucleus and several nuclear groups whose significance is, as yet, completely problematical. These all lie mesially from the peduncles. But just at this place there pass into the medulla the Tractus vago- et quinto-cerebellares and from the medulla afferent bundles to the apparatus of equilibrium, which may pass into the Nervus vestibularis and into the Oliva superior. The middle peduncle reaches a considerable size only in the mammals, where it carries large bundles of fibers from the ganglia of the pons up into the cerebellum. The termini of these fibers—the cortex of the cerebellar hemisphere—are completely lacking in other animals, in which only the midportion—the Vermis—develops. One set of fibers which lies in the middle peduncle is also demonstrable in lower vertebrates. That is a fasciculus which passes ventrally from the cerebellum, curves around the medulla ventrally for a short distance, just to where it reaches the median line, where it bends upward, ascends within the raphé, finally decussates, and is lost in the lateral portions of the medulla,—the *Tractus cerebellotegmentalis.*

The relation of the arms within the cerebellum of the lower vertebrates requires elucidation. There is an open field here for the degeneration-method. Not the least of the difficulties in the study of the intact organ is the fact that several tracts cross in the cerebellum and pass to little known gray masses. In teleosts whose large cerebellum is quite free from the tracts from the cerebrum more is known with certainty than is the case in the other vertebrates. Particularly so among the decussation-fibers, the largest are those which belong to the Tractus nucleo-cerebellares of the Vagus and the Trigeminus, as well as fibers from the terminal region of the Acusticus. A large part of this decussation lies on the ventral side of the cerebellum (Fig. 60) close above the roof of the ventricle. There one finds in teleosts a good point of orientation in the decussation of very thick medullated fibers. They come from the Nervus trochlearis, which, without exception in the animal kingdom, decussates here on the boundary between the midbrain and the oblongata. Just behind this begin the ventral decussations of the cerebellum. The most anterior belong to the Tractus cerebello-nucleares Trigemini: the most posterior one to the tract of the Acusticus. However, the separate elements of the ventral decussation of the cerebellum are not yet sufficiently known.

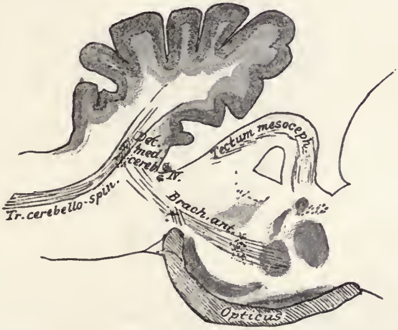


Fig. 61.—Sagittal section far to one side of the median plane through the brain of an eight-day chick. Only a part of the fibers are medullated. Showing the origin and course of the superior and inferior cerebellar peduncles.

There are also dorsal decussations in the cerebellum. They arise mostly from the Tractus cerebello-spinales, probably also from cerebellar nuclei (see Fig. 210).

Within the cerebellum there are everywhere associated bundles. The largest of these are found in teleosts, where a large bundle of medullated fibers joins the posterior portion of the cerebellum with the anterior (Fig. 86). Then there are always numerous short association-bundles, some of which pass ventral to the Purkinje cells in the inner lamina and a part dorsal to it in the molecular lamina. What further connections are possible through the medullated nerve-processes may be better studied in the description of the mammalian brain.

To Summarize.—In the cerebellum we have an organ into which nerve-tracts enter from the interbrain, the midbrain, the medulla, and the spinal cord: an organ that in mammals is also indirectly connected with the cerebrum. Into this organ pass bundles from several sensory cranial nerves, especially from the nerves of equilibration.

Fig. 62.—From the cerebellum of the minnow: *Phoxinus lævis.* *a*, Purkinje cells. *b*, Cells of the granular layer, of which one sends its neuraxons up into the association-net of the zona molecularis (*c*).

Within the cerebellum manifold connections are possible through cell-processes, as well as through contact with the numerous local cells.

It is easily conceivable that in this range of possible connections with tracts from almost every part of the brain is laid the foundation for *co-ordination* of *movements* and for the *maintenance* of *muscle-tonus*: functions which must be ascribed to the cerebellum.

The loss of the cerebellum has no vital significance in lower vertebrates. It appears that a part of the functions performed by it may be suspended, to be replaced in some way by another part of the brain. Even the minimum development of the organ in creeping animals indicates that it has essentially functions which in some way are connected with locomotion.

Though the cerebellum possesses connections with many parts of the brain, it is not traversed by a single tract passing from lower to higher levels. These all remain in the base of the oblongata, thence to pass to the base of the midbrain.

CHAPTER IX.

THE MIDBRAIN, OR MESENCEPHALON.

THERE is no part of the brain into which such large tracts enter, none from which so many tracts emerge for distribution to remote parts of the nervous system, and none within which are furnished so many connections between right and left side as the MIDBRAIN: THE MESENCEPHALON of the lower vertebrates. Only in mammals, where the cerebrum is developed into the great organ peculiar to that class, does there arise a brain-segment which contains still more extended connections and still greater commissural tracts.

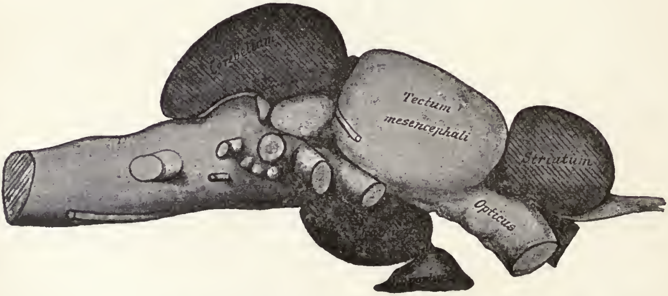


Fig. 63.—Brain of the cod: *Gadus æglefinis.*

Even the external appearance is suggestive of the significance of the structure. The accompanying figure (Fig. 63) of the brain of the cod shows at once how relatively great is the development of the mesencephalon, and that it is approached in size only by the medulla, which is the origin of the large cranial nerves. The cerebrum and, indeed, even the cerebellum—always unusually large in teleosts—are hardly to be compared in size with the midbrain and medulla.

In the description of the midbrain it is advisable to differentiate at once a *roof-segment* and a *basal segment.* Throughout the entire animal kingdom the roof exhibits fewer changes than any other part of the brain. The relative size only changes, and one who is acquainted solely with the relatively small *corpora quadrigemina* of man is surprised when he sees the immense *optic lobes* of a fish or a bird. But the minute structure is always the same. In the dorsal layers of the hemisphere—partially divided dorsally by a sagittal fissure—the *optic nerve* always ends. From the ventral layers always arises a system of sensory fibers: the deep marrow, which contains, among others, the already described Tractus tecto-spinales et tecto-bulbares.

This is very beautifully seen in the sagittal section of the brain of an amphibian larva, because here scarcely any fibers in the midbrain except these two tracts are medullated.

The roof of the midbrain is so large in fishes, and birds especially, because it produces such an unusually large opticus. In amphibians and reptiles it is also relatively larger than in selachians and mammals. The ventricle of the midbrain in the first-named animal is correspondingly large (see Fig. 68), while it is reduced to a crevice—the aquæductus Sylvii—in selachians and mammals. The extension of the roof in birds and in the teleosts has also led lateral pendulous projection over the base of the midbrain (see Fig. 55, *D*). One, therefore, sees the roof-formation inclosing the base externally. If one lay the brain of a bird or of a fish with the base up, he will see, on either side, the optic, arising from great white prominences, which, in spite of the fact that they embrace the base, are, on inspection, evidently nothing else than the strongly developed midbrain-roof.

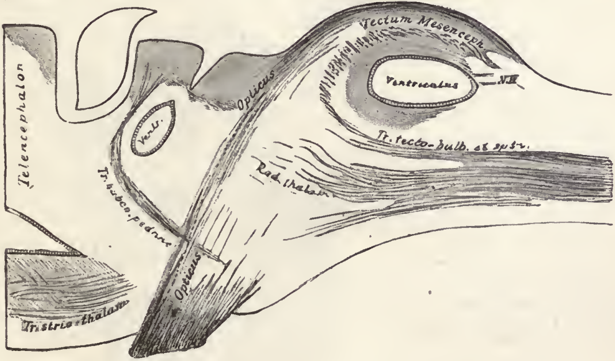


Fig. 64.—Sagittal section of the brain of *Axolotl*, the amblystoma-larya of Siredon.

The Tectum mesencephali is practically the ganglion of origin and the terminal ganglion for both of the kinds of fibers mentioned; also for a great number of intratectal association-tracts. It receives, also, an afferent bundle from the Thalamus, and in birds and mammals such a one from the cerebrum.

In the posterior portion of the midbrain lies, in all animals, a single nucleus, from which fibers join the deep marrow; this nucleus is called the *Corpus quadrigeminum posterius* (Fig. 65). In mammals, where the anterior part of the roof remains relatively small, this corp. quad. post. reaches a size almost equal to that of the anterior bodies.

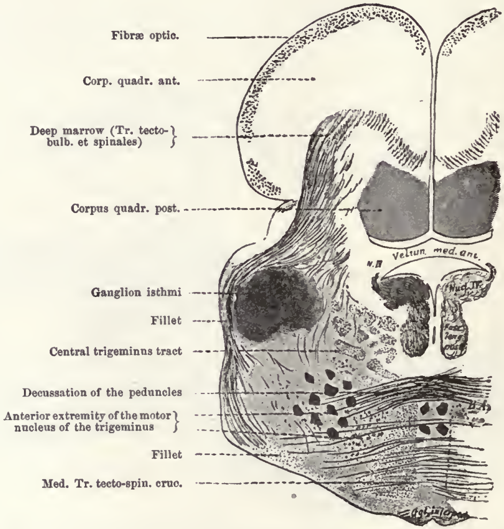


Fig. 65.—Frontal section through the most posterior portion of the midbrain of a lizard.

In the same manner in the anterior division of the roof there lies imbedded on either side of the middle line a beautifully outlined, roundish nucleus, which, up to the present, has only been found in lower animals, and whose demonstration in mammals has not yet been accomplished: *Nucleus prætectalis.*

The base of the midbrain is formed of those masses of fibers which arise in the forebrain and interbrain and pass the midbrain on their way to parts beyond. Then there are fibers which pass into the base from their origin in the roof. Finally, a number of nuclei have been found there, from which arise bundles which pass, in part, into the cerebellum, in part, to the brain-surface as peripheral nerves: Oculomotorius, Trochlearis (see Fig. 68).

From the roof of the midbrain passes from one side to the other of the brain a large commissure: *Commissura posterior cerebri.* It lies in the roof-plate itself, and borders entirely upon the posterior wall of the epiphysis (see Figs. 18 and 89).

The minute structure of the roof of the midbrain is exactly known only through the researches of R. y Cajal, of Fusari, and especially of von Gehuchten and P. R. y Cajal, in representatives of the different classes of vertebrates.

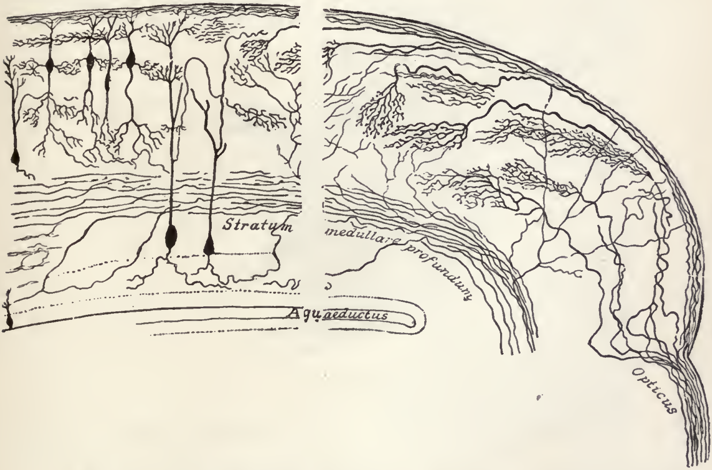


Fig. 66.—Showing the minute structure of the midbrain-roof. Two sections placed side by side for comparison of the layers. After Pedro R. y Cajal. Right-hand section from a frog. Note opticus *fibers* entering and ramifying in different layers. Sagittal section (compare Fig. 64). Left-hand section from a lizard. Note the *cells.*

It becomes evident that the different layers into which the roof-plate may, in all animals, be subdivided arise in a relatively simple manner (see Fig. 66).

Into the outer layer enter the fibers of the optic nerve with innumerable terminal ramifications. There are similar nerve-terminations in several of the deeper layers. The terminal ramifications come into manifold relations with the dendrites of cells which lie at various levels. A small number of such cells appear to send fibers down into the optic nerve itself, but the majority—especially a long layer of very large cells—send their neuraxons ventrally, where they form a definite layer of the deep medullary layer: *Stratum medullare profundum.* But into this layer, as into the optic layer, numerous fibers enter from other terminal ganglia. *Through this structure there arises an extraordinarily great opportunity for the transmission of light-impressions to the general sensory tract,* since the deep medullary layer, as far as now known, is in connection with ends of other sensory nerves.

Refer to Figs. 64 and 71, and see how, at the posterior end of the midbrain, the complex of Tractus tecto-spinales et tecto-bulbares just anterior to the cerebellum rises abruptly into the midbrain and there enters the deep medullated layer. There we have again found connection with a bundle already familiar, and may turn our attention to others.

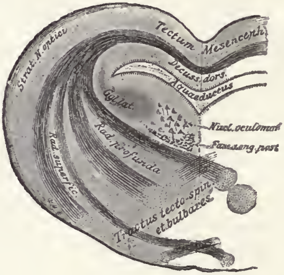


Fig. 67.

Naturally, it is not very easy in all the fiber-systems which fill the ventral portion of the midbrain to recognize the separate relations. To solve this problem in adult animals seems quite impossible. As most welcome simple objects, the larvæ of amphibians offer themselves. Here the system of the deep medullary stratum develops itself before all other fiber-systems of the midbrain, even earlier than the optic nerve. This layer has medullary sheaths at a time when no other system in this region is medullated, except, probably, the nuclei of the cranial nerves. If one, in observing a frontal section, passes from the ventricular epithelium outward, one comes first upon a layer of loose tissue with few cells,— the Ependym,—then a simple tissue with large ganglion-cells, and beyond it into the only medullated layer of the roof-plate: the *stratum medullare profundum.* Still beyond that one recognizes cells and thin non-medullated fibers. What becomes of the medullated layer may be easily understood (see Fig. 67). A part passes direct to the side of the midbrain and down to the base, thence posteriorly: a second part goes the same way, except that it first crosses the median line before it turns downward. This decussation was formerly called *Commissura ansulata.* These two parts together represent the lateral division of the deep medullary layer. The fibers of the median division which lies next to the ventricle do not turn toward the base of the midbrain.

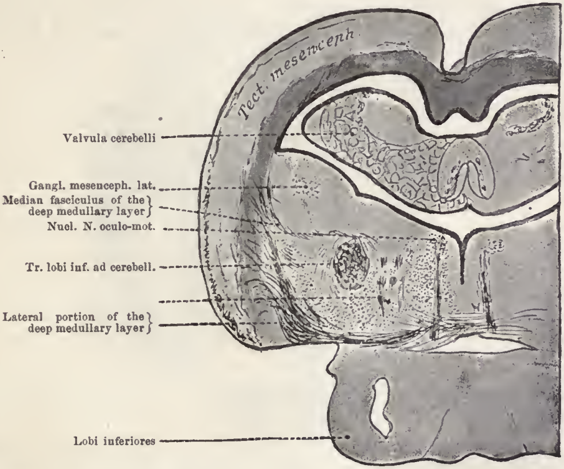


Fig. 68.—Frontal section through the midbrain of a teleost, *Rhodeus amarus.*

For a short distance they pass parallel to the ventricular wall and then divide, like the lateral portion, into a direct and crossed bundle.

The direct portion ends mostly in a ganglion,—*Ganglion laterale mesencephali* (see Fig. 68); the crossed portion encircles the floor of the ventricle, which presents here only a narrow cleft, and forms under it in beautifully plaited lines the *tegmental decussation* (*Haubenkreutzung*). Afterward it passes posteriorly close to the middle line, ventral to the fibers of the posterior longitudinal bundle (see Fig. 91).

Thus, all of these are bundles which connect the deep layers of the midroof with more posterior segments. Most of them end in the medulla, in the nuclei of the posterior columns, and in the gray matter of the spinal cord: Tractus tecto-spinales et tecto-bulbares. In adult animals the deep medullary layer of the midbrain may be best studied where it is best developed: *i.e.,* in birds or in fishes. The teleosts present the especial advantage that the region in which the Stratum medullare prof. lies is relatively simple in structure; so that the tracing of the fibers is facilitated. If one becomes once familiar with the relations in teleosts he may find them readily again in any of the higher vertebrates.

In Fig. 68 one may find several of the structures above mentioned. The tegmental decussation is not, however, to be readily found. In the enormous extension of the roof, which is found in the teleosts, these fibers have come into another position. They lie now directly upon the decussation which the lateral position of the medullated stratum makes, and thus increases the commissura ansulata. In horizontal sections one may readily separate the two parts of the commissure (see Fig. 91).

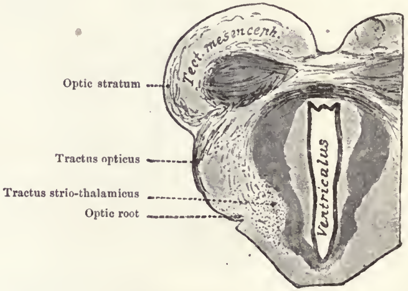


Fig. 69.—Transverse section through the midbrain of a toad: *Buf. cin.*

The fiber-system of the medullary stratum from the roof of the midbrain fills a large part of the basal portion of that brain-segment, encircling and traversing it. Because of the great number of transverse fibers, the base of the midbrain has been called the *Pars commissuralis.*

The roof of the midbrain gives origin to still another system from the same layer: viz., the fibers which, taken together, are much greater than parts mentioned, and which, throughout the whole roof region, pass in lateral direction from right to left or *vice versâ.* Through these fibers there is formed in the median line the dorsal decussation of the midbrain. The whole structure is the *Lamina commissuralis mesencephali.* This decussation is exceedingly constant, and from Petromyzon to man it is always present. In Fig. 68 it may be seen as a shaded inner layer of the roof. It joins anteriorly with the transverse fibers, which, as Commissura posterior, pass along the frontal end of the midbrain-roof (Fig. 69). But, through the narrower caliber of its fibers and their somewhat more dorsal position, the bundle is always readily distinguished from the posterior commissure.

The optic nerve arises, in all lower vertebrates, chiefly from the roof of the midbrain. Figs. 64 and 70 give a good view of this origin.

Only in the higher mammals does the opticus origin in the ganglia of the thalamus appear to play a greater rôle. The roof of the midbrain is a segment of a sphere. From the ventral chiasma a curving tract of manifold bundles encircling the whole mass of the midbrain passes to the Opticus.

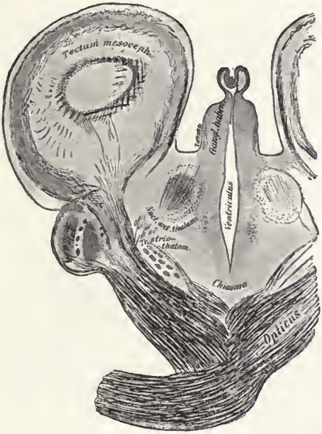


Fig. 70.—Transverse section of *Rhodeus amarus* through the region of the chiasma. Note that the Tectum mesencephali covers the Opticus. The median portion of the figure belongs to the thalamencephalon.

Most of the bundles lie near the surface, and, like the partially flexed fingers of a hand, inclose the spherical mass; but a smaller number of bundles, especially those which are destined for the more posterior portion of the Opticus, turn inward just before reaching the roof of the midbrain, and pass toward their terminus, breaking through the basis of the midbrain-roof, thus, in a measure, passing under it.

These different bundles have been described as different "roots": viz., as "median, lateral," etc.; but this has little to recommend it, for, though some of the bundles vary their course somewhat, they all pass to the same end.

Since the optic tract enters the frontal end of the midbrain, one will meet it only in sections which are cut far forward. Such a section (as shown in Fig. 70) encroaches upon the interbrain.

The Tectum mesencephali is, in all lower vertebrates, brought into intimate relations with the great nuclei of the interbrain (thalamencephalon) through a large bundle: the *Tractus tecto-thalamicus.* The bundle is so large that it will doubtless be found in mammals also. It is lost between the layers of the roof. The cerebral connections probably exist in reptiles; in birds and mammals, however, its existence is certain.

Important in the investigation of the brain of lower vertebrates is the large-celled *roof-nucleus* (*Dachkern*). The nucleus in question lies close on either side of the median line, but does not occupy the whole length of the roof. It is not present in mammals, but one meets there a group of quite similar cells, which degeneration-experiments have shown to belong to the fiber-system of the Trigeminus: *Radix mesencephalica Nervi V.* It has not been demonstrated, however, that the origin of the midbrain-root of the Fifth nerve is a homologue of the *Dachkern* in question.

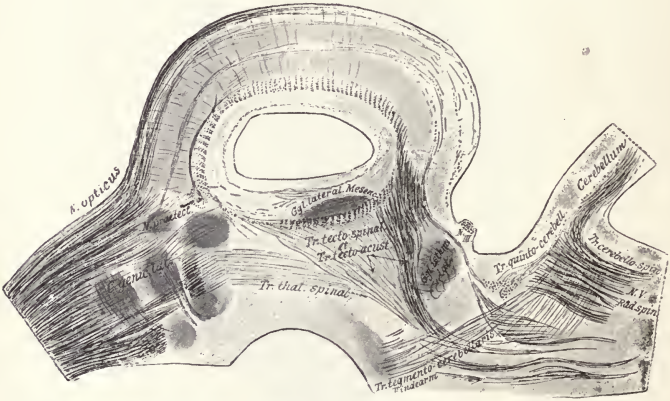


Fig. 71.—Sagittal section of a lizard-brain, showing the position of the nuc. lat. mesencephali; also showing well the different bundles of the Opticus and the course of the fibers from the deep medullary stratum into the fillet.

The basis of the midbrain is distinguished by the numerous already described decussations which lie in it, but the fact that several important bundles pass into it from the interbrain, and finally by the presence of several separate nuclei.

In birds and fishes where it is widely spread out on account of the large roof, where also the ventricle comes into relation with not a small part, it is especially favorable for study. One recognizes at once that the central gray, which everywhere incloses the ventricle, covers everywhere the surface of the midbrain-base, which lies next the ventricle. In this gray matter—that is, in the dorsal portion of the midbrain-base—lie several important nuclei. Near either side of the median line may always be seen a number of small masses of cells, which send out ventrally the fibers of the *Nervus oculomotorius* (see Fig. 68). Even in the lowest vertebrates these leave the base of the brain, always at the same place, as two not unimportant nerves, which turn toward the eye-cavity. Just posterior to the nucleus of the Oculomotorius one finds aggregations of cells (Fig. 65) from which the Trochlearis arises. In all animals yet studied the nerve crosses to the other side in the *Velum medullare posticum* (Fig. 60). In order to reach this dorsally located decussation, its fibers must, just after their origin, pass somewhat backward and then turn dorsally. Thus, the nerve which passes off quite dorsally always appears in the narrow crevice which remains between the midbrain-roof and the cerebellum (see Figs. 56 and 74).

Lateral from the nuclear origin of this nerve there lies, in the midst of the central gray, a large nucleus: the *Nucleus lateralis mesencephali.* The thin layer of nerve-netted gray matter around the aqueduct in mammals scarcely suggests what important structures are here represented in a process of retrogression. If one dissects off the roof of the teleostean midbrain, one will see, under the same, the protruded part of the cerebellum as a large evagination divided in the median line (see Fig. 86). Laterally from this one finds on either side an elongated, somewhat curved projection, which may not, like the cerebellum, be lifted from the floor of the midbrain; in fact, it belongs to this. This growth was known to the old anatomists, and was designated by them as *Torus semicircularis.* The Torus arises through the location of the lateral mesencephalic nucleus (especially large in fishes) in the lateral part of the central gray of the midbrain. The same nucleus is also demonstrable in birds, even though it does not reach in them the relative size which it has in fishes. In selachia its presence is, to me, doubtful; but in reptiles it is evident, and in amphibia it is, through the location at least, to be recognized (Fig. 72). From the nucleus lateralis mesencephali arises a large bundle: the *lateral longitudinal bundle.* It may be followed through the entire medulla oblongata, and probably passes into the lateral columns of the spinal cord.

That a part of the longitudinal fiber-system in the midbrain-base arises from the thalamus (Fig. 71) was mentioned above. Three of the bundles which lie here deserve especial mention before we consider the thalamus, because they give to the medullary white matter of the base its characteristic feature. The first is the *Fasciculus longitudinalis posterior* (Fig. 44). It arises with its most anterior fibers from a single nucleus of the most posterior part of the Thalamus, but reinforces itself in its backward course, while it passes the nucleus of the Oculomotorius. The bundle lies on either side of the middle line quite dorsally, partly imbedded in the nuclei in question and partly ventral to them (Fig. 65). In a similar way from a nucleus which is readily to be seen in the ventral part of the thalamencephalon in all lower vertebrates—*Nucleus tegmenti*—arises the *Tractus tegmento-cerebellaris,*—the peduncle of the cerebellum. It traverses the midbrain for only a short distance, and crosses to the other side just behind the last roots of the Oculomotorius (see Fig. 65). The decussation of the Tractus tegmento-cerebellaris lies dorsal to the decussation of the tegmental tract from the roof: *Commissura ansulata.*

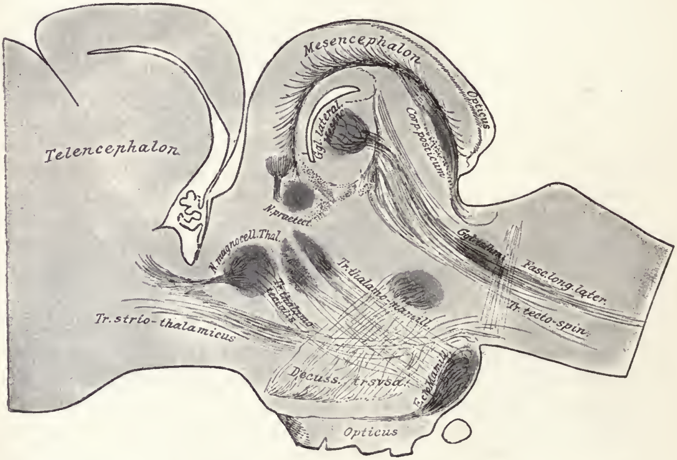


Fig. 72.—Sagittal section of brain of chick on eighth day after hatching, showing origin of the Fasc. long. lateralis.

The third longitudinal fasciculus of the midbrain-basis arises from the *commissura posterior* (Figs. 69 and 73), whose limbs turn backward after the decussation quite anterior to the midbrain-roof, describing the outline of a horseshoe. The posterior end is still unknown. There is strong evidence that in the lateral parts of the posterior longitudinal bundle fibers from that commissure pass far back. According to Kölliker and others, the whole system arises from a nucleus lying in the region of the Nucleus fasciculi posterior. The author is unable to differentiate a separate nucleus. The relation of the posterior longitudinal fasciculus to the posterior commissure requires further elucidation. This has been retarded, because both bundles are so difficult to bring to degeneration *in continuo.*

Quite ventral in the anterior part of the midbrain-base lies a flat lenticular ganglion, which receives bundles, among which are some from the Corp. striata of the cerebrum. So far as the author sees, it is best defined in the reptiles and birds. The mammals have, in the same location, two ganglia: one behind the other, the anterior one being called *Corpus subthalamicum,* and the posterior *Substantia nigra.* Which one of these corresponds to the basal ganglion of lower vertebrates is yet uncertain, the term *Ganglion ventrale tegmenti* being used to designate the structure (see Fig. 73).

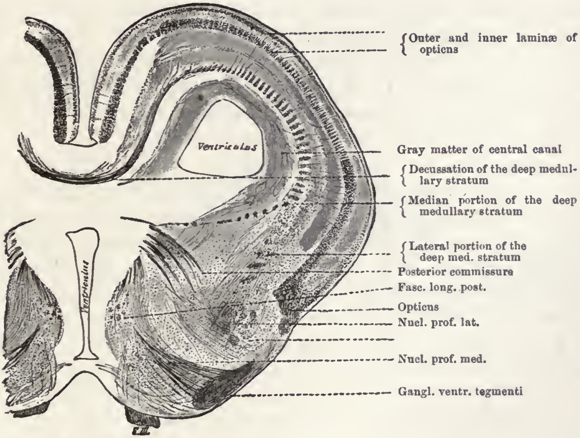


Fig. 73.—Frontal section through the midbrain of *Lacerta.*

To the special ganglia of the thalamencephalon must be reckoned two not clearly defined cell-aggregations: one lying in the lateral portion of the base and one close beside the median line. Into both pass portions of the deep medullary stratum: into the lateral one, the uncrossed fibers, and into the median one the crossed fibers of the median portion of the deep medullary stratum. The nuclei may be designated as the *lateral* and *median deep midbrain-nuclei* (*nuc. profund. lat.* and *nuc. profund. med.*, Fig. 73).

The midbrain-base is naturally, in fishes, traversed also by those fibers which pass from the thalamus to the cerebellum; furthermore, fibers from the *Decussatio transversa* (Fig. 72), which cross posterior to the chiasma and turn backward to the midbrain-wall on either side until they reach the most posterior region of the midbrain-roof, probably ending in the ganglia of the posterior quadrigeminal bodies or in the *Ganglion isthmi*.

Having presented the gradual development of the mesencephalon, let us, without a more detailed account, turn to a summary of the most important features.

Summary.—From the roof of the mesencephalon arises the optic tract from cells which, through their dendritic processes (*Endstätten*), are in communication with the great roof commissure and with the bundles to the sensory terminal nuclei in the oblongata and the spinal cord. From the gray matter ventral to the aqueduct arise fibers of the *Nervus oculo-motorius* and of the *Fasciculus longitudinalis*.

The base is occupied mostly with longitudinal bundles, tracts, and fasciculi to the spinal cord and to the cerebellum; and the whole is embraced ventrally by the decussation of the deep medullary stratum and laterally by the uncrossed fibers of the same,—the fillet.

The structure of the midbrain is, as far as known, in all animals the same, except that those portions of the fibers which pass downward from the roof of the organ,—*i.e.*, the Tractus opticus and the fillet,—are much more highly developed in fishes and birds than in mammals. In the latter, therefore, there has taken place a relative retrogressive development.

In other places a relative increase of the volume of the midbrain has taken place; not, however, conditioned upon a change in the structure of the midbrain itself,—that remains the same,—but upon the tracts which pass through the organ. In mammals large tracts arise destined for the pons or spinal cord. These tracts find no room in the structure described above as typical for lower vertebrates. They pass quite ventral to that, giving rise to a new external ventral layer: the *cerebral peduncles*. Lying dorsal to this is the *tegmental system*, common to all vertebrates; the *cerebral peduncles* represent a *novum additum* which appears only late in the animal kingdom.

So the midbrain offers again a good example of the fact that in the animal series (Taxonomic Series) no one segment of the brain undergoes a step-by-step progressive development which is even approximately parallel to the rank of the animal as determined by its general structure. There is a particular organ gradually developed, which may be highly developed in organisms of median rank, while in organisms of higher rank it may be weakly developed, as we have seen to be the case in the midbrain. The case may be further complicated by the association, here and there, of new tracts arising in brain-segments which, in particular classes, are especially developed.

CHAPTER X.

THE INTERBRAIN: THE THALAMENCEPHALON.

THE anatomical apparatus which has been described is so constructed that it may be looked upon as, in the main, complete in itself. Only a very few bundles pass anteriorly from the organs above described. Moreover, in the lower vertebrates at least only a few small tracts pass from those brain-segments anterior to the midbrain into the ganglia which lie in the midbrain and oblongata, or into the spinal centers. Consequently, fishes, amphibians, and reptiles never show so marked derangement of functions where all of the brain anterior to the posterior commissure is removed as when the midbrain, with its great association-bundles and important tracts, is injured or when one injures the oblongata or the spinal cord.

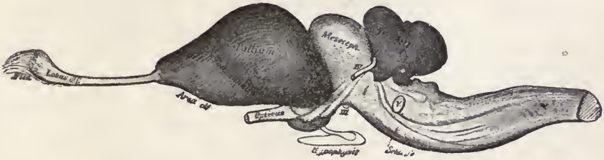


Fig. 74.—Brain of a Nile crocodile, natural size. The cerebrum covers the thalamus anteriorly; the Tractus opticus covers it laterally; so that only a small part of the hypothalamus remains visible.

Regarding the physiological significance of that part of the brain between the midbrain and the cerebrum—viz., the *Thalamencephalon*—we know practically nothing and we stand only on the threshold of morphological knowledge.

Doubtless, however, the thalamencephalon is an important segment of the brain. Since from Petromyzon up through the vertebrates, however weakly one or the other brain-segment may be developed, one uniformly finds the interbrain anterior to the midbrain. In the external view of the brain it is scarcely visible, because, even in those cases where it is not enmantled by the hemispheres, still the midbrain-roof protrudes beyond it, and, furthermore, it is completely covered laterally through the great fiber-system of the optic tract, which passes down to the chiasma from the roof of the midbrain.

The best starting-point is the very simply constructed thalamencephalon of the amphibian. It is an elongated body of oval cross-section, continuous anteriorly with the prosencephalon and posteriorly with the mesencephalon. Close behind the plexus chorioides of the cerebrum is located on either side a small ganglion,—*Corpus habenulæ,*—and this division is designated the *epithalamus.* On the ventral side lie several prominences and aggregations of ganglia which are, in part, readily distinguished from the rest of the thalamus, and are grouped together as the *Hypothalamus.* The principal body which lies between these two just named retains the name *Thalamus.* These three divisions are practically demonstrable in all vertebrates, but the epithalamus alone is uniform in its structure, the other divisions varying much in different genera.

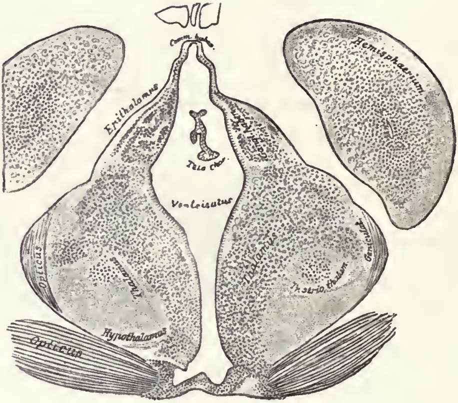


Fig. 75.—Section through the Diencephalon of *Bufo*: toad.

The central cavity of the thalamencephalon is closed dorsally with several folds of the same epithelial plate as had formerly constituted the entire encephalon (see Figs. 18 and 20). Besides this, the roof contains the fibers of a small commissure: *Commissura habenularis.*

Anteriorly the interbrain is separated from the cranial cavity by the *Lamina terminalis* (see Chapter IV, page 49). It is always narrow, and on either side of it an opening leads into the central cavity of the hemispheres, which even in the embryonic period are evaginated dorso-laterally from this location.

The lamina terminalis of the brain, before turning backward to form the roof of the interbrain, passes first a short distance dorsally,—*Lamina supraneuroporica,*—and then falls in the usually sail-like, pendulous *Tela chorioidea,* from which, through anteriorly-directed evaginations, the *Plexus chorioidei* of the ventricle is formed. In several amphibians (Fig. 55, *B*) and in the Dipnoi, whose brain can scarcely be differentiated from the typical amphibian brain, the *Tela* grows exuberantly into the central cavity of the interbrain by the addition of numerous tap-like processes. Close to the epithelium there always lies a rich, vascular plexus. It is probable that the structure is an organ of secretion. Posterior to the Tela chorioidea are one, or frequently several, dorsally directed projections called Paraphysis and *Epiphysis,* according to their relative location (see Figs. 76 and 86).

Fig. 76.—Median sagittal section through the brain of the lizard: *Varanus griseus.*

Just anterior to the epiphyseal evagination, the entrance to which is not shown in the figure, lies regularly the *Commissura habenularis.* It belongs to the system of fibers which pass into the *Ganglia habenulæ* from the posterior olfactory region, and will be considered later.

The epiphyseal tube is very constant. In several selachians and in many reptiles this structure passes through a hole in the skull to a sense-organ under the skin which has a striking resemblance to an eye. One can recognize in this impaired parietal organ a cornea, a lens, a retina, and, below this, a pigmental layer. We are indebted to Graf and Spencer for its discovery. In other vertebrates one finds in the adult stage no connection between the epiphyseal tube and the sense-organ. The epiphysis has withdrawn within the skull, and the parietal eye is so completely lost in the amphibian and reptilian transitional forms that in birds and mammals no trace of it remains. The blunt, often enlarged end of the tube remains as a little tubercle,—*the pineal gland,*—just anterior to the midbrain.

The base of the thalamencephalon is, in the median line at least, separated from the skull by only a thin membrane. Within it and under it pass important systems of transverse fibers, and just at the middle line the hypothalamus is thickened into a structure of varying form. Ventral to the commissural region of the cerebrum the lamina terminalis has a small evagination anterior to the chiasma: the *Recessus præopticus.* It then covers the basal wall over the chiasma, through which it is strongly curved inward (Fig. 76), and then curves outward, forming the *Recessus postopticus.* Still farther posterior follows always a deep recess, which often ends in a narrow, often thread-like tube: the *infundibulum* or *Recessus infundibularis.* The projection which this makes upon the base of the brain is called the *Tuber cinereum.* To the terminal tube of the infundibulum is applied the *hypophysis*: an outgrowth from the oral epithelium to the base of the skull. In mammals it grows so fast to the infundibulum that it is customary to refer to the end of the infundibulum as the cranial part of the hypophysis.

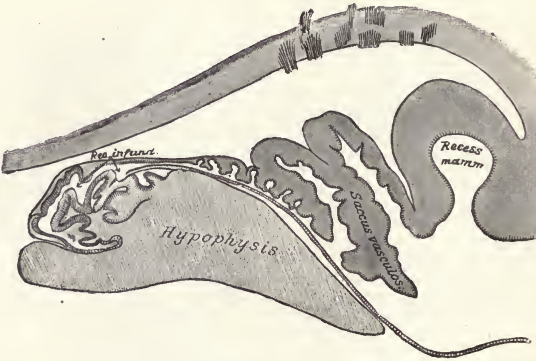


Fig. 77.—Sagittal section through the infundibular region of a shark: *Scyllium canicula.*

Kupffer made a discovery a few years ago that is destined to throw new light on the significance of this structure. In the embryos of lower vertebrates—Petromyzon, sturgeon, and others—there exists, for a period, a peculiar evagination from the dorsal side of the primitive pharynx and directed forward. He called this the *preoral gut.*

It is known that in the sturgeon a passage leads from the exterior into this preoral gut: *i.e.*, the fundament of a separate mouth is established over the permanent mouth. This whole structure—the preoral cavity and the preoral gut, into which it leads—*becomes the hypophysis.* According to Kupffer, the evagination from the oral cavity of craniate vertebrates—the hypophysis—is a vestige of this old preoral cavity.

In lower vertebrates dorsal to the infundibulum the posterior wall of the infundibulum is evaginated into a long, narrow epithelial tube whose walls are thrown into numerous folds through the pressure of numerous blood-vessels. The structure is called the *Saccus vasculosus* (see Figs. 59 and 77). When the posterior end of the ventral wall of the interbrain joins to the base of the midbrain one always finds a farther small evagination: the *Recessus mammillaris.* In selachia it contains large ridges and nodules of epithelium, and forms a richly vascular structure evidently functional.

Fig. 78.—Horizontal section through the hypophysis of the ray: *Raja clavata.*

Now that the dorsal and ventral portion of the interbrain have been described, we may turn to the consideration of the lateral portions. Close to the epithelial roof there lie the *Ganglia habenulæ*, one on either side, the distinctive ganglia of the *Epithalamus* (Fig. 75). In many of the lower vertebrates there is a difference in the size of the two ganglia; otherwise, however, the Ggl. habenulæ offer a good example of a markedly constant brain-structure, varying neither through progression nor retrogression. From Petromyzon to the mammals one always finds them on either side and a little to the front of the epiphyseal process. They consist of two bodies,—a lateral and a median,—and are always separated from the epiphyseal sac posteriorly by the *Commissura habenularis* (Figs. 76, 79, 86). In amphibians and reptiles where the other ganglia of the thalamus are only slightly developed relatively, or in fishes where they are placed more to the ventral position, the Ggl. habenulæ occupy a position in front of all the other interbrain-ganglia. When in birds and mammals the other constituents of the thalamencephalon develop more and more, they press the epithalamus somewhat back; so that the whole remaining part of the interbrain lies between it and the forebrain. The relative location of the epiphysis remains, in the meantime, unaffected.

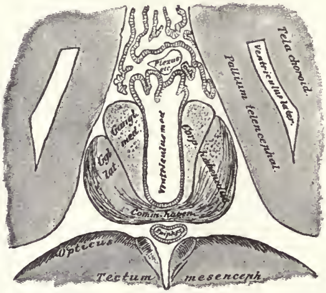


Fig. 79.—Horizontal section through the Gang. habenulæ of a turtle: *Emys europ.*

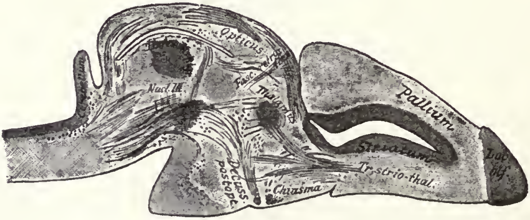


Fig. 80.—Sagittal section through the brain of Triton, lateral from the median line, showing the Fasciculus retroflexus; also the Tr. Strio-thalamicus ending in three places in the interbrain.

The tracts which pass to the epithalamus are as constant as the development. First, it always receives anteriorly from the olfactory region of the cerebrum an afferent tract: *Tractus olfacto-habenularis.* To this is associated in those vertebrates above the amphibia a bundle from cerebral cortex: *Tractus cortico-habenularis.* Both together form the *Tænia thalami* (see Fig. 100). Several smaller afferent bundles need not be mentioned. Remember simply, that in the Ggl. habenulæ an important connecting bundle ends, which is composed of fibers from the posterior olfactory lobe and fibers to the olfactory cortex.

A large part of the fibers of the Tænia thalami end, not direct in ganglia of the same side, but cross to the one on the opposite side through the Commissura habenularis. The tænia consists of a medullated and a non-medullated portion; the same is true of the commissure. Figs. 99 and 100 show the plan of the connection of the olfactory apparatus and the Ggl. habenulæ.

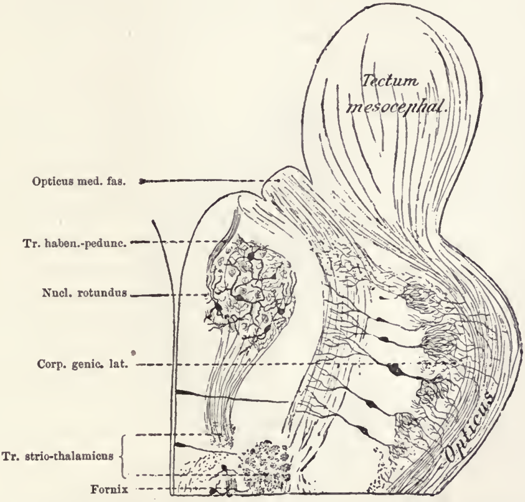


Fig. 81.—Frontal section through the dorsal portion of the thalamus opticus of the "blind snake": *Anguis fragilis.* Golgi method.

The more median of the two ganglia sends out a bundle ventrally: *Tractus habenulo-peduncularis,* or *Fasciculus retroflexus* (see Figs. 64 and 80). Its fibers traverse the whole base of interbrain and midbrain and end not far posterior to the Oculomotorius in a small ganglion lying quite ventral in the base of the medulla, in the *Corpus interpedunculare* (Fig. 65). Here they break up, and their terminal fibers decussate with those of the other side. The fasciculus and the corpus interpedunculare are absolutely constant throughout the whole vertebrate series.

The ganglia peculiar to the thalamus may only be sharply differentiated from those of the hypothalamus in the mammals and birds; in lower vertebrates the two regions merge into one another.

To the author the Thalamus of the reptile is best known, and, since the transition from this to the same organ of birds and mammals may be readily made, it will be advisable to begin with a close study of the former.

Anteriorly there enters into the thalamus from the corpus striatum of the cerebrum a large bundle: *Tr. strio-thalamicus.* The bundle splits up in such a manner that each one of the ganglia to be named immediately receives fibers which, separated from the others, pass to it direct. This characterizes all the thalamic ganglia.

The nucleus which strikes one first is a large, round one, composed of immense multipolar cells,—the *Nucleus rotundus thalami.* It is found likewise in birds, here with a retort-shaped, posteriorly directed projection. In fishes, also, it is a very large ganglion. In the nucleus rotundus the bundles of the Tr. strio-thalamicus split up into fine rays (Fig. 81), and from it arises a fasciculus which, passing backward, ends in the roof of the midbrain: Tr. thalamo-tectalis (Fig. 83). The appearance of this nucleus and its connections are especially characteristic and very constant.

Somewhat anterior and dorsal to the Nuc. rotundus in the neighborhood of the Ggl. habenulæ lies the *Nuc. anterior* (Figs. 70 and 83). From it arises a characteristic bundle,—characteristic of reptiles, birds, and mammals,—which, traversing the whole thalamus quite parallel to the Tr. habenulo-peduncularis, passes to the base and is lost in the Corpus mammillare located there: *Tr. thalamo-mammillaris* (Fig. 83),—in mammals called the *fasciculus of Vicq d'Azyr.*

Ventral to the two described nuclei one finds in reptiles and birds, probably also in fishes, in the midst of the gray matter that surrounds the median ventricle, an elongated nucleus of large cells: *Nuc. magno-cellularis strati grisei.* It is probably fibers from it that pass ventrally to cross just over the infundibulum as the *Decussatio supra-infundibularis.* Besides this, it probably sends bundles off posteriorly.

In many reptiles, especially turtles, in mammals, and possibly in birds, the two sides of the ventricular wall fuse together for a little distance in the midst of the thalamus. Thus arises the *Commissura grisea thalami*: the Commissura mollis in mammals. In crocodiles, turtles, and snakes there lies here a large nucleus,—median nucleus (Fig. 82),—the connections of whose fibers are not yet clear. At any rate, it receives fibers from the striatum and sends fibers out laterally. The median nucleus is not sharply defined, but there lie in the gray matter of the thalamus, some near to the median nucleus and some farther away, numerous apparently similar cells, which surround all of the other more clearly defined nuclei. I will designate the whole as the *Nuc. diffusus thalami.*

As was already mentioned, nearly the whole external surface of the thalamus is covered by the descending fibers of the optic tract. Between the optic tract and the two described thalamic ganglia lies a double ganglion-complex, which is very constant and is, indeed, to be reckoned in with the fundamental ganglia of the opticus system: the *Corpus geniculatum laterale* (Figs. 81, 82, 83, and 84). It is present in all vertebrates. In reptiles the author differentiates an antero-ventral from a postero-dorsal portion (see Fig. 82). It is possible that the latter merges into what in man is called the Corpus geniculatum mediale. At least an analogously located line may be seen in birds arising from the Decussatio transversa and which may, in mammals, be followed as far as to and into the Geniculatum mediale. There arises from the Corpus geniculatum laterale—probably also from the Corp. genic. med.—a posteriorly directed *Stilus corp. geniculati,* which is lost in the posterior portion of the midbrain-roof, possibly communicating, on the way, with the nucleus prætectalis, later to be described. In birds with enormously developed geniculatum it is very large.

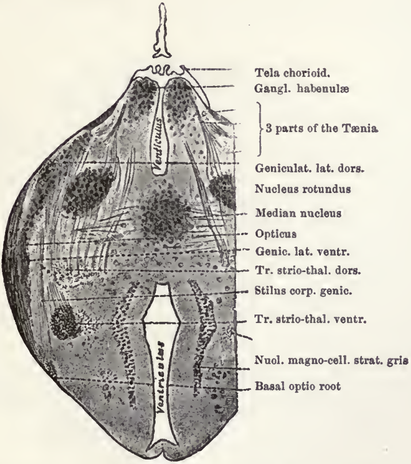


Fig. 82.—Frontal section through the Thalamus opticus of a young alligator.

In the geniculatum a part of the optic nerve ends in striking ramifications in whose midst are the dendrites of elongated fusiform cells whose median end ramifies within a bundle which probably, also, belongs to the optic system. These structures are well represented in Fig. 81.

In the midst of all these ganglia end the *Tr. thalamo-bulbares et spinales.* It is, however, still impossible to designate just what nucleus is the terminal one (see Fig. 64, *Rad. Thal.*).

With the mention of the *Nuc. entopeduncularis,* a group of large ganglion-cells median to the Tr. strio-thalamici, I have enumerated the most important ganglia characteristic of the thalamencephalon of lower vertebrates.

Fig. 83 shows a schematic representation of the nuclei of the thalamus in the pigeon. It gives a good general idea of the structural relations already quite complicated in birds and as yet not well known.

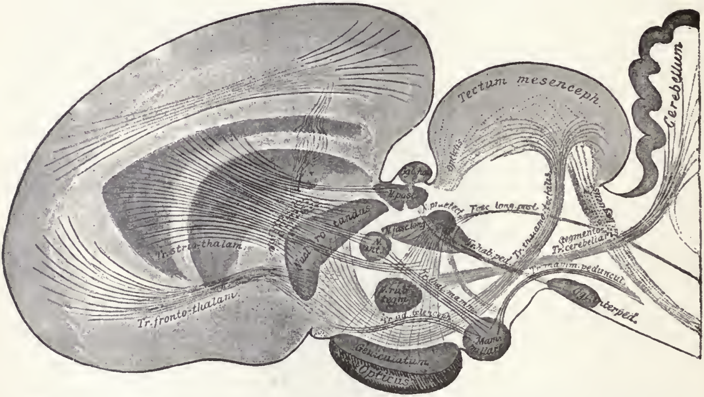


Fig. 83.—Schema of the principal nuclei and tracts of the interbrain of the pigeon.

What is recognized as common to the nuclei of the thalamus in all lower vertebrates may be thus summarized: *The nuclei of the interbrain receive fibers from the basal ganglia of the forebrain, and give off posteriorly new tracts to centers which lie at a lower level. Furthermore they are joined to the ganglia of the hypothalamus in manifold combinations.* The fibers which pass to the roof of the midbrain and to the medulla and spinal cord have already been mentioned. We will soon find that also from the nuclei of the hypothalamus tracts lead to the cerebellum and to other regions of the midbrain than to the roof. *So we see in the thalamencephalon a great* *center* which is inserted in between an important part of the cerebrum and nearly all other parts of the brain.

Traces of a progressive development of the thalamus are found in the reptiles, where from the frontal cerebral cortex a bundle arises which, ending in the thalamus, represents a direct cortico-thalamic tract. In birds the same thing is even more evident, and one may recognize how, *with the development of an extended cerebral cortex, more and more bundles appear which pass from it into the ganglia of the thalamus.* In mammals these *Tr. cortico-thalamici* have undergone such a great development that they make the greatest system of the thalamencephalon, and taken together are designated *Corona radiata* of the Thalamus. With this transformation there goes hand in hand a gradual enlargement of the ganglia; so that it is no longer possible to recognize the comparatively simple relations which exist in reptilia and to homologize with certainty the large thalamic nuclei of

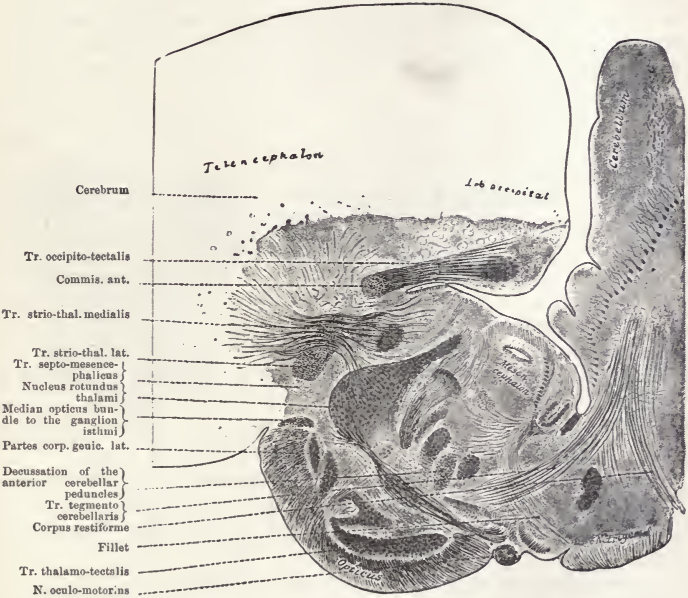


Fig. 84.—Sagittal section through the Thalamus opticus of the domestic pigeon. Hæmatoxylin staining.

mammals with the previously described nuclei of reptilia. It will require much work yet before it is known what new structures have been introduced and what is to be attributed only to the increase of structures already present. As yet, it is not possible to determine more than that, *in mammals, fibers from the Tr. strio-thalamici end in all or nearly all of the thalamic ganglia,* and that *the Tr. thalamo-bulbares et spinales are developed from one of the ventral nuclei.*

Only a few thalamic nuclei of mammals may be homologized with those of lower vertebrates; and these will be more minutely described, because, in them, we have learned to recognize the whole process of the addition to already existing systems of cerebral tracts which are not necessary to the existence of lower vertebrates. First, there is the *Corp. geniculatum.* In all animals fibers from the the optic nerve pass into it. From birds upward in the vertebrate series there is formed a tract from the cerebral cortex to the optic center. Whether in birds it reaches the geniculatum is not known, but that it does so in mammals has been conclusively demonstrated. So you see, anatomically recognizable, how the primitive terminal center of the optic nerve passes, in higher animals, into relations with tracts which arise in the organ of thought, of memory, of association, etc.

For the ventral nucleus in which the tracts to the medulla and spinal cord end, a similar relation has also been recognized in the mammals. Here it receives afferent bundles from the cerebral cortex, indeed, from psychomotor areas: from cortical areas whose loss diminishes the ability to carry out acquired movements or movements which are the result of associative reflexes.

Though these nuclei exist in lower vertebrates, it is only in the highest of the series that the cerebral tracts are added.

So much for the ganglia peculiar to the thalamus. There still remains for consideration a narrow region that is usually reckoned in with it: the boundary region between the interbrain and the midbrain,the *metathalamus.*

Just anterior to the roof of the midbrain and continuous with it, simply extending out into the thalamus anteriorly, we find the *Nuc. prætectalis.*

It has not been demonstrated yet in mammals, though I believe that it is to be recognized in the most anterior portion of the ganglion reckoned until now as belonging to the gray matter of the anterior quadrigeminal body. Of this nucleus something has been said before (Figs. 71 and 72), and also of the fact that in it probably bundles from the stilus of the geniculatum end (Fig. 83). Median from it lies a not very sharply defined nucleus, from which the bundles of the commissura posterior—*Nuc. commissura posterioris*—appear to develop, and ventral to it one finds, throughout the whole vertebrate series, the *nucleus* of *origin* of the *posterior longi-*

tudinal bundle (Fig. 44): an elongated, perpendicularly placed nucleus which lies near the median line, one on each side. From it develop the most anterior fibers of the *Fasciculus longitudinalis posterior,* the bundle which we have repeatedly met from the spinal cord on to the interbrain. That it later receives bundles from the nuclei of the cerebral nerves has already been mentioned.

The nucleus of the posterior longitudinal fasciculus lies rather far ventral, and might, in fact, be reckoned with the hypothalamus instead of the metathalamus. In fishes it certainly belongs to the former.

Lateral from it—*i.e.,* in the postero-lateral portion of the thalamus—lies the *nucleus ruber tegmenti*: a usually well-defined nuclear mass from which fibers arise which decussate soon after their origin, pass dorsally, and end in the cerebellum. These bundles are comprehended under the term *Tractus tegmento-cerebellaris*: the anterior peduncle of the cerebellum. For the nucleus see Fig. 83; for the tract see Figs. 71 and 84, and for the decussation see Figs. 65, 83, and 84.

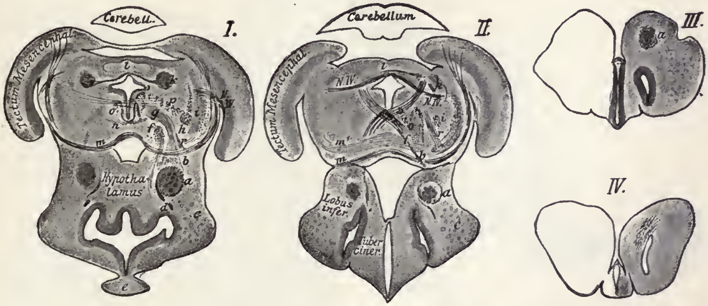


Fig. 85.—Frontal sections through the boundary between the base of the midbrain and lobi inferiores. From the teleost: *Zoarces viviparus.* (A young specimen three centimeters long.) *a*, Nucleus rotundus thalami. *b*, Supplementary nuclei of the same. *c*, Post. ganglion of inferior lobe. *e*, Infundibulum. *f*, Tr. lobo-cerebellaris frontalis. *g*, Tr. lobo-cerebellaris caudalis. *h*, Fritsch's commissure. *i*, Ggl. profundum mesencephalici lat. *k*, Ggl. lat. mesencephalici Torus semic. *l*, Valvula cerebelli. *m*, *m′*, *n*, Single portions of the fiber-bundles from the roof (see also Fig. 67). *o*, Nucl. N. Oculomot. and Fasciculus longitudinalis post. *p*, Commissura post.

We turn our attention[1] now to the structure at the base of the inter-

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[1] Seven pages of the original (131 to 137) are here briefly summarized.

brain,—to the *hypothalamus,*— depending largely upon the figures for our medium of expression.

Of the many decussations in the base of the interbrain the most important is that of the tractus optici: *the chiasma.*

Just behind the chiasma, and very closely associated with it, lie the tracts from the *Ganglion ectomamillare* (Fig. 87), which together form the *Commissura post-chiasmatica.*

Somewhat dorsal to them we find the bundles of the *Decussatio transversa,* or *Gudden's commissure* (see Fig. 89). They arise from the most posterior portion of the midbrain, possibly from the Ggl. isthmi, which lies close under the cerebellum (Fig. 88).

Farther dorsal lies a large-fibered decussation whose constituents descend from the gray matter of the central cavity of the third ventricle: the *Decussatio supra-infundibulus.* In the brain of the selachians and amphibians it is easy to get the greater part of the Decussatio transversa in a single section, as shown in Fig. 89.

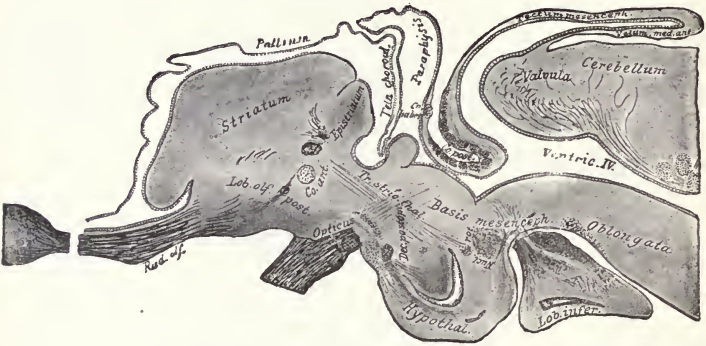

Fig. 86.—Sagittal section of brain of barbel: *Barbus fluviat.*

From the somewhat uninspiring picture which the present condition of our knowledge of the hypothalamus of the lower vertebrates yields let us turn to a more encouraging one.

To the few really well-known tracts in the brain belongs that one which serves the function of vision. The optic nerve has already been mentioned incident to the description of the roof of the midbrain; but, since we find all of its fibers united just anterior to the hypothalamus, it will be profitable to view the whole tract together.

We know at present that parts of the optic nerve arise from the large ganglion-cells of the retina (S. R. y Cajal, Monakow), and we know that another part passes from the roof of the midbrain itself to be distributed in the retina. The retina itself may be looked upon as a system of neurons arranged in strata one above the other. A part of these neurons stand in direct relation to the Opticus, as just stated; while a part are connected with other cells, of the second, third, and fourth orders, propagating the stimulus received by the peripheral neurons of the first order. In the midst lie many cells the distribution of whose processes make it evident that they connect one part of the retina to another.[1]

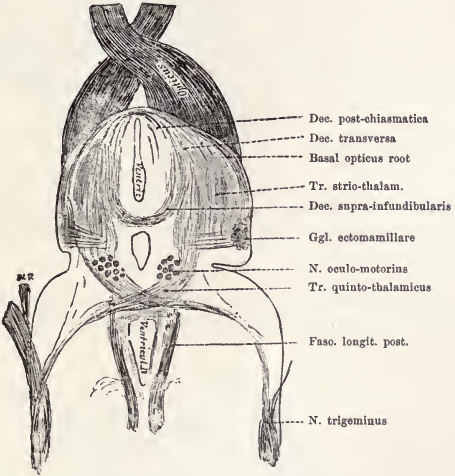

Fig. 87.—Horizontal section through the hypothalamus, chiasma, and medulla of a lizard.

From the eyeball the optic nerve passes into the cranial cavity. In fishes whose eyes are relatively much larger than man's, also in birds, the nerves in question are enormous, and in brain-sections of these animals dominate the field. At the base of the skull they cross in the chiasma, which lies, as above stated, just anterior to the hypothalamus. This decussation is, in most animals, complete, but in some birds and probably in the

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[1] For a more exact description see S. R. y Cajal's monograph on "The Retina." There is a German translation by Dr. Greef.

majority of mammals the decussation is only partial. That probably depends upon the position of the eyes which, in the lateral position, as in fishes, reptiles, etc., have no part of the field of vision in common, while, in the position found in the owls, the ape, and man, the visual field is quite separate only in the lateral portions, the images of the median portion being coincident. So it is explained why careful investigations on the chiasma

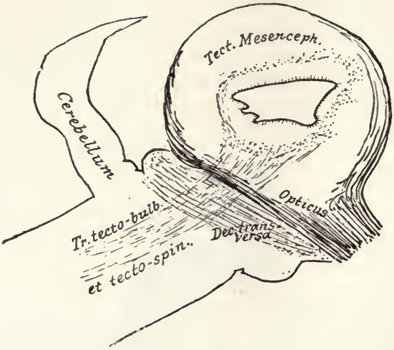

Fig. 88.—Sagittal section some distance from the median line of the brain of *Varanus griseus,* showing the course of the Decussatio transversa from the chiasma to its terminus.

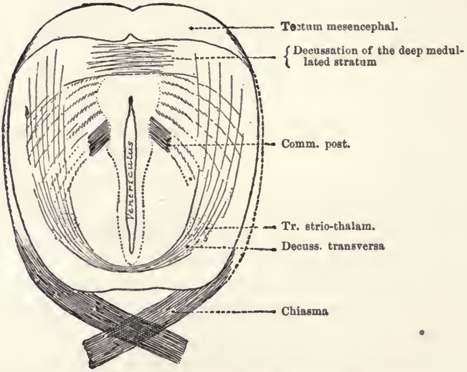

Fig. 89.—Frontal section through the midbrain of *Scyllium canicula.*

have led to very contradictory results over the decussation, according to the animal which the investigator has studied. Possibly the conditions vary even for different individuals of the same species. We are quite certain of the partial decussation in mammals, especially man, where degenerations

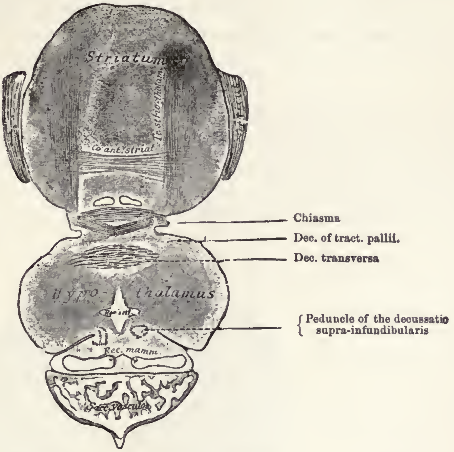

Fig. 90.—Horizontal section through the thalamus of an adult shark: the *Scyllium canicula.*

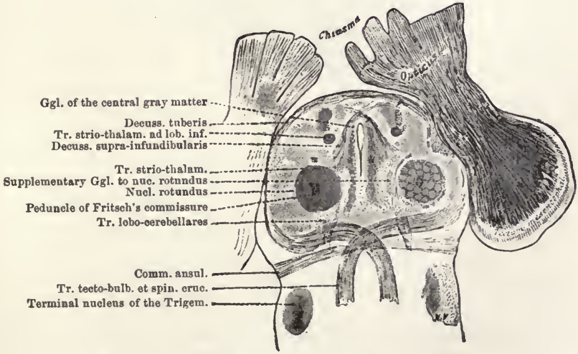

Fig. 91.—Horizontal section through the thalamus of a teleost: *Gobio fluviatilis.*

in the optic nerve after loss of the eyes could be compared with the visual images received during life.

The decussation is not, however, so simple as represented in Figs. 87 and 89. The bundles are plaited together more or less, in fishes one nerve passing through a slit in the other.

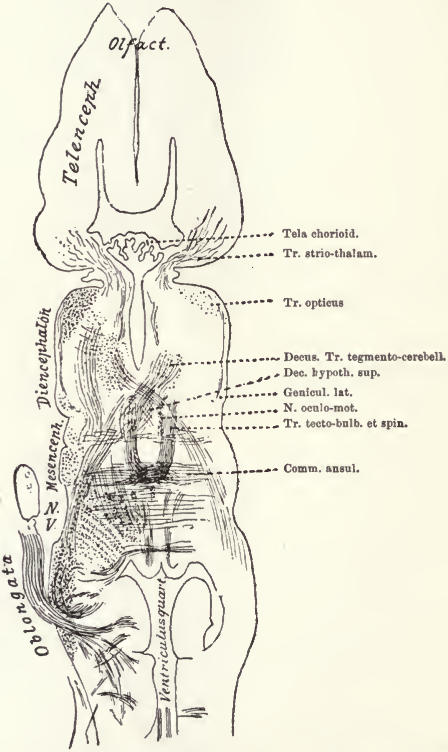

Fig. 92.—Horizontal section through the brain of the *Scyllium canicula* to show the decussations in the base of the brain.

Beyond the chiasma the reunited fasciculi pass backward and upward (Fig. 88), inclose the thalamus, sending into the externally located Corpus geniculatum a large portion of the collaterals from the fibers (compare Figs. 81 and 82). The tract thus becomes little poorer in fibers. Splitting up into numerous branches it now passes to the roof of the midbrain, where it is already familiar to you. These tracts ascending to the corpora quadrigemina might be called the peduncles of the quadrigemina, as they have been in mammals, but it is preferable to retain the term *"roots,"* because these tracts contain in mammals also fibers from the cerebrum.

In Fig. 66 one sees a part of the ends of the optic fibers. One may note here that they stand in close relation to those tracts which arise in the deep medullated stratum of the midbrain. Not only do the dendrites of these cells from which arise the bundles to the sensory nuclei of the medulla and spinal cord dip into the midst of the optic system, but *bundles of axis-cylinders pass into the optic layer* from the sensory fiber-system above mentioned.

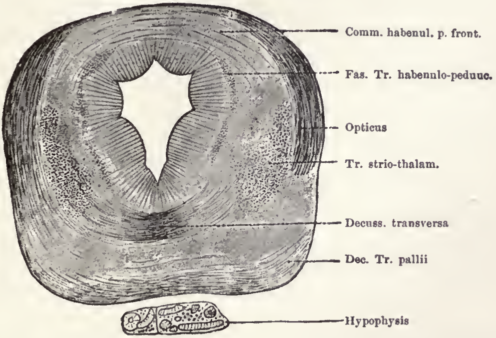

Fig. 93.—Cross-section through anterior portion of thalamus of *Scyllium canicula.*

In mammals a majority of the fibers of the optic end in the Geniculatum laterale and the remainder in the Tectum mesencephali.

We will not leave the consideration of the Thalamencephalon without impressing the fact that this segment of the brain, in lower vertebrates at any rate, is joined to the cerebrum by relatively small tracts. I, therefore, present at the close of this chapter a section from the most anterior portion of the interbrain of the *Scyllium canicula* just behind the Ggl. habenulæ.

Note that nearly the whole section is filled with the opticus and with the commissures associated with the optic system; also a few which correspond to the system of the ganglion habenulæ. Note that to the cerebrum the somewhat ventral bundles of the Tr. strio-thalamici pass out. When the cerebral cortex becomes prominent, as in the higher animals, this tract is associated with those which pass from the cortex into the thalamus and also those which pass through and beyond the thalamus. But even up to mammals in the vertebrate series one can differentiate from the great fiber-systems,—the *Capsula interna,*—severed at this point, the bundle to the striatum: the Tr. strio-thalamicus. But in mammals they play a subordinate rôle as far as size indicates.

CHAPTER XI.

THE CEREBRUM: THE PROSENCEPHALON.

FROM those brain-segments already considered in different classes of vertebrates very varied direct tracts pass into the anterior segment: the cerebrum. In frogs the interbrain only is connected with it; in other vertebrates the midbrain also, and, finally, in mammals it receives a connection with the spinal cord, whose centers are, in other animals, much more independent of it. A direct tract from cerebrum to cerebellum is not known, but even here there is, in mammals, a possible connection through the tegmental nucleus and through the frontal ganglia. *The influence which the cerebrum must exert over the lower centers direct is in varying strength according to the vertebrate class.* This fact, so evident to the comparative anatomist, remained, curiously enough, up to the present quite ignored in the interpretation of physiological and psychological phenomena.

It is important, naturally, to designate which part of the cerebrum is connected with other parts of the brain. You will see at once that especially important tracts, those from the cortex, appear relatively late in the series, and much later still do they reach comparative perfection; indeed, it is only in mammals that such tracts pass to most of the other parts of the brain.

We can imagine a schematic cerebrum. Picture to yourself the ovoid vesicle which evaginates from the common ventricle near the *terminal lamina* on either side. It increases in thickness at the base, forming there a large body: the *Corpus striatum.* In the floor of the vesicle end the olfactory nerve-fibers, and we may at once differentiate the *olfactory apparatus* from the corpus striatum. Thus we have a second—indeed, characteristic—division of the cerebrum,—sometimes, in fact, given the dignity of a position co-ordinate with the brain-segments, and called the Rhinencephalon. The portion which remains of the vesicle—namely, the roof and sides—is called the *Pallium,* or *Mantle.*

The mantle may consist of (1) a simple epithelial plate, as in teleosts; (2) the lateral portions may thicken into nerve-areas, as in cyclostomes; (3) lateral walls and anterior walls may be thickened, as in selachians, or, finally (4) nearly the complete mantle may be transformed into brain-substance, only the most posterior part retaining its epithelial character and persisting as the Tela chorioidea. Thus is constructed the brain-mantle in amphibians and reptiles, in birds and mammals. The development of the mantle is of especial interest. From a small beginning in teleosts it develops into the enormous organ which we recognize in man as the cerebral hemispheres, and with this development progresses the capacity for the higher psychical activities.

Fig. 20 shows well the separate parts of the embryonic human brain, which may serve here as a prototype, since in the depicted one only structures appear which are constant in their recurrence. Study, also, Fig. 55, and note the varying development of the mantle shown in the four sagittal sections given.

I. THE OLFACTORY APPARATUS AND THE CORPUS STRIATUM.

These structures, together with the spinal cord, cerebellum, and midbrain, show, through the whole series, little essential difference.

Except the Ggl. habenulæ and optic system, no other portion of the brain is so constant in structure as the olfactory apparatus. Only the relative size varies; the structural features remain unchanged. For our knowledge of the structure we are especially indebted to S. R. y Cajal, Van Gehuchten, Kölliker (and Edinger).

From the epithelium of the nasal mucous membrane (Fig. 16, *a*) long terminal fibrillæ run backward. They are called Fila olfactoria, and pass through the cribriform plate into the cranial cavity.

Within the cranium they reach, after a longer or shorter course (according to the class), the anterior end of the brain, where they enter within it. The whole bundle, which may be subdivided, is called the *Nervus olfactorius.*[1]

The Fila olfactoria pass to an anteriorly directed evagination of the forebrain-vesicle. This evagination forms on the base of the brain a more or less elongated tube which, in most animals, remains hollow. This tube is called *Lobus olfactorius anterior.* From the place where it passes into the base of the brain begins the posterior olfactory region, which in mammals is called the *Lobus olfactorius posterior.* Since in lower vertebrates the homology is not yet certain, we will designate the anterior simply as *Lobus olfactorius,* and the posterior, which includes the whole base of the brain, as *area olfactoria.*

At the place where the Fila olfactoria enter the anterior end of the olfactory lobe they break up, sometimes, after decussation and exchange of fibers, into very fine terminal ramifications. These enter the apex of the lobe, where they meet the terminal ramifications of cells which lie in that

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[1] The term *Radix olfactoria* would be a better one, since Figs. 15 and 16 show the Fila olfactoria and the "olfactory nerve" to be homologous to the roots of the spinal and of most of the cranial nerves, being the *neuraxons* of the neurons involved.

region. Thus the fine ramification of the olfactory neuron of the I order comes into close relation with the dendrites of cells which represent the olfactory neuron of the II order.

The united terminal ramifications are to be seen, even with low power, on all sections through the apex of the lobe as spherical structures located just beneath the fibers of the olfactory nerve: *Glomeruli olfactorii.* From the olfactory cells of the II order arise new neuraxons, and these pass backward toward the area olfactoria.

The entering and freely decussating Fila olfactoria, the dendrites of the olfactory cells (II order), and the glomeruli together make, at the apex of the lobe, a characteristic picture, which is called *Formatio bulbaris.*

In most animals it makes a swelling anteriorly, which is called the *Bulbus olfactorius.* Sometimes, however, the apex of the lobe is overlaid with the Formatio bulbaris farther back than the visible bulb reaches. Certain amphibians and reptiles especially show a second ovoid bulbar formation on the median side of the lobe somewhat back of the usual position.

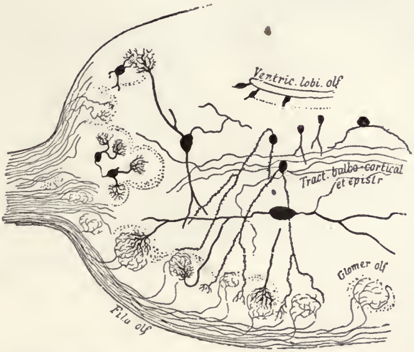

Fig. 94.—Sagittal section through the Bulbus olfactorius of a frog. (After P. R. y Cajal.)

Emerging from the posterior and lateral pole of the spheroidal bulb one always sees the olfactory tract of the II order,—*Tractus olfactorius,*— which, at first, covers the olfactory lobe, but later collects in one or more bundles at its outer side and passes posteriorly. This second olfactory bundle is so large that with the unaided eye it may usually be seen as a white bundle. In several teleosts the olfactory bulb is very large and located far forward in the skull. Thence the tracts pass as two great white fasciculi on either side backward into the brain. They might easily be mistaken for the olfactory nerve, which, however, terminated at the inconspicuous olfactory lobe, and the part of the olfactory apparatus which passes from the lobe to the brain—to the Lobus olfactorius posterior—must be designated the olfactory tract.

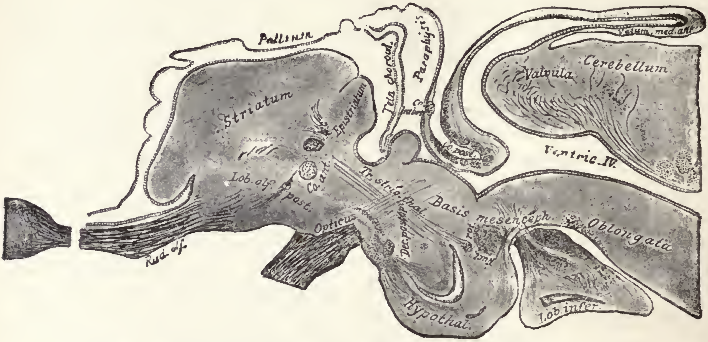

Fig. 95.—Brain of the barbel: *Barbus fluviatilis.* (Sagittal section near the median line.)

In the brain of the barbel (Fig. 95) one sees the long course of the tract, also the entrance of the fila into the bulbus, which lies far anterior to the rest of the brain. In the perch, however, the bulbus is so close to the brain that the olfactory tract (*Rad. olf.*) is very short.

Fig. 96.—Brain of *Perca fluviatilis.* Olfactory apparatus and corpus striatum only shown. (Sagittal section somewhat lateral.)

The posterior end of the secondary olfactory fibers was long unknown until C. L. Herrick was able to show that one part ends in the basal portion of the Lobus olfactorius posterior, and another part farther dorsal in a part of the brain which lies upon the corpus striatum. The author has carefully studied the relations in fishes and reptiles and has determined that, in the recurrence of the same relation in animals so far remote from each other in the series, we have to do with a fundamental principle. This newly outlined portion of the brain, which always lies close to the corpus striatum, I have designated the *Epistriatum.*

The Epistriatum is most sharply defined in the reptilian brain (see Fig. 97), where it is also differentiated in its minute structure (compare also Fig. 118).

In amphibia the fibers of the olfactory tract are, for the most part, nonmedullated, and in birds very sparingly so, since these animals have a somewhat atrophic olfactory apparatus. Hence it has not been possible to demonstrate, in both, the course of the fibers in question or the location of the *Ggl. epistriaticum.* In mammals the tract from the bulb is well known. One sees it pass backward on the base of the brain, and recognizes that bundles pass continuously from it into the Lobus olfactorius posterior, possibly into the cortex of the Lobus olfactorius anterior. The posterior end has, as yet, not been with certainty located. It is possible that the structure known as Nuc. amygdalæ corresponds to the Epistriatum of the lower vertebrates.

Fig. 97.—Brain of the lizard (*Varanus*), showing the course of the median fibers from Bulbus olfactorius and the Epistriatum. Lob. olf. post., with its fibers, not shown.

The median portion of the secondary olfactory tract ends, then, in the Epistriatum, while the lateral portion ends farther ventral in the Lobus olfactorius posterior.

Even in the teleosts—the carp, for example—one sees that, lateral to the large bundles *en route* to the epistriatum—viz., the *median fasciculus*—smaller bundles pass into the area olfactoria. This *lateral olfactory fascicu-*

lus disappears in the midst of the Lobus olfactorius posterior, which, moreover, is not, by superficial examination, to be differentiated from the striatum, whose ventral portion it forms.

The olfactory apparatus of amphibia has not yet been thoroughly studied, but in reptiles and in mammals one can readily recognize that many fibers pass into the base of the brain, into the Lobus olfactorius posterior; also that fibers disappear in the Lobus olfactorius anterior. They plunge in, to break up into fine terminal ramifications and come into relation with the dendrites of the large cells,—here called cortex-pyramids. Corresponding with this distribution, we had to assume two classes of fibers: the *Tr. bulbo-epistriatici* and the *Tr. bulbo-corticales*; in the last-named tract were differentiated fibers for the anterior, and fibers for the posterior portion of the olfactory lobes. Finally a connection probably also exists,

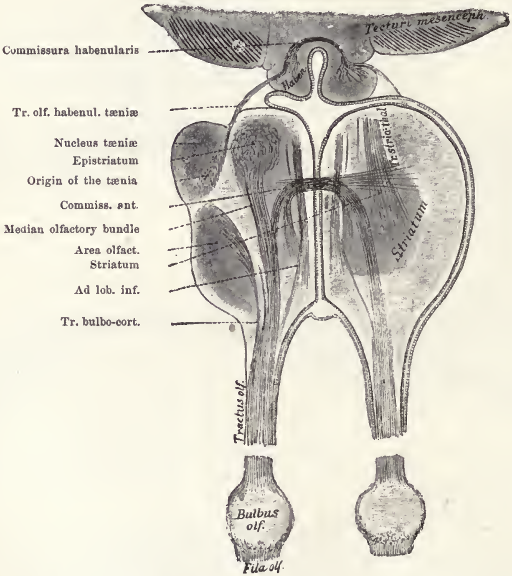

Fig. 98.—Schema of a horizontal section through the brain of *Cyprinus carpio*, showing subdivisions of the corpus striatum; also the course of the olfactory fiber-system.

at least in large reptiles, between the cortex of the olfactory lobes and the epistriatum: *Tr. cortico-epistriaticus.*

The olfactory apparatus, then, as far as described, consists of a combination of at least two neurons: a peripheral neuron of the I order, from the nasal mucous membrane to the bulbus; and a central neuron of the II order, from the bulbus to one of the several termini above enumerated. But from these terminations proceed other tracts of the third, or higher, order. In the first place, the olfactory centers—*i.e.*, the terminations of the II neuron are uniformly connected by a tract with the Epithalamus, especially with the Ggl. habenulæ. Carefully study these relations in Fig. 98.

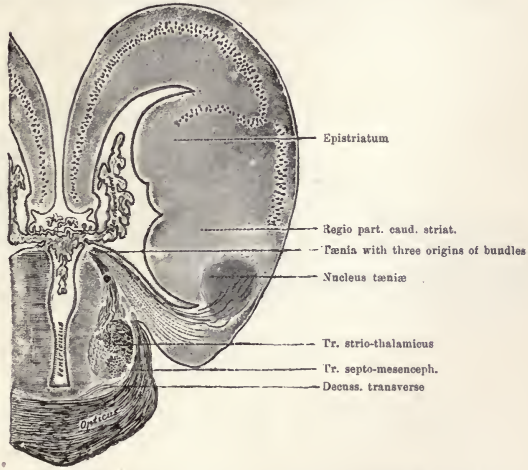

Fig. 99.—Frontal section through the most posterior portion of the Cerebrum of the Swamp-turtle: *Emys lutaria.* Note dorsally the mantle with its cortex, ventrally the transition to the thalamus with the underlying chiasma, at the right the posterior end of the olfactory region.

A second connection passes from the olfactory center to the brain-cortex. This tract might be designated the *Tr. cortico-olfactorii.* It is absent in fishes, is probably present in amphibians and birds, and is well developed in reptiles and mammals.

The cortico-olfactory tract is, as you will find later, the first connection which was established between the brain-cortex and any sensory apparatus. Just because of this important fact this tract will be discussed later in connection with the development of the brain-mantle.

The cortical center of the olfactory apparatus reaches in mammals its highest development. Here there are developed numerous association-bundles, and the surface is enormously enlarged, including whole lobes: *Lobus cornu Ammonis* and *Lobus pyriformis.*

These portions of the brain are to be looked upon as highly-organized centers which receive their stimulation from the lower olfactory mechanism, but which, through their structure, are made capable of extended independent activity.

Thus, in the vertebrate series there is added to the lower olfactory mechanism a higher one, which gradually increases in extent.

Having given a general view of the olfactory apparatus as at present understood for the vertebrates, let us study in the accompanying figure (Fig. 100) an ideal sagittal section through a lizard-brain, where the parts already described may be again viewed, with their connections. The olfactory lobe lies anteriorly, covered by the Formatio bulbaris, into which the Fila olfactoria from the nasal mucous membrane pass. Posterior to the Lobus olfactorius lies the Area olfactoria, and still farther back the Nuc. tæniæ (*Tub. Thæn.*), above which are the epistriatum and striatum. Over the whole is spread the mantle, which bears the cortex. Except for the mantle connections, which appear first in the amphibia, the schema holds for all vertebrates. That the cortical connections are not absolutely essential to the sense of smell is demonstrated by the fact that fishes have a finely developed olfactory apparatus, but possess no sort of a cortical connection.

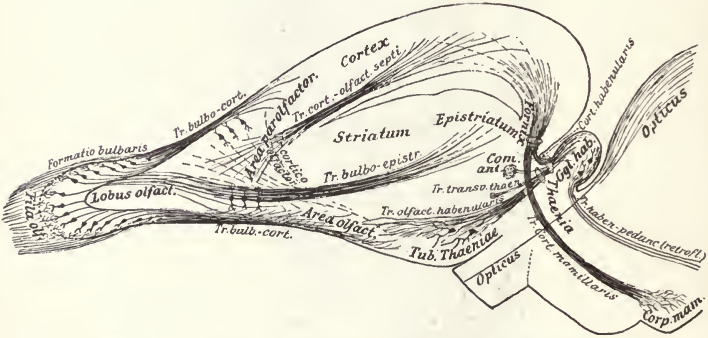

Fig. 100.—Schema of the olfactory apparatus of a lizard-brain.

All portions of the brain which are in any way brought into relation with the olfactory apparatus are connected with the corresponding portion of the opposite side through strong commissural fibers. These bundles all cross the median line at one place, designated the *Commissura anterior.* This commissure lies in the Lamina terminalis near the base, and is exceedingly constant (Figs. 18, 76, and 100). The various bundles are best known at present in the reptiles. Everything now known indicates that the relations are the same in the other vertebrates as in reptiles.

The commissures of the olfactory apparatus are shown schematically in Fig. 101.

II. THE CORPUS STRIATUM.

The *Corpus striatum* lies above the olfactory apparatus. It is a somewhat ovoid body which projects up into the ventricle of the cerebrum from the base of the cerebrum, occupying the same place in all animals from the fishes to man.

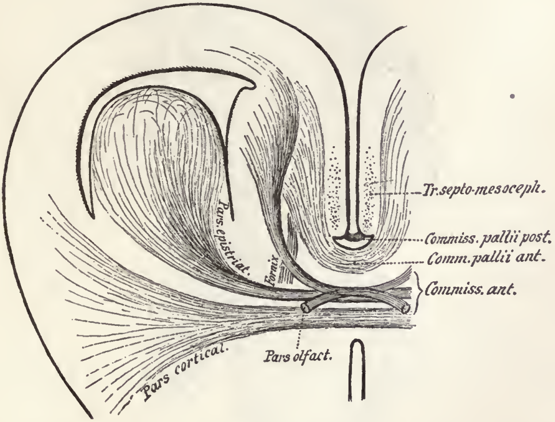

Fig. 101.—Schema of the commissures of the olfactory mechanism of the reptile (compare Fig. 98). *Pars epistriat.*, Epistriatic commissure. *Pars cortical.*, Commissure of olfactory cortex of one hemisphere with that of other. *Pars olfact.*, Ramus connectens Lobi olfactorii.

It is not usually to be seen in the uncut brain, because it is covered in by the brain-mantle, and lies really in the floor of the enmantled ventricle. Only in fishes, where the mantle is represented by a thin membrane, is it to be recognized through the mantle. In this case it forms what is called the frontal lobe. The more highly developed the mantle,—as in mammals,—the more unimportant appears the structure—so large relatively in the lower vertebrates. In the figure of the cod-fish brain (Fig. 38) one recognizes the corpus striatum in the large prominence at the frontal end. If one wished to change this figure to represent a mammalian brain, he would have to draw the hemispheres, wholly wanting in the teleosts, over the basal structures of the forebrain. The figured fish-brain is to be compared morphologically to a human brain, from which one has dissected off the hemispheres, leaving the striatum *in situ*.

The investigations of V. Gehuchten on teleosts and those of the author on reptiles, established the fact that, from the great multipolar cells which lie just in the center of the striatum, large bundles of fibers arise; also that fibers which come to that organ from behind end there in ramifications.

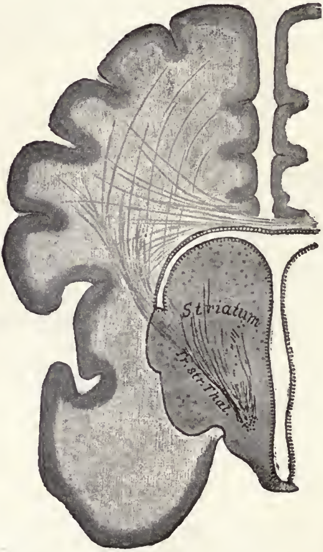

Fig. 102.—Frontal section of the forebrain of a teleost, bounded above by the columnar epithelium, which incloses the ventricular cavity. The fish-brain is drawn within the contour of a mammalian brain in order to show the relation in size and position of the structures under consideration.

The whole fiber-system has been previously designated the *basal forebrain-bundle*; but since all of its fasciculi end in the ganglia of the thalamus or metathalamus, a more appropriate name would be *Tr. strio-thalamici.*

This tract has already been encountered in the description of the interbrain. A careful review of Figs. 72 and 80 will be profitable in this connection.

Through the *Tr. strio-thalamici* the basal ganglia of the forebrain are most intimately connected with the ganglia of the interbrain. These tracts are exceedingly constant, and, though they are recognized with especial ease in teleosts because of the lack of other fiber-systems from the forebrain, yet it is possible to demonstrate them in amphibians (Figs. 75 and 80), in reptiles (Figs. 72, 81, and 82), in birds (Figs. 83 and 84), and in mammals. They are naturally less prominent in the last, where the fiber-system from the cortex to the interbrain and to parts of the brain located still farther posterior is especially highly developed. Their discovery was first made possible through embryological methods; later, also, through the study of degenerations. If one remove the whole mantle from a dog's brain,—a feat successfully accomplished by Monakow on the newborn animal and by Goltz on the adult,—all the bundles which arise from the mantle degenerate, and those which arise from the striatum remain *intact.* In the stained section these are brought out into prominence. In Fig. 102 it has been attempted to make the mantle more clear by inscribing a section through the corpus striatum of a teleost within the contour of a human brain. One sees at once that the fiber-system of the striatum falls in the region which in mammals is designated as the anterior limb of the *Capsula interna.* In the teleost the thin mantle is insignificant in comparison to the striatum; in mammals the relation is nearly reversed; but in birds, where

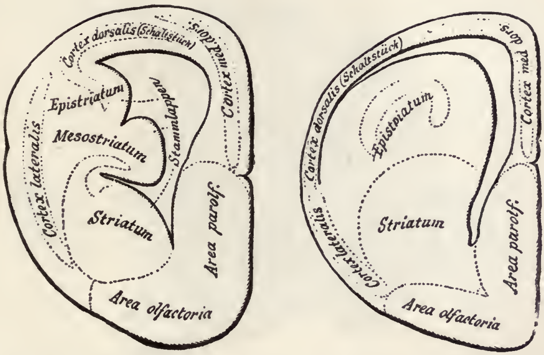

Fig. 103.—Diagrammatic frontal section through the brain of a turtle (left) and of a lizard (right).

the corpus striatum reaches remarkable size, it makes the major part of the forebrain, notwithstanding the presence of a fairly developed mantle.

In turtles the enormous development of the basal ganglia, especially the development of a *mesostriatum,* and of the epistriatum and the disappearance of the lateral horns of the ventricle makes a cross-section which is completely different from the brain of other reptiles, and reminds one strongly of the bird-brain (study Fig. 103).

The chelonian brain, with its enormous basal ganglia and slight development of the mantle, is more like the avian brain than is any other reptilian brain.

The *Corpus striatum* of birds and mammals is, up to the present, well known only in its principal features; much yet is lacking to furnish a clear understanding of it, especially in its subdivisions. The author's experiments in degeneration show one thing, however: Neither in reptiles, in birds, nor in mammals can one through removal of the corpus striatum cause degeneration of parts posterior to the midbrain. This indicates that *that important and constant structure, the striatum,* confines its efferent fiber-system essentially to the thalamus and the hypothalamus. The individual bundles of the strio-thalamici are developed to a varying degree, according to the size of the thalamic ganglia to which they go. For example, the bundle to the large hypothalamus in the teleost is enormous,—*Tr. strio-hypothalamus,*—while in other animals it is often difficult to find.

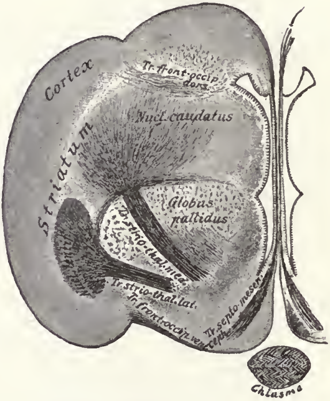

Fig. 104.—Frontal section through the brain of a parrot. A somewhat schematic composite of several serial sections into one figure.

The higher vertebrates—the birds and the mammals—manifest in the structure of the corpus striatum an especial construction. In mammals it is divided into a lateral and a median portion by fibers from the cerebral cortex which bisect it. The lateral portion is designated as the *Putamen* and the median portion as the *Nucleus caudatus.* Several ganglia—*Globus pallidus*—lie on the median side of the Putamen, whose nature is not yet understood, and which are so closely associated with the Putamen that they are grouped with the latter and the whole ganglion-complex called the *Nuc. lentiformis.* This will be more fully discussed subsequently. In birds the Putamen and both portions of the Globus pallidus are demonstrable, but the divisions of this portion of the striatum from the Nuc. caudatus is not so sharp as in mammals, because the fibers from the cortex which, as *Capsula interna* in mammals, separates the two portions are in birds only slightly developed. Notwithstanding that, one can with certainty recognize in birds that from the Putamen, located extremely laterally, a thick bundle passes inward, where it meets those fibers which arise in other parts of the striatum. The two bundles together pass to the nuclei of the thalamus (see Figs. 83, 84, and 104).

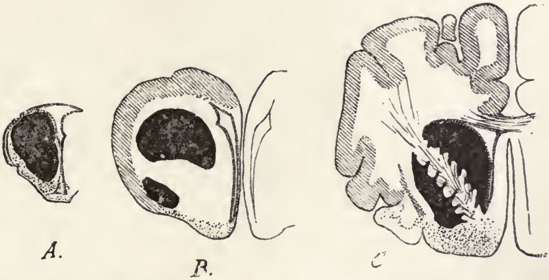

Fig. 105.—Schematic frontal sections of the forebrain, to show the position of the striatum and its fiber-system in relation to the whole. *A*, Brain of a Teleost; *B*, of a Bird; *C*, of a Mammal.

Thus the Tr. strio-thalamici are composed in the bird, as in the mammal, of a median bundle and of one which joins it from the outer side. The lateral bundle includes in mammals the greater part of the fibers of the cerebral base which pass down from the cortex. It is there called the "loop" of the Nucleus lentiformis. The median portion corresponds in birds and mammals according to its position exactly the same as is shown in Fig. 102 for the fish-brain. Thus it belongs to that collection of fibers which is designated as the *Capsula interna.*

Of the physiological significance of the corpus striatum we know nothing at all. All experiments carried out on the brains of fishes have only induced disturbance of the sense of smell when the anterior lobes were severed. Up to the present no animal from which the striata alone had been removed has been observed for any considerable time. This operation seems to be possible only in the teleosts, where there is no mantle to complicate the operation.

Even for the olfactory apparatus, experiments which throw light upon it are few. It has become possible only through the experiments of the last years to give it the anatomical dignity of separating it into different territories. Probably the comparative observation of animals with a cortical olfactory apparatus and animals without it will lead to the desired results.

The questions are: Do fishes smell in the same manner as do the higher vertebrates? Do they interpret their olfactory impressions differently? Are they able to retain these impressions in their memory?

CHAPTER XII.

THE CEREBRUM, OR PROSENCEPHALON (*Continued*).

III. THE CEREBRAL MANTLE.

WITH the olfactory apparatus and the corpus striatum, we have described everything that is common to the Prosencephala of all vertebrates. We come now to the consideration of the variable portion of the forebrain, namely, the *Mantle.*

As mantle, or pallium, we have designated all of those portions of the wall of the cerebral vesicle not included in the olfactory apparatus and the striatum; that is, the dorsal and lateral walls of the cerebrum. It has already been mentioned that in several lower vertebrates the largest part of it is formed of a simple epithelial plate. Of the epithelial mantle of the teleost Figs. 86 and 107 furnish a sufficient picture. In cyclostomes portions of the wall on either side of the basal ganglion extend upward, ending in a folded epithelial membrane. Studniczka has recently designated these structures as lateral areas of the mantle. Their minute structure is, however, too little known to justify a decision. It is possible that we have to deal here with simply a dorsally directed extension of the striatum. In rays and sharks, representatives of the selachians, the mantle is developed; indeed the most anterior portion is so enormously thickened and the lateral portions project so far inward that in the greater part of the forebrain of selachians the ventricle is obliterated, and in rays it is to be demonstrated in only the most posterior portions. In most sharks it is present, and even its projections into the olfactory lobes are to be recognized. But even here, since the anterior wall of the brain is disproportionately thickened, it projects mostly far over the region of origin of the olfactory lobes, so that they do not lie anteriorly, as in the other vertebrates, but laterally and remote from the frontal portion of the cerebrum. In this way the brain of the selachian diverges much in form from the brains of other vertebrates, as is shown in Fig. 106. It thus comes that through the thickening of the walls the division into hemispheres is often so masked (Fig. 106, *B*) that it is only recognizable microscopically through the finer fibers and through the narrow vascular cleft between the right and left hemispheres.

In the mantle of all other vertebrates a deep groove separates the right from the left ventricle. It reaches posteriorly to the Lamina terminalis, near which the cerebral vesicles have evaginated. All of the commissures which join the hemispheres to the striatum traverse the Lamina terminalis (see Fig. 101). In mammals for the first time there arises late in the embryonic period, dorsal and anterior to the Lamina terminalis, a new system of transverse fibers destined to connect cortical regions of one hemisphere with those of the other: *Corpus callosum.*

The mantle of higher vertebrates is differentiated from those of teleosts and ganoids through a very essential feature. It is no longer simple epithelium, but consists of numerous cells which receive and send out nerve-fibers; that is, the mantle has become a nervous mechanism. This mechanism, which is not much developed in the amphibians, reaches, in the reptiles, the condition of a well marked brain-cortex, differentiated from the other layers of the mantle.

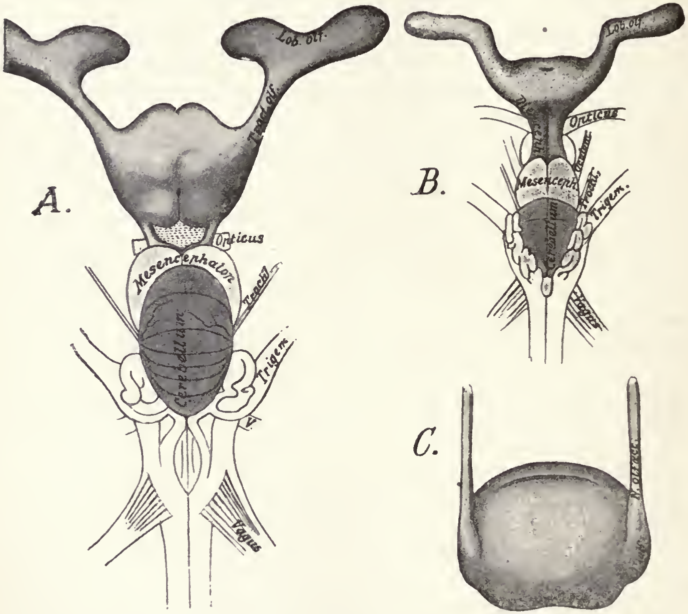

Fig. 106.—Selachian brains, showing the various development of the brain-mantle in different species. *A*, Brain of *Galeus canis*; *B*, of *Raja miraletus*. *C*, The cerebrum of *Carcharias*. All are shown in natural size. In *A* the Tela chorioidea is removed, giving a glimpse of the ventricle of the Thalamencephalon.

There is no other part of the brain which approximates the cerebral mantle in the great changes in the progression and retrogression manifested; and, since this is involved in the existence of certain higher psychic activities, let us now proceed with the consideration of the most interesting field of brain-anatomy.

First, as to the outer form. What has already been said regarding the selachian mantle has shown that in that class of vertebrates only the anterior region of the mantle is of nerve-tissue, but that larger or smaller portions—according to species—of even the posterior part of the mantle have given up the character of simple epithelium.

Note in Fig. 107 the thin mantle of the trout as compared with the enormous thickening which the anterior portion of the mantle has undergone in the ray (Fig. 108). Then note that in the amphibia (Fig. 109) the thickening has progressed much farther posterior. Further note that the brain of the reptile, with its already developing cortical substance (Fig. 110), forms a transition to the birds, on one side, and to mammals, on the other side (Figs. 111 and 112).

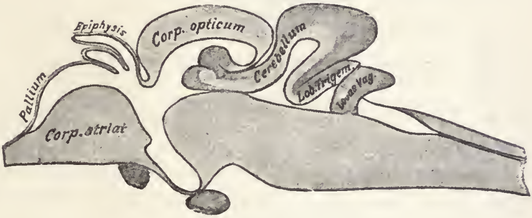

Fig. 107.—Schematic sagittal section of an embryonal teleostean brain (trout).

In our description of the hemispheres, which we will always find in amphibia and upward in the vertebrate series, it will be best to take as a starting-point the *ovoidal form.* In amphibians and reptiles the smaller anterior end of the ovoid merges into the olfactory lobes, while, on the median side,—the one turned toward the other hemisphere,—there takes place so marked a flattening that only a vertical cleft remains between the two halves of the brain.

In the midst of the cleft the two halves of the brain are connected by the unpaired Lamina terminalis, which passes in a convex line from above downward and forward. But the hemispheres have been developed, not only anteriorly from the Lamina terminalis, as is stated in the embryological introduction. They usually extend dorsally as well as ventrally from the lamina. The dorsal portion is directed posteriorly and may be designated as the *Polus occipitalis pallii.*

The ventral projection, which is present only in a rudimentary form in amphibians and reptiles (Fig. 113), should be called *Polus temporalis.* Into both these poles the ventricular cavity extends, forming a *posterior horn* and an *inferior horn.*

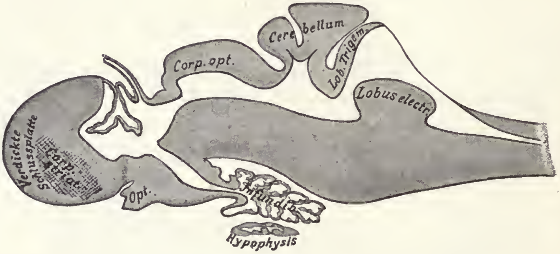

Fig. 108.—Sagittal section of a selachian brain (the ray).

The nearly ovoid hemispheres of the amphibian correspond most closely to this schematically described brain. But even in the reptiles the outer form manifests quite marked variations in the development, according to the families. When one finally passes up through the birds and mammals he soon meets the widest variations in form.

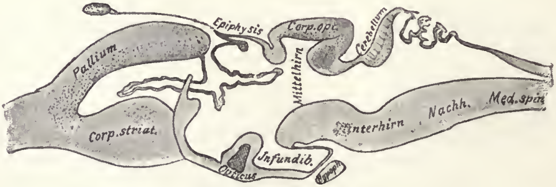

Fig. 109.—Sagittal section of an amphibian brain.

At first there is, in amphibians, a hardly noticeable groove between the olfactory lobe and the mantle, running outward and downward on the margin of the mantle, called the *Fovea limbica.* This groove, separating the olfactory apparatus from the mantle, is always clearly marked in mammals. The development of the individual poles offers essential differences. Some have suggested for the Polus frontalis of the lower vertebrates the term frontal lobe, for the Polus occipitalis, temporal lobe, etc. But this is incorrect, since that which bears the name in mammals is a product of late development. For example, the occipital lobe of mammals does not exist at all in reptiles. It appears for the first time in birds. The occipital lobe is not alone a prominence of the occipital pole, but a definite portion of cerebrum with a specialized cortical character and a fixed relation to the origin of the Opticus.

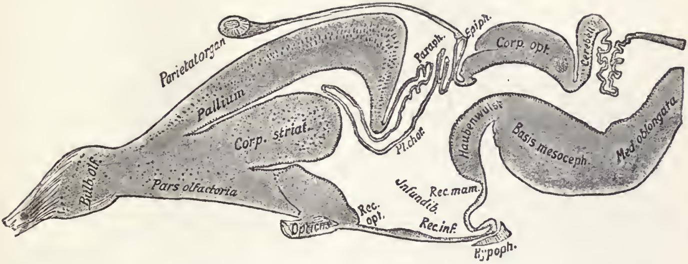

Fig. 110.—Schematic sagittal section of a reptilian brain.

So we find that even in the lower vertebrates the form of the brain varies in different orders. When, for example, one compares the above illustrated lizard-brain with that of a turtle the compressed form of the latter will certainly be apparent. It is brought about, on the one hand, by the development of the striatum, which, as above described, causes a simi-

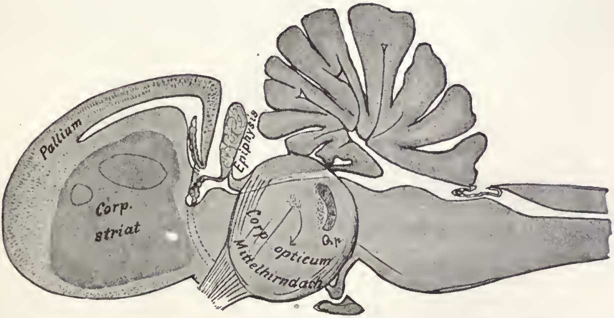

Fig. 111.—Schematic sagittal section of an avian brain.

larity between the turtle-brain and the avian brain; and, on the other hand, by the development of the skull, which is never without influence.

In higher vertebrates with the great development of the mantle appear the grooves, or sulci. Since they are particularly developed in the mammalian brain, they will be minutely described in a later chapter. The brains of most reptiles possess only the Fovea limbica as boundary between two different portions of the mantle. However, there is recognizable in the large snakes and still better in turtles another shallow groove, which lies near the upper edge of the mantle and extends for a shorter or longer distance parallel to it. In birds this *Fovea collateralis* is more clearly developed. It is not a real sulcus such as traverse the mammalian brain. We have to do here with a ventral and dorsal projection of the mantle, which is dependent upon the

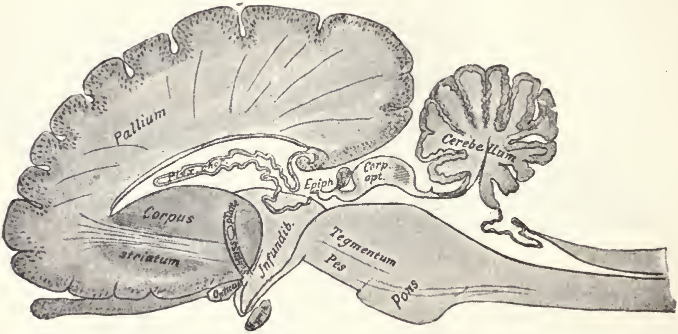

Fig. 112.—Schematic sagittal section of a mammalian brain.

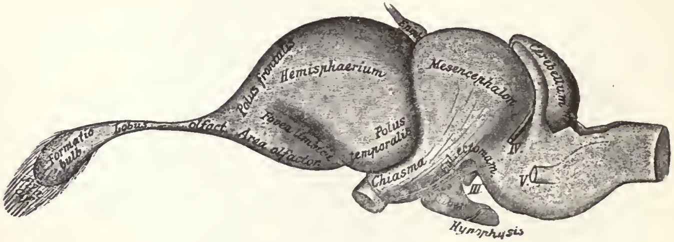

Fig. 113.—External view of the brain of the lizard: *Varanus*. (Enlarged four times.)

development of the striatum (see Fig. 105, *B*). Between the two projections remains the groove, which has been designated the Fovea collateralis.

Somewhat more complicated than the arrangement of the outer aspect of the hemispheres is that of the median wall. In the amphibia this wall has undergone so little differentiation, that in certain species—indeed, in different specimens of the same species—it may be grown to the adjacent wall of the other hemisphere for a greater or less distance.

Such is not the case in reptiles. While all the features to be here described are present in amphibia in a rudimentary form, it is only in the highly organized reptilian brain that they come out into prominence. Here one can easily make several subdivisions, subdivisions which, as will be brought out later in the description of the mammalian brain, will serve as important points of departure in following its further development.

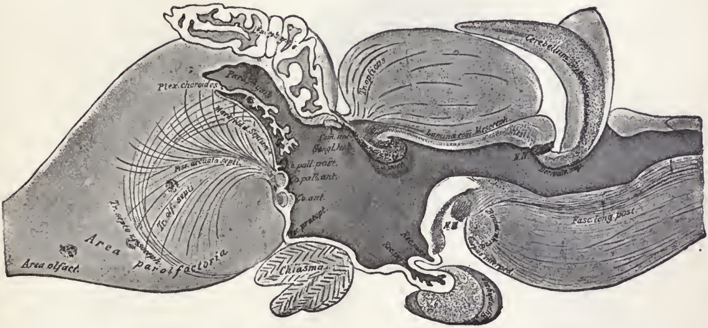

Fig. 114.—Inner wall of a hemisphere of the reptilian brain: from *Varanus griseus.*

1. The median surface of the olfactory apparatus near the base: *Area parolfactoria.* In reptiles there are prominent aggregations of ganglia here, which give rise to bundles of fibers.

2. Posterior to this and somewhat farther dorsal lies that portion of the median wall designated the *Septum,* which also contains a ganglion in reptiles, in birds is strongly atrophied, while in mammals, again, it contains a small ganglion and is called the *Septum pellucidum.*

3. Dorsal to the two portions named is the *cortical portion* of the *inner wall.*

In the dorsal portion of the area parolfactoria there begins regularly a deep sulcus, which, running to the Lamina terminalis in the upper margin of the septum, divides the whole inner side into a dorsal and a ventral portion. Only the dorsal portion is covered with cortical tissue. This sulcus, which thus forms the ventral boundary of the brain-cortex, persists throughout the whole animal series after its appearance in the reptiles. In the accompanying figure (114) it is called *Fissura arcuata septi,* but in mammals it is called the "inner marginal fissure."

Into the cortex which covers the dorsal portion of the septum an important bundle regularly enters: the *Tr. olfactorius septi.* It arises from the olfactory apparatus of the base of the brain; its fibers converge toward the median brain-surface, thence pass upward and backward into the cortex. The region in which it ends is, on this account, called the olfactory cortex. In amphibia, with uncertainty, demonstrable; this bundle is always prominent in reptilia and mammalia (see Fig. 114). In birds, however, it is veiled by a bundle, which is especially developed in these animals—*Tr. septo-mesencephalicus*—and which, arising in a wide origin from the dorsal portion of the cortex near its edge where it turns outward, is spread out upon the inner surface of the avian brain like a broad, white fan. Reaching the base of the brain, it encircles it with externally directed fibers, and just anterior to the optic tract, which it reaches on the lateral aspect of the brain, passes again upward and backward to disappear in the most anterior portion of the roof of the midbrain. Thus this tract connects the midbrain with a particular cortical region (Fig. 115). It is foreshadowed in reptiles, but has not been located in mammals.

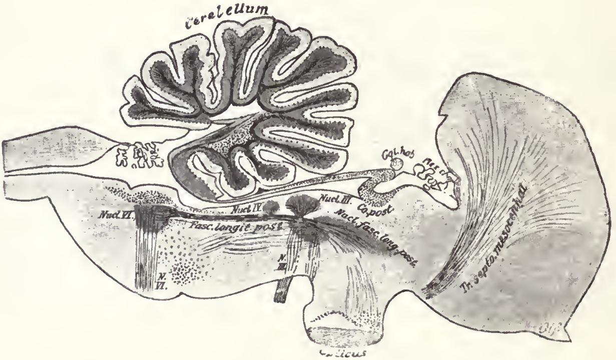

Fig. 115.—Sagittal section through the brain of a chicken.

If one makes a frontal section through the forebrain of any of the higher vertebrates, the more anterior sections always show an approximately oval outline on whose base the corpus striatum lies (see Fig. 103); farther posterior (Fig. 101) one finds the septum on the inner wall, which loses its previously simple features; and finally one comes (Fig. 99) to the place where the mantle merges into the choroid plexus and becomes purely epithelial (Fig. 120). At this point in the base of the brain the boundary between the forebrain and the interbrain is usually reached, and one sees upon the sections the tracts which unite these two segments of the brain.

The author assumes that this brief description illustrated by the figures has sufficiently familiarized the reader with the outer form of the cerebrum, and will now describe the structure of certain parts of the mantle.

As the cross-sections of the whole amphibian brain is strikingly like the embryonic brains of the other vertebrates, so even in the forebrain a structure will be found which always recurs in higher vertebrates in the embryonic period. Thus, one can, in a section through the cerebral wall, usually differentiate only two layers: an inner one rich in cells and an outer one sparsely filled with cells. At several places in the mantle,—near the olfactory apparatus, for example,—in the anterior part of the Regio parolfactoria, and then in the postero-median region of the mantle the inner layer shows especial projections: evidently a greater development of the cells which constitute it. Good sections well stained show that the inner layer next to the ventricle is formed of epithelial cells, which send their long branching processes up through the entire mantle to the outer surface, thus making a frame-work for the brain-mantle (see Fig. 116, the left margin). This frame-work, formed of the terminal processes of epithelial cells, is, besides this, present, also, in all portions of the brain posterior to this, and is persistent even in the reptilia. In birds and mammals a large part of the terminal processes disappear in post-embryonal life. Then, farther outward

Fig. 116.—Section through the mantle of a frog-brain. (After Pedro Ramón y Cajal.)

there are numerous cells, which, for the most part, cannot be recognized as ganglion-cells, but rather retain the character of neuroblasts throughout life. Between them, however, lie true ganglion-cells, with profusely branching dendrites and slim neuraxons. The majority of these neuraxons may be traced upward toward the brain-surface; but a small minority take their course between the ganglion-cells and the epithelial cells, and mark the beginning of the *subcortical medullary layer.* Whither they go in amphibia is not known, but it is probable they go mostly in the commissures of the mantles. From single fibers which pass outward from this subcortical medullary layer and from those which pass direct from the cells to the surface of the brain there is formed just under the surface of the brain a fine net-work: the *tangential reticulum.* Besides the two sources named, the neuraxons of cells which lie in the tangential reticulum itself participate in the formation of the net-work.

This quite irregularly disposed apparatus must be looked upon as the fundament of a brain-cortex, because in reptiles one finds just the same elements, only in much greater number and thickness, arranged, furthermore, in more regular and unmistakable strata. In these animals no further doubt can exist that one has in this structure to deal with a cortex, from which, as we shall see later, the highly specialized and well known cortex of higher vertebrates may be derived.

It is, indeed, one of the greatest services which S. Ramón y Cajal has bestowed in the field of brain-anatomy that he has demonstrated the *type* which recurs in the structure of the brain-cortex in all classes of vertebrates and that he designated the features that characterize a brain-cortex. The author's own investigations on amphibia and reptilia coincide throughout with the important discovery of the Spanish *savant.*

A most essential feature of the cortical structure, and one always recognizable, is the fact that these fibers originate and end, and that there exist innumerable possibilities for the association of incoming and outgoing fibers.

In the cortex of the reptile one may from without inward differentiate (1) the *tangential* layer of fibers, (2) a *molecular* cell-layer, (3) a layer of *pyramidal* cells, (4) the layer of the *Plexus subcorticalis,* (5) the *medullary center,* and (6) the *ventricular epithelium* (compare Fig. 117).

This relatively simple apparatus is, however, so constructed, even in vertebrates of so low rank as the reptiles, that it affords an almost infinite possibility for combinations of single cells and tracts (study, again, Fig. 117).

But the cortex is not, by any means, uniform over the whole mantle. Even in reptiles one can differentiate particular cortical areas one from another. The author would differentiate at least three separate areas in the cortex of the reptile (see Fig. 103), to which might be added as a fourth the cortex on the Conus frontalis pallii, which belongs possibly to the olfactory apparatus; furthermore, this area sends out a separate bundle which probably ends in the thalamus. Of those cortical portions depicted in Fig. 103, the one designated as dorso-median area is especially interesting. It covers the whole median side of the brain, passes the dorso-median edge, extends out laterally over the outer surface of the brain, and includes that olfactory bundle mentioned in the last chapter. External to this and separated from it by a narrow cleft lies another interesting cortical portion. This, the *dorsal area* or plate, covers not only the dorsal portion of the outer wall, but turns toward the median line on the ventral surface covering the epistriatum. These relations are preserved throughout life in the turtle. They are well shown in Fig. 118. Note, also, in this figure how the medullated tangential layer bends inward toward the epistriatum. Note, also, the Tr. bulbo-epistriaticus. Ventral from the dorsal plate lies the *lateral plate,* which adheres closely to the striatum (is possibly identical with it), called, in mammals, the *Claustrum.*

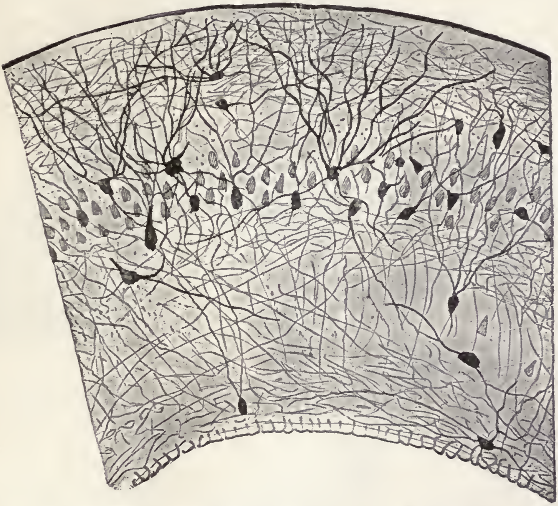

Fig. 117.—Section of cortex near median dorsal edge of the mantle of *Lacerta agilis.* Golgi staining.

It is interesting to note that the cortical area which receives the oft-mentioned olfactory bundle remains on the inner edge of the hemisphere, not only in the reptiles, but also in mammals. In most reptiles it presents a smooth surface, but in several species one recognizes that it experiences an increase in area through folding. In mammals this folding reaches the extent of a complete rolling in of the whole cortex, at least in adults, while in the embryonic state the relations are the same as in reptiles, where the structure first made its appearance (see Fig. 119).

This rolled in portion of the cortex that always receives a bundle from the olfactory apparatus has long since been designated as the *Cornu Ammonis.*

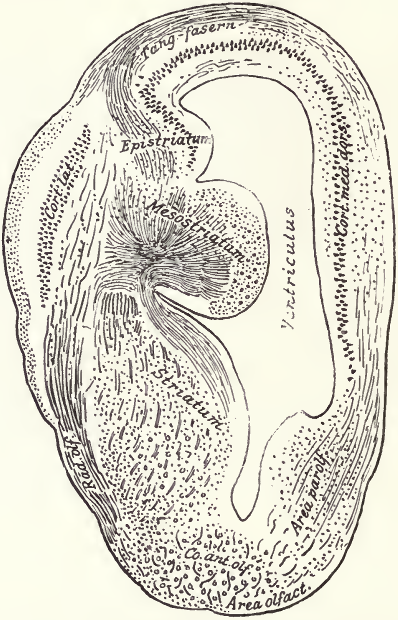

Fig. 118.—Frontal section through a hemisphere of the giant turtle: *Chelone midas.*

The investigation of the amphibian brain makes it very probable that exactly the corresponding region of the mantle-wall receives olfactory connections.

Broca, and later Zuckerkandl, demonstrated, after numerous comparisons, that in mammals the extension of Ammon's horn and the cortex lying anterior to it under the limbic fissure is completely dependent upon the development of the olfactory apparatus; so dependent that, in aquatic mammals with atrophied olfactories, this cortical area is demonstrable only in rudimentary form, while in the burrowing rodents it may attain an enormous development.

Through these investigations the demonstration seems complete that the cortical portion just described is the cortical center for the sense of smell.

Not only does a fiber-system end in the Cornu Ammonis, but a bundle arises from it and commissures enter it. A large assortment of fibers come into relation with this cortical area. Before they enter they all distribute themselves along the ventral margin and form an important collection of nerve-fibers designated the *Fimbria*. The fimbria always occupies the same position in all vertebrates; it accompanies the ventral margin of the cornu, and, therefore, in reptiles lies dorsal to the Fissura arcuata septi. In the posterior portion of the hemispheres where the median wall of the brain merges into the Plexus chorioideus the fiber-system of the fimbria lies between these structures and the cortex. Let us now consider the fibers which arise in the olfactory cortex, and also the commissural fibers.

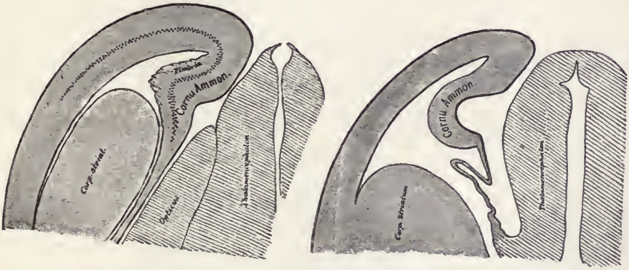

Fig. 119.—Section through the posterior portion of the left hemisphere: *A*, of a Lizard—*Varanus griseus*; *B*, of a Mouse-embryo.

Reptiles and mammals which have well-developed olfactory cortices, probably also amphibians and birds, possess two bundles which characterize this cortical region and always occur in the same place. The two bundles are generally together designated the *Fornix*. But it is more advisable to subdivide the bundle into two parts according to their terminations. Coming from the posterior part of the olfactory cortex they together pass a short distance ventrally to about the level of the commissura anterior, and then they turn toward the posterior. Here the previously united bundle divides into two parts: one bundle going to the Ggl. habenulæ,—*Tr. Cortico-habenularis,*—and another one to the *Corpus mamillare* on the base of the hypothalamus,—*Tr. cortico-mamillaris* (see Fig. 100). The latter, especially, is a well defined bundle easily followed in its course, long known in mammals as the *Fornix column.* In birds it is very thin. In birds and reptiles the fornix passes in a rather straight course from its origin to its terminus. But in mammals, where, through the great development of the mantle, the olfactory cortex recedes far to the posterior and in part bends ventrally (Figs. 132, 133, and 143), the *Tr. cortico-mamillaris* must follow the margin of the hemisphere and run a rather long arcuate course before it can turn down to the corpus mamillare just behind the commissura anterior.

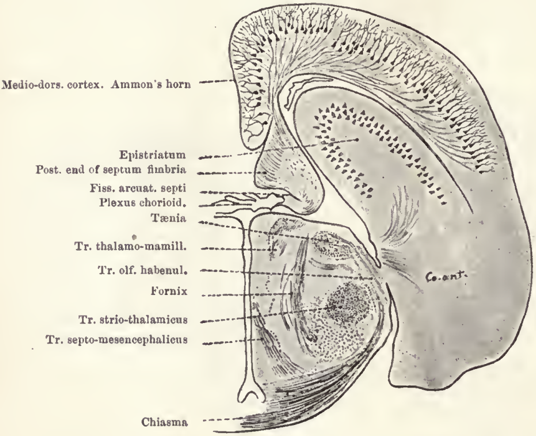

Fig. 120.—Frontal section through the posterior cerebral portion of the giant snake: *Python bivittatus.* Dorsal, the mantle; ventral, the transitional region of the Thalamus.

Besides the Fornix system the olfactory cortex is characterized by a commissural system which connects the right side with the left. Its bundles are designated as *Commissura ant.* and *post. pallii.* In mammals the whole complex is called the *Psalterium.* In the lowest orders of mammals it forms the only mantle commissure; in the higher orders there is a second commissure, the *Corpus callosum.* The latter connects mantle-areas which do not belong to the olfactory apparatus, and is usually, especially in man, much larger than the commissures of the olfactory mantle, because, as we shall see later, of the high development of mantle not yet described. The corpus callosum always lies dorsal to the olfactory commissure and is naturally correspondingly longer and thicker the more the mantle is extended. It is longest in apes and in man and shortest in rodents and in insectivora.

The physiological significance of the brain-cortex has come to be known through a great number of admirable studies on the mammalian brain in the course of the last twenty-five years. The experiments upon animals and the observations upon man, observations which daily lead to new and interesting results, have yielded the following: *The cortex may be accepted as that part of the brain which serves as the basis of the highest psychic functions. Upon the normal existence and condition of the brain-cortex depend all of those abilities which may be acquired by study, nearly all of those activities which are executed by the use of memory-pictures, and especially all of those psychic processes which we term associations.*

One may conceive the whole cortical apparatus as a gigantic association-center, to which from without through relatively narrow tracts such impressions may be conducted as have already found their first termini in deeper centers: *primary brain-centers.* From this cortical association-center tracts pass down to more posterior brain-regions which are adapted to call forth movements, etc., through their agency. The sum of all these tracts is designated *Corona radiata.*

That which determines the size and extent of the cortex-bearing mantle is not the usually narrow tracts, but the development of the association-fibers which afford the possibility to receive the afferent sensory impressions in the very greatest variety of ways, to inhibit or suppress, to evaluate, to associate with previously received ones, and finally to harmonize the activities with acquired memory-pictures. We know also that special activities are performed by special cortical areas; that the cortex subdivides into a number of separate regions which are functionally different. Numerous investigations of the last years have made us more definitely acquainted with the surface of the mammalian brain-mantle. The results of these investigations taught us that certain areas, varying according to the species, are more developed, and certain ones less so. Our knowledge of the physiological significance of these cortical areas is, in many cases, slight, but it is the task of the immediate future to study the development of these cortical areas: a task which, happily, is already undertaken for certain species of mammals.

Thus, since, according to the present state of our knowledge, the cortex may be accepted as the location of those psychic functions which are consciously executed after consideration, through use of memory-pictures, so is the demonstration of a cortical bundle to the nucleus of a special sensory apparatus of great interest to comparative psychology.

Hence it seems to me the most important result under consideration up to the present time, that we have been able to demonstrate that *the first cortical area developed in the animal kingdom was the olfactory cortex.* The olfactory cortex is the cortex of the dorso-median area, because just this area is where the fibers from the terminus of the secondary olfactory tract end. A clew which could throw light on the functional significance of other cortical areas in reptiles has not been found. They may belong to the olfactory apparatus, but not necessarily so.

That the oldest cortex represents essentially only a single sensory center—the olfactory center; that all associations which serve them as a foundation, all memory-pictures which they retain, are such as serve especially the sense of smell; these facts furnish a point of departure for new investigations in the field of comparative psychology. Studies in animal psychology have, up to the present time, been based upon too complicated psychic phenomena. We must first know what sensory impressions a lower animal may *receive*, what it may *retain*, and how far—directly or through associative thought—it is able to *interpret* these impressions. Then only shall we be prepared to approach the complicated problems which have usually been attempted.

Let us now turn back to the purely morphological considerations, and determine first how, in the course of the vertebrate series, other tracts have been associated with the cortical olfactory tracts; how the complicated apparatus which we see in the mammalian brain came to be.

Unfortunately there is not much that can be reported. There are everywhere gaps in our knowledge, everywhere it requires more diligent collaboration in the field only recently discovered.

We have set aside the olfactory center while we studied the connections which joined the olfactory apparatus with the cortex. Though we may not find with certainty also in reptiles another and similar connection, we may turn to the avian brain, which will furnish a number of other bundles connecting the cortex with parts of the brain lying farther back.

Most interesting to me from the stand-point of comparative psychology is the bundle which arises in the occipital region of the brain, passes forward to bend sharply downward and backward, and thence passes to the termini of the optic nerve in the midbrain. The *Tr. Occipito-mesencephalicus* is so enormously developed in the pigeon that it appears to be one of the very largest bundles of the whole brain. The reptiles possess, apparently in the same location, a thin bundle; it is not, however, absolutely certain. A pigeon in which one has severed this bundle appears to be blind in the eye on the side opposite the severed bundle, taking its bearings with difficulty and always with the eye that has the uninjured central visual field. We know that up to mammals and man there exists such a tract from the primary optical centers to the occipital lobes, and I will show later how in mammals all of those functions which we conceive as "seeing with understanding, recognition and interpretation" are dependent upon the entirety of the occipital lobe. *Thus, in birds, first in the series, the primary optical apparatus is connected with the cortical mechanism.* Undoubtedly a greater capacity for service is thus made possible for the visual apparatus.

It will now be more easily understood how birds work—in part—with very highly developed possibilities for visual memories. The interpretation of olfactory impressions may be sufficient for the supply of life-necessities for the earth-groveling lower vertebrates, but for birds the same thing would not be advantageous. For, flying far above their food, their homes, etc., they must be able to recognize these by sight, and, more than that, to differentiate them from all other similarly appearing objects. Recall in this connection the unerring swoop of the bird of prey upon its victim; the migrations, the certain return of the carrier-pigeon, etc.

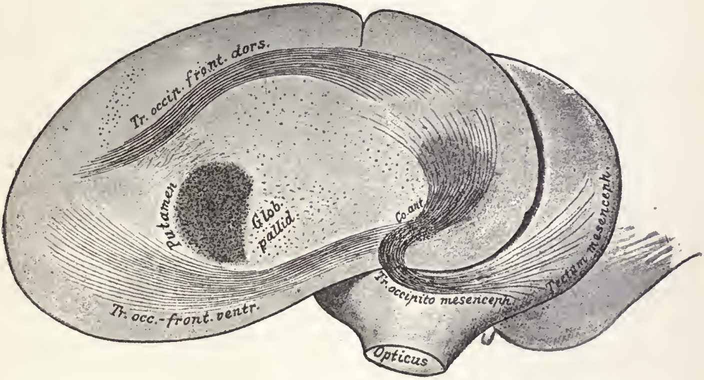

Fig. 121.—Composite of several lateral sagittal sections from a pigeon's brain showing the course of the Tr. occipito-mesencephalicus.

Another bundle which arises in the cortex of the avian brain has been mentioned already—the *Tr. Septo-mesencephalicus* (Fig. 115). This stands in close connection with the terminations of the optic nerve and with the sensory functions of the midbrain. Regarding the functions whose bearer it is we know nothing as yet with much certainty. Its severing does not cause disturbance of vision (Jensen), nor does it cause indubitable motor disturbances.

We are yet far short of answering the question which presents itself at once after these observations: What functions has the primary end-apparatus—*i.e.,* the deep center—of the sensory nerves in the brain? We know simply what occurs in mammals when they are deprived of their connection with cortical center. Now, it is not at all improbable that, in the measure that the psychical activity of the cortex increases, the activity of the deeper center decreases. Fortunately we possess in the teleosts organisms which possess no cortex at all and only the lower centers. On these new observations should be instituted. It is asked: What is the reptile more capable of accomplishing in the realm of *smell*—in the interpretation of his olfactory perceptions—than a fish, now that it is demonstrated that to the olfactory apparatus of the reptile a cortical center has been added? Similar investigations are needed for the visual apparatus, since a difference must exist between the vision of a teleost, whose optic tract ends in the midbrain, and that of a bird or mammal, which possesses, from the primary optical center to the cerebral cortex, a tract which meets there an extension association-apparatus.

The brain-cortex enters into connection with a number of connections which are located far posterior to the cerebrum. These come into prominence for the first time in all their complexity in the mammals, and we shall have to study them more closely when the mammalian brain is under consideration. But as low in the series as the reptiles one finds a portion of the *Corona radiata* coming from the frontal pole and ending probably in the Thalamus—*Tr. cortico-thalamicus.* This very cortico-thalamic connection becomes later very strong, as already incidentally mentioned in the description of the thalamic nuclei. Other very thin fasciculi of the *Corona radiata* have been observed in birds, but, since their termini are insufficiently known, their enumeration would be of little interest here. Though there are in reptiles and birds no cortical connections to parts which lie posterior to the thalamus, yet such connections occur in mammals more and more in the ascending animal series. The cortex becomes ever larger, ever more important for the activity of the animal organism when the mechanisms which develop under the influence of use and thought are perfected.

The great importance of the brain-cortex for activity in association is evident, not only from the observations which have been made on animals deprived of cortical areas and on men with diseased cortical areas, but also from its structure, since, as you have already seen, the cortex of the reptiles affords extraordinarily great possibilities for association of afferent impressions. Innumerable contacts connect there the cells and the tracts of the most varying provinces. In birds, but still more in mammals, there are still several long bundles which pass from one portion of the cortex to another. These are called *Association-bundles.* In Fig. 121 there may be seen depicted in the pigeon two of these bundles which are for the purpose of connecting the frontal with the occipital segment of the mantle. The dorsal one passes close beneath the cortex, while the ventral one passes over the surface of the mantle, just like the fibers of the layer of cortical association (see also Fig. 83).

The mantle of birds is, so far as we now know, not much more extended than that of reptiles. Only in the frontal portions, and then in the occipital lobe,—appearing here for the first time,—does it manifest any essential progress.

In order that you may quite clearly recognize the development of the brain-mantle,—the increase of the cortical area,—I present in Fig. 123 a reptilian brain which I have inscribed within the brain of one of the lowest mammals: a marsupial. The reptilian brain is so inscribed that the two *Psalteria* coincide (see page 172).

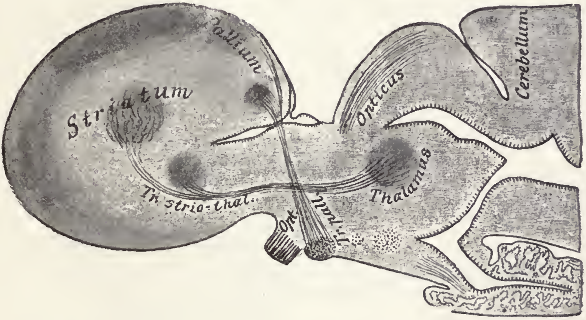

Fig. 122.—Sagittal section through the brain of an adult ray.

The similarity of the two brains is at once apparent; one notes that the Gyrus limb—*cornu Ammonis*—of the one corresponds to the same feature of the other; indeed, one recognizes that the olfactory tract, which enters into Ammon's horn anteriorly from the base, exactly corresponds in the two figures. Compare especially Fig. 114, where, in the brain of the lizard, this bundle appears just like the above. But this experiment has not its sole significance on the morphological side. It should also show especially in what directions the farthest development of the brain proceeded, using the reptile's as a starting-point. In the first place, one recognizes that from the brain of the reptile to that of the marsupial is a much shorter step than that from the brain of the marsupial to the brain of man.

But only in mammals does the mantle with the cortical portions become a powerful structure which leaves the striatum far behind in size, and grows out over the posteriorly located interbrain and midbrain, even extending beyond the cerebellum in man. Very highly developed brains show, besides this posterior growth, also a bending of the posterior half of the mantle ventrally (Fig. 136).

The most anterior part of the hemispheres—the frontal lobes—make their appearance only in the highest mammal, viz.: man.

From the great cortical extension of the mammalian mantle comes a great mass of fibers; others pass into it. These fibers, collectively designated the *Corona radiata,* pass from the cortex posteriorly, to end in the thalamus, cerebellum, medulla, and spinal cord. Other large bundles traverse the hemispheres, connecting one territory of the mantle with another.

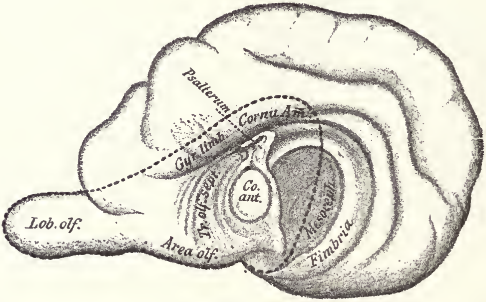

Fig. 123.—The brain of a marsupial (*Thylacinus*), within which the brain of a reptile is so inscribed that the Psalteria coincide (compare Fig. 114). (After Flower.)

All of these taken together form under the cortex a great mass of white, medullated substance, whose extension is relatively greatest in man; in lower mammals it is only small, in many—the mouse, for example—it is quite unimportant.

While the Corona radiata passes backward, it courses between the two nuclei of the striatum and associates itself with the fibers arising from them. The whole fiber-complex is designated as the *Capsula interna.* How the capsule is composed of fibers from the cortex and the striatum may be seen in Fig. 102, which shows a mammalian brain with that of a fish inscribed.

But all of these outgoing and incoming fibers lie in the brain-mantle closely associated into a bundle which spreads out anteriorly. If the cortical apparatus is disproportionately larger, if it is more strongly developed in its individual features, then it must spread out over this smaller radiate bundle of fibers into folds. Such brain-folds, or *Gyri*, are lacking in only a few mammals (lissencephalic mammals); in all others they are present in greater or less abundance (gyrencephalic mammals). The arrangement of the folds, convolutions, or gyri, which is constant within certain limits for single animals, depends, indeed, upon two factors: (1) upon the extension of the brain-cortex which the species in particular has acquired in the course of development, and (2) upon the relative size of the cranial cavity, which naturally must not proceed in equal steps with the cortical development, since it is dependent upon other factors.

One can, therefore, recognize no progressive development of brain-fissuring within the animal series or even within a single family. For example, in the Monotremata the Ornithorhynchus has a perfectly smooth brain, while the Echidna has a richly convoluted one. Even among the Primates the ape, Hapale, has a brain which is almost completely free from convolutions.

Not only on the richness of convolutions, but also on the course of the convolutions, the two mentioned factors have an influence. When the brain-surface of man is better known to you it will be advisable to cast a glance at the various directions of the sulci in the animal series.

It is the object here to show how, from modest beginnings, is developed that great organ—the Mantle—which, as bearer of the highest psychic activity, predominates over the lower brain-centers.

The subject having now been developed to that point, the comparative anatomical treatment of the subject should be brought to a close.

If the foregoing presentation has been attentively followed, two points will not have escaped the reader, namely: (1) *that in different classes the different brain-segments may be developed in varying degree*; (2) *that there are really lowly organized brains in which no single part has reached a high development.* Furthermore, the brain and spinal cord of the urodelate amphibians is, in the main, very little different from that of larval or embryonic stages of higher animals. The medulla and spinal cord, especially, correspond to those of the human embryo of about the second and third month. In fact, the observation of tailed amphibians—the anura takes a somewhat higher rank—teaches us that they lead a soulless dream-life and that they are capable of psychic activities hardly recognizable to us now.

In comparative psychological questions we still stand quite in the beginning of our knowledge. That anatomical investigation can here usefully co-operate—indeed, that to it it is granted to gain a certain insight just where pure psychological observation is not yet sufficient—has possibly been shown in these chapters in which the genesis of the brain has been followed.

PART III.

THE SPECIAL ANATOMY OF THE MAMMALIAN BRAIN, WITH ESPECIAL CONSIDERATION OF THE HUMAN BRAIN.

CHAPTER XIII.

THE FORM-RELATIONS OF THE HUMAN BRAIN.

ACQUAINTED with the fundamentals which characterize the central nervous system of vertebrates, we will now give our attention especially to the mammalian brain. Seeing, as you have, how it has been slowly evolved through a long series of transitional forms, it will certainly be gratifying to investigate the entire structure, somewhat more thoroughly, in an example of the highly specialized brains. The preceding description has directed your attention principally to the morphology, and to some extent the psycho-physiology, of the central nervous system. At present, however, we must attempt to make good the demands which medicine, far advanced as it already is in the diagnosis of nervous diseases, must necessarily make of the physician.

The old physicians have studied and described the human brain almost exclusively; thus we have the best knowledge of its form-relations. The numerous investigations on brains of those who have suffered *intra vitam* from nervous affections, investigations which we again owe almost entirely to physicians, have increased our knowledge to such an extent that it is now possible, in a measure, to survey and describe the human central nervous system more accurately—at least in its most important relations.

Although these chapters are not intended for beginners, but for students who are already acquainted in general with the grosser anatomy of the human brain, it will not be entirely superfluous to review these relations. These outlines of the map, on which later all the points of importance are to be designated, are once more accurately established by recapitulating what has previously been learned. Guided by embryology, you certainly will easily understand the morphological relations presented by the adult organ.

A fresh brain is laid on its base. You will notice at once the great fissure which separates the hemispheres; and the fissure of Sylvius, which arose with the development of the temporal lobe. Since the forebrain has grown over most of the other parts of the brain (see Fig. 19), these latter could be made visible posteriorly by raising up the hemispheres and uncovering them. It can also be accomplished by separating and partially removing the hemispheres. The second method is more advantageous, because a better view of the lateral ventricles and the corpus striatum is thus obtained. Let us, therefore, proceed in that manner.

The knife held horizontally passes simultaneously through both hemispheres, and removes sections two to three millimeters in thickness. The first and second of these sections contain very much gray cortex and relatively little of the inclosed white matter; but even in the third section a large, white, medullary field is uncovered in the middle of each hemisphere. This is the *centrum semiovale.*

In it run all the tracts which pass down from the cortex and a portion of the fibers which unite the various regions of the brain with one another.

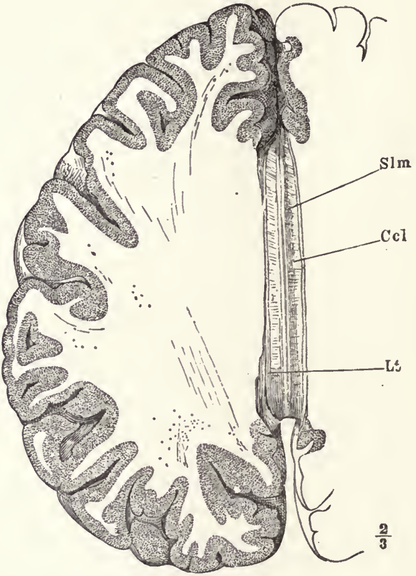

Fig. 124.—Forebrain from above. The hemispheres have been removed down to the level of the corpus callosum (*Ccl*). The white space between *Ccl* and the cortex is the centrum semiovale. *Lt,* Ligamentum tectum or stria longit. Lancisi: a part of the cortex which borders on the corpus callosum. *Slm,* Striæ longitudinales mediales: long, white bundles of fibers which interlace on the middle of the corpus callosum. (After Henle.)

On examining Fig. 22 we should expect that on farther section only a thin epithelial layer would be found lying over the ventricles in the median line, between the hemispheres. This is not the case, however. During a later embryonic period dense masses of fibers have grown transversely over the ventricles from hemisphere to hemisphere (at *a*, in Fig. 22). For this reason, therefore, the ventricle is not found at the bottom of the great fissure, but the *corpus callosum,* as this mass of transverse fibers is called. The corpus callosum is now divided, and, after removing what white matter still remains

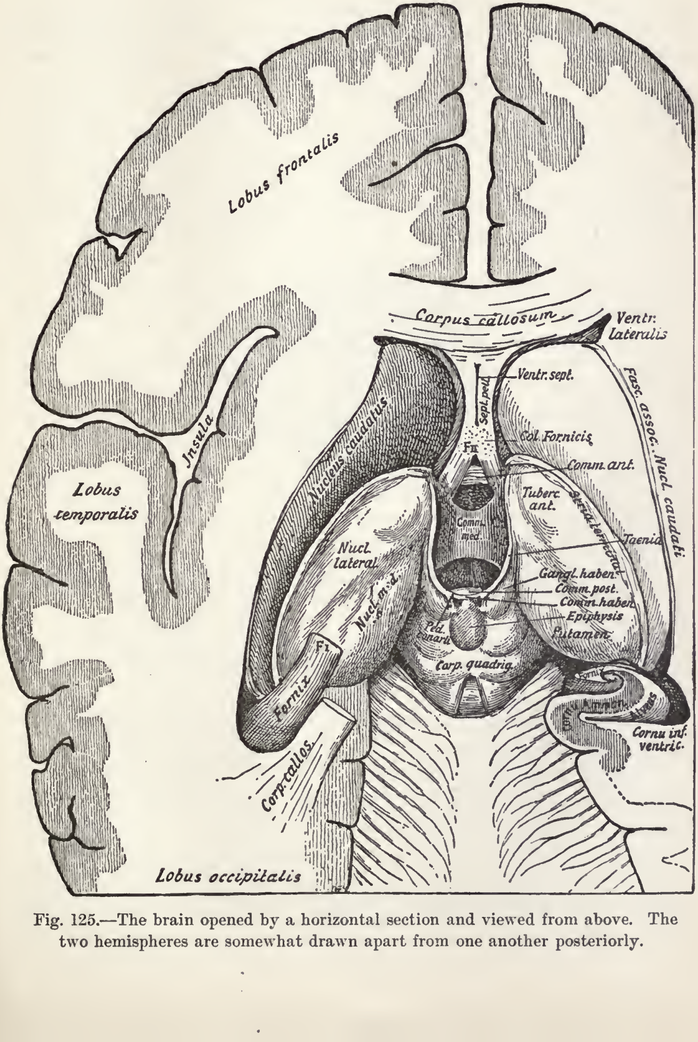

Fig. 125.—The brain opened by a horizontal section and viewed from above. The two hemispheres are somewhat drawn apart from one another posteriorly.

over each lateral ventricle, it is cut off anteriorly and posteriorly. It is then seen that it is united by its under surface to thin, white bundles of fibers, which, arching over the cavity of the ventricle, descend anteriorly and posteriorly into the depth of the same. They belong to the *fornix.*

The fornix is a combination of bundles of fibers which pass continually along the edge of the hemispheres. They arise, on each side, from the mesial border of the inferior horn as the *crura fornicis* (Fig. 125, posterior); then converge over the posterior portion of the thalamus and unite with one another above the ventricle to form a broad tract: the *corpus fornicis.* In the angle where they meet a number of fibers pass across them transversely, thus forming a triangle. This triangle is known as the *lyra Davidis,* or *psalterium.* It lies under the posterior end of the corpus callosum and, for the most part, is united with this. At this point, consequently, the corpus callosum lies close to the edge of the hemisphere. It occasionally happens, however, that the fornix is situated at some distance from it; a small cavity, the *ventriculus Verga,* is then observed between the fornix and corpus callosum. In the anterior part of the brain the corpus callosum recedes constantly from the edge of the hemispheres, and a portion of the inner sagittal wall of the hemisphere remains between it and the ventricle. This portion of the median wall, situated below (posterior, in the horizontal section) the corpus callosum, is the *septum pellucidum.* That part of the great fissure found between the two septi is called the *ventriculus septi pellucidi.* Imagine the corpus callosum removed in Fig. 125; the continuation of the wall of the hemisphere into the septum and the significance of the ventricle are then evident at once. This is not a true ventricle, but, as already stated, only a portion of the fissure between the hemispheres covered over by the corpus callosum.

The fornix naturally borders this portion of the wall of the hemisphere also. It again divides at the anterior end of the corpus callosum into two bundles, the *columnæ fornicis,* which descend in front of the thalamus as a posterior thickening of each membrane of the septum pellucidum, and terminate provisionally at the base of the brain at the boundary-line between the forebrain and interbrain.

The corpus fornicis has been removed, along with the corpus callosum, in Fig. 125 and only the anterior and posterior portions remain visible. In the right, where the section passes somewhat deeper through the white substance, the fornix is divided in that part known as the fimbria. It there lies near to its point of origin, the cornu Ammonis. On the left I have divided it just where it arches over the surface of the thalamus.

Unite the points F and F^1 by a gentle curve passing over the thalamus, and the course of the fornix is reproduced. It will also be clear to you from the accompanying median, longitudinal section through an embryonic brain.

You observe there that, arising from the apex of the temporal lobe, it arches over the interbrain in a curve and descends in front of this to the boundary between the forebrain and interbrain.

After the fornix, and the *plexus chorioideus* attached to it, is divided and cut away, a view of the opened ventricles is obtained (Fig. 125). The unpaired ventricle lying in the median line is the cavity of the primary forebrain, now called the *ventriculus tertius.* At its anterior end the fornix ascends from below. Then, on each side of the fornix there is found a communication of the ventriculus medius with the ventriculi laterales: the *foramen Monroi.* The part of this ventricle which lies in the frontal lobe is called the anterior horn, the part in the occipital lobe the posterior horn, and that in the temporal lobe the inferior horn. A finger could easily be introduced into each of the horns. The basal regions of both hemispheres are connected with one another by means of the *commissura anterior.* The bundles of white, medullated fibers composing it are seen passing across in front of the pillars of the fornix.

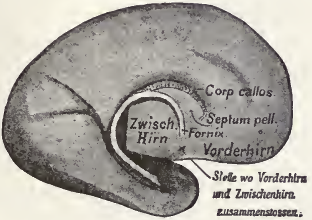

Fig. 126.—Inner aspect of the embryonic hemisphere shown in Fig. 23. Shows the inner lower border of the hemisphere, which becomes thickened into the white medullary line of the fornix. The latter, however, only becomes medullated after birth. *Zwischenhirn*, Interbrain. *Vorderhirn*, forebrain. *Stelle*, etc., Point where the forebrain and interbrain meet.

The *nucleus caudatus* rises from the floor of the lateral ventricle. Farther posteriorly parts become visible which no longer belong to the hemispheres: the interbrain (*thalamus opticus*) and the midbrain (*corpora quadrigemina*). Behind these is seen the roof of the hindbrain (the *cerebellum*).

The cavity between both thalami, the ventriculus medius, was at one time the cavity of the interbrain-vesicle. It is closed in above by the plicated plexus chorioideus, at the posterior end of which lies the conical projection, the *corpus pineale,* now become solid. The floor of the interbrain, which is naturally formed in front by the embryonic terminal lamina, consists of gray matter descending like a funnel toward the base of the brain. This protuberance is called the *tuber cinereum*, its cavity the *infundibulum*. In Fig. 125 it is not visible, but may be seen in the median section shown in Fig. 133 and in front of the chiasma (*lam. t.*) in Fig. 135.

The fissure between the thalamus and the nucleus caudatus is traversed by a long vein, beneath which is constantly found a slender tract of white fibers: the *stria terminalis*, or *tænia semicircularis*. Isolated depressions may be more or less distinctly recognized on the surface of the thalamus. They separate from one another the elevations which correspond to the thalamic ganglia.

The *tuberculum anterius*, the arched surface of the nucleus anterior thalami, is always demonstrable. The line of division between a mesial and a lateral thalamic nucleus is also pronounced at times. The entire thalamus is covered within by the central gray matter, which is connected for a short distance with the gray matter of the opposite side to form the *commissura mollis*. At the extreme anterior end the pillars of the fornix dip into this gray matter. Near the place where this occurs a small bundle of fibers is seen on each side to ascend from below, reach the surface of the thalamus, and pass backward close to its mesial edge. It then passes, anteriorly to the midbrain, for the most part into an elongated body, the *ganglion habenulæ*, on the dorsal edge of the thalamus. The bundle is called the *tænia thalami*, and forms an afferent pathway, passing from the olfactory apparatus at the base of the brain to the interbrain.

A part of the tænia, receiving other fibers on its way, passes farther backward posterior to the ganglion habenulæ, and then runs to the other side directly in front of the pineal body. The portion between the ganglion and the pineal body is called the *pedunculus conarii*, because the body appears to rest on it.

The decussation of the bundles lying just in front of the epiphysis is designated as the *commissura habenularum*. This decussation lies directly dorsal and anterior to the commissura posterior, from which in most cases it is not separated at all (see Fig. 144 also).

The gray mass of the thalamus is overlaid by white fibers, the *stratum zonale*, which, in part, pass into the optic nerve. An enlargement of the posterior portion of the thalamus, the *pulvinar*, forms the chief point of origin of these nerves. The largest part of the optic nerve disappears in this ganglion and in a protuberance which lies on its under side: the *corpus geniculatum laterale*.

The tracts of nerves from the hemispheres, which were situated deep down between them and the interbrain, emerge in great part from the cerebral mass posteriorly to the interbrain, and then lie exposed as two thick strands on the under surface of the midbrain. Taken together, they are called the *crura* of the brain, or the *pedunculi cerebri*.

The roof of the midbrain commences behind the pineal body. The commissura posterior, the crura of which pass backward through the midbrain, is regarded as the most anterior portion of its roof. The corpora quadrigemina, appearing just behind this commissura, will be considered more closely later.

Only the mesial portion of the corpus striatum, the nucleus caudatus, is visible if the brain is opened, as has just been done, from above downward. The lateral portion, the nucleus lentiformis, lies deeper and is covered by the medullary masses passing over it into the capsula interna. It could be exposed by opening downward outside of the nucleus caudatus. A better idea of its form is obtained, however, by making a frontal section transversely through the entire brain at the point in Fig. 125 where the thalamus begins, just behind the thickest part (caput) of the nucleus caudatus; that is to say, just posteriorly to the ascending pillars of the fornix.

Fig. 127.—Frontal section through the brain of the adult. Explanation in the text.

It is not very difficult to understand the section (Fig. 127) made in this manner, if the relations shown in Fig. 22 are borne in mind. The wall of the brain is decidedly thicker than during the fœtal period, but the corpus striatum still projects from the floor into the cavity of the ventricle, as in that section. The outer fissure is now obliterated, since the coronal fibers from the cortex have increased in late embryonic life. At the bottom of the great fissure the ventricle is seen to be covered by the dense transverse fibers of the corpus callosum. To these there ascend from below the two pillars of the fornix, leaving the ventriculus septi pellucidi free between the thin membranes of the septum pellucidum. They project freely into a cavity: the lateral ventricle. This cavity is bounded without by the corpus striatum. Just here it may be beautifully seen how the corpus striatum is penetrated, and apparently divided into two ganglia, by the thick masses of fibers forming the internal capsule. In the lenticular nucleus—that is to say, in the outer part of the corpus striatum—three divisions are easily distinguished. Only the outer one of the three parts, the *putamen* (shaded heavily in Fig. 127), is regarded in common with the *nucleus caudatus* as a source of fibers. The significance of the two inner parts, *globus pallidus,* is not clear as yet. Sometimes the globus pallidus consists of three or more divisions. Externally to the lenticular nucleus there lies a thin, gray mass in the wall of the hemisphere known as the *claustrum.* The space between it and the lenticular nucleus is called the *capsula externa.* Still farther out lies the cortex of the *island of Reil.* The gray mass in the floor of the middle ventricle belongs to the wall of the infundibulum, the *tuber cinereum.* With its continuations, it is spoken of as the *central gray matter* of the ventricle. At the point where this central gray matter and the cortex of the temporal lobe are continuous with one another there lies a large, roundish nucleus: the *nucleus amygdalæ.* It probably stands in some relation to the terminal apparatus of the olfactory nerve. From the neighborhood of the nucleus amygdalæ, probably from the nucleus itself, there arises a portion of those bundles of fibers which pass as the stria cornea between the thalamus and the nucleus caudatus.

We know from comparative anatomical investigations that the space between the infundibulum and the nucleus amygdalæ, shown in horizontal section in the illustration and included with the central gray matter, is a cortical region which is very much atrophied in man. It is designated as the *olfactory field.*

Between the pillars of the fornix the *anterior commissure* is seen (Fig. 125). Its fibers curve backward as they pass through the corpus striatum. Thus it happens that we again meet with them in transverse section, just below the outer part of the lenticular nucleus (Fig. 127, below and to the left).

I cannot urge you too strongly to look up in the fresh brain all the structures just mentioned and to become acquainted with their relations by making preparations of your own. Descriptions and illustrations will probably give you a good idea of them, but they can never supply what is to be gained by the study of the brain itself.

We will now consider the convolutions and fissures of the surface of the cerebrum.

It is not so very long ago that anatomists manifested little interest, and physicians none at all, in the study of the conformation of the cerebral surface. Neither is it so very long since order was brought out of the seeming chaos of the convolutions, and clear and accurate illustrations took the place of those old plates concerning which an author pertinently remarked that they resembled a dish of macaroni more than the brain. Interest was first actively stimulated in regard to the human brain only after physiology, followed shortly by pathology, had shown how differently irritations, extirpations, and diseases appear according as they involve this or that convolution of the hemisphere.

It will be impossible to become as thoroughly acquainted with the course of the convolutions as is desired, merely from descriptions and diagrams. Take a brain, therefore, and, following my description, trace out for yourselves sulcus after sulcus and gyrus after gyrus.

Fig. 128.—Brain of a human fœtus of the thirteenth week.

The hemispheres, primarily lens-shaped, grow out anteriorly and posteriorly. In the middle only, at a point corresponding to the corpus striatum within, the wall fails to follow this expansion as rapidly, and thus gradually becomes more deeply situated. The flat depression, which in this manner arises on the stem of the hemisphere, is called the *fossa Sylvii*, and that part which lies in the depression, the *lobe* of the *stem*, or the *insula Reilii*. The island is, therefore, that part of the cortex which adjoins the ganglia of the cerebrum from without. At first it is entirely uncovered, but later is more and more concealed by the expanding hemisphere overlapping it.

This depression is easily found on the adult brain, likewise its posterior continuation, the largest of the brain-fissures: the fissura Sylvii. If the fissure is drawn apart, the island of Reil is discovered at the bottom traversed by several perpendicular and oblique sulci. Even in the fifth month of pregnancy two divisions of the Sylvian fissure, an anterior and posterior, are distinctly to be seen. All the rest of the brain is still smooth (compare Fig. 23).

From this developmental period on, fissures (*sulci*) are formed on the surface of the hemisphere by local elevations (*gyri*) of the cortex. These sulci and gyri increase more and more in the later months of fetal life, until, at the time of birth, almost all the fissures and convolutions which the adult brain will possess are clearly defined.

The following drawings, purely diagrammatic, may serve as guides in the study of the surface of the hemispheres. Only the more important and constant fissures and convolutions are therein indicated. A simple diagram is more easily remembered than representations of the surface of the brain, which reproduce the smaller gyri and shallower sulci, all of which are inconstant, alongside of those which are more pronounced and constant.

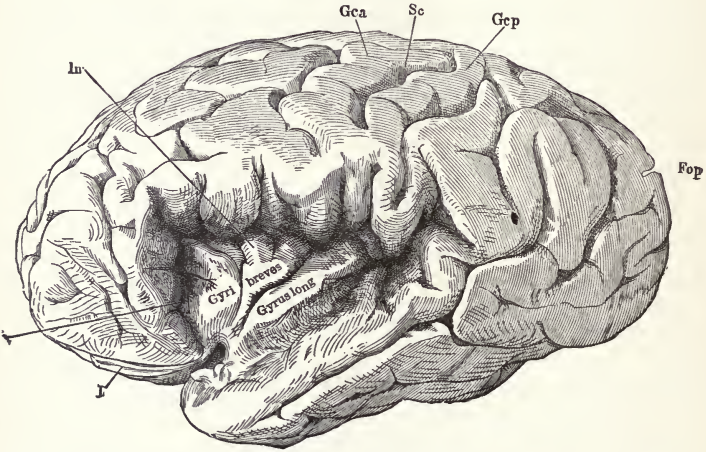

Fig. 129.—The left hemisphere with the fissura Sylvii drawn apart in order to show the insula (*In*). *Sc*, Sulcus centralis. *gca, gcp*, Gyrus centralis anterior and posterior. *Fop*, Fissura parieto-occipitalis. (After Henle.)

First locate the fissure of Sylvius. It separates the greatest part of the temporal lobe from the rest of the brain. A long posterior limb and one or two short anterior branches, which are directed upward, are distinguished on it. The mass of the brain which lies at the point where these join one another covers the island of Reil and is called the *operculum*. If those parts of the brain which surround the fissure of Sylvius are separated from one another, as has been done in the preparation shown in Fig. 129, the island lies in full view. The island is then seen to be divided into two small lobules by means of a deep fissure, the *sulcus centralis insulæ,* which passes obliquely upward and backward from below and in front. Several, almost perpendicular, sulci divide the anterior broader lobule into three or four gyri breves insulæ. The posterior lobule is really nothing but a single, longer gyrus: the gyrus longus. It borders directly on the temporal lobe. An important fissure, the *sulcus centralis* or central fissure, begins in the operculum, and ascends from there to the median edge of the hemisphere, which it frequently incises. At the bottom of this fissure a small annectant gyrus not infrequently divides it into a superior and inferior portion. Recent surgical operations, as well as the knowledge gained from physiological studies, have made it desirable to divide the fissure in parts. The two genua, the *superior genu* and the *inferior genu* of the *central sulcus,* respectively indicated in the diagram by an asterisk, serve as such points of division. Locate the fissure in Fig. 130. This central sulcus separates the *lobus frontalis* from the *lobus parietalis.* All that lies below the Sylvian fissure is called the *lobus temporalis.* In front of the sulcus centralis lies the *anterior central gyrus,*[1] behind it the *posterior central gyrus.*[2] The region in front of the

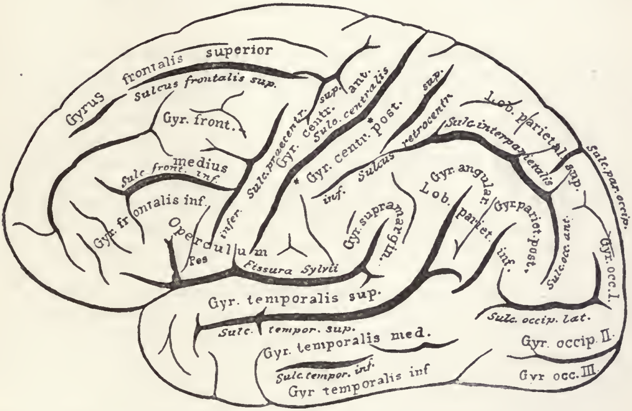

Fig. 130.—Lateral aspect of the brain. The gyri and lobuli are designated by Roman letters, the sulci and fissuræ by italics.

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[1] Circonvolution frontale ascendente of the French writers.

[2] Circonvolution pariétale ascendente of the French writers.

anterior central convolution, the frontal lobe, is divided by two fissures, the superior and inferior frontal sulci, into three gyri: the *superior, middle,* and *inferior frontal gyri.* These convolutions are not always sharply separated from one another along the entire extent of the frontal lobe, inasmuch as the fissures are frequently interrupted after a short course by annectant gyri. These three divisions of the frontal lobe, lying above one another, are readily found on all brains. It will probably be observed also that they are connected with the anterior central convolution by means of several annectant gyri. From the central convolution, they are separated by a fissure, the *sulcus præcentralis,* of variable length and depth. Besides an inferior, more constant, part, this sulcus has a shorter superior part, which is demonstrable at times. According to the investigations of *Schnopfhagen,* the relation here shown diagrammatically in Fig. 130 is said to be the most common one.

On the broad middle convolution of the frontal lobe there has lately been distinguished a mesial, from a lateral, division. The inferior frontal convolution is incised by the two short anterior branches of the fissure of Sylvius. They join the main horizontal limb in the form of a V. This V-shaped region is the portion of the gyrus designated as the *pars opercularis.* Considerable variations occur at this point, which depend on the degree of intellectual development of the individual. That portion is especially subject to variations which lies between the posterior arm of the V and the anterior central gyrus: the *pes* of the *inferior frontal convolution.* It is a simple convolution, which often shows indentations, extensions, etc. On the brain of Gambetta, a famous orator, it consisted of a double convolution on the left side.

The brain of the anthropoid apes is surprisingly similar, as regards convolutions, to that of man. That which especially distinguishes it from that of man, however, is the development of the frontal convolutions. The superior and middle gyri are always very much shorter, and only rudiments of the inferior gyrus are demonstrable. It is highly probable that this is the anatomical expression of inferior intelligence, particularly of the utterly undeveloped faculty of articulate speech. As we probably owe the perfection of our intelligence to our faculty of speech—not as individuals, but as a race—the reason for the inferior development of the entire frontal lobe in apes may, perhaps, be found in the imperfect development of the inferior frontal gyrus.

The *temporal* lobe is traversed by several sulci, which run parallel with the fissura Sylvii, and, more or less distinctly separate from one another, a *superior, middle,* and *inferior temporal gyrus.* In most cases only the first two of these gyri are plainly distinguishable throughout their entire extent.

Now observe the region behind the central fissure and above the temporal lobe; it is called the parietal lobe. It is divided into a *superior* and an *inferior parietal lobule* by the *sulcus interparietalis,* which arches around the end of the fissure of Sylvius and the first temporal sulcus. Throughout most of its extent, the superior lobule is not separated from the posterior central gyrus, unless, as often happens, a branch of the sulcus interparietalis ascends toward the edge of the hemisphere and thus considerably interrupts the continuity.

This branch, the *fissura retrocentralis superior*, often occurs independent of the interparietal fissure. The interparietal fissure allows the recognition of three divisions, which are occasionally separate from one another. The anterior division is called the *fissura retrocentralis inferior*, the posterior the *sulcus occipitalis anteterior* or *perpendicularis*.

The portion of the inferior parietal lobule which surrounds the end of the fissure of Sylvius is called the *gyrus marginalis*. The part that lies just back of this and arches around the superior temporal sulcus is the *gyrus angularis*. The former gyrus is at once observed on every brain; the latter must be searched for with some diligence. It is found in the space bounded above by the interparietal fissure and below by the superior temporal sulcus; that is to say, its end. Its posterior part, indeed, just surrounds the end of this sulcus. The region of the gyrus angularis is an important one, and it is therefore advantageous to be able to locate and bound it well. The small gyrus directly posterior to it is the *gyrus parietalis posterior*.

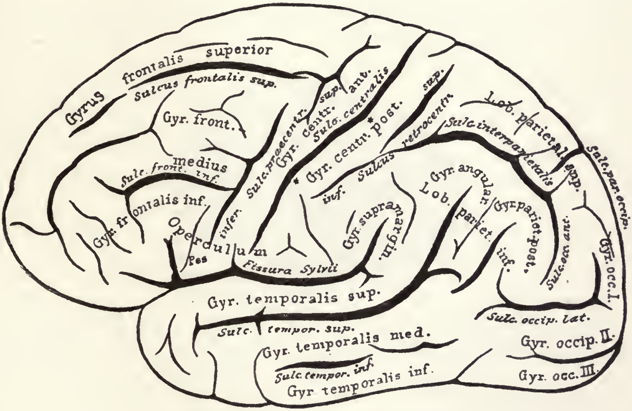

Fig. 131.—Lateral aspect of brain.

The *occipital lobe* is not so uniformly fissured in all brains that the convolutions described by writers as *superior, middle,* and *inferior* may be easily identified without elaboration. It is commonly separated from the parietal lobe by the *anterior occipital sulcus,* which passes vertically downward behind the lobulus parietalis inferior. One or two small sulci, placed somewhat horizontally, separate the small gyri from one another.

When all of these fissures and convolutions have been found, cut the brain in two along the line of the great longitudinal fissure, and study the mesial side of the hemisphere.

The most important parts of the mesial wall of the hemisphere are already familiar to you from the study of their embryology in the second chapter. It was there learned that the edge of the hemisphere, thickened to form the fornix, follows in curved line the hemisphere, which grows out posteriorly and inferiorly; that anteriorly, where the corpus callosum passes across from one hemisphere to the other, the portion of the inner wall which lies between the fornix and the corpus callosum remains as the septum pellucidum.

From its embryology, the section previously made through the brain of the adult is easily understood. In the preparation from which the accompanying illustration was made (Fig. 133), as well as on the embryonic brain now again demonstrated (Fig. 132), all the parts that lie behind the middle of the thalamus have been cut away, because they conceal the under surface of the temporal lobe and prevent us from following the fornix.

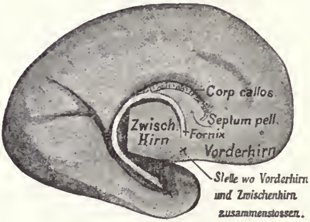

Fig. 132.—Inner aspect of the embryonic hemisphere shown in Fig. 23. It shows the inner, inferior edge of the hemisphere, which becomes thickened to form the white, medullated line of the fornix. This, however, becomes medullated after birth only. *Zwischenhirn*, Interbrain. *Vorderhirn*, forebrain. *Stelle*, etc., Place where forebrain and interbrain meet.

The interbrain—that is, its lateral wall, the thalamus opticus—is therefore now observed in the center on the longitudinal section. The margin of the hemisphere, thickened to form a white, medullary band, the fornix, passes in a curved line along the boundary between the interbrain and the cerebrum. It first appears near the base of the brain in the gray matter behind the lamina terminalis; ascends dorsally as the columna fornicis;

then accompanies the margin of the hemisphere still farther; curves with it into the temporal lobe, and ends only at its apex.

The horizontal mass of transversely-divided fibers above the fornix belongs to the *corpus callosum.* On this there is distinguished anteriorly the *genu,* posteriorly the *splenium,* and between the two the *body.* Between the corpus callosum and the fornix lies the triangular field of the septum. Moreover, just in front of and below the fornix the commissura anterior is seen in transverse section; it lies in the middle of the lamina terminalis. The lamina terminalis then continues ventrally into the floor of the interbrain, and is here somewhat infolded by the chiasma—also cut transversely.

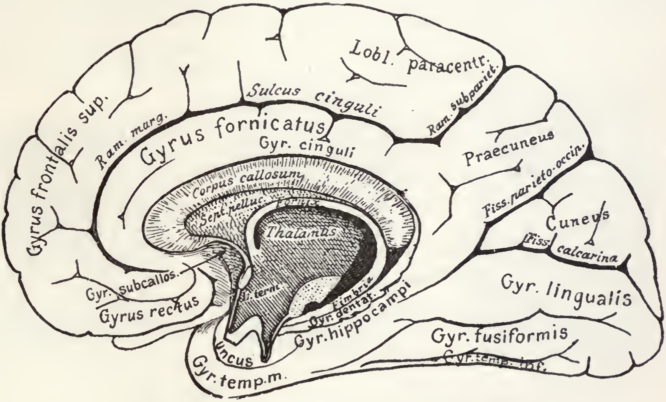

Fig. 133.—Longitudinal section through the middle of an adult brain. The posterior portion of the thalamus, the crura cerebri, etc., have been removed, in order to expose the inner surface of the temporal lobe.

These structures, in part membranous, have been purposely left intact in the preparation in order that the floor of the middle ventricle might be seen once more. The posterior wall—the infundibulum and its transition into the ventral region of the midbrain, the prominence of the tegmentum—has also been left in place. In your own preparations, however, remove all of these gray parts and observe how the fornix terminates behind the region designated as *uncus.*

The portion of the wall of the hemisphere which lies above the corpus callosum is traversed by few and rather constant fissures.

First of all, the *sulcus cinguli* runs parallel with the corpus callosum.

Posteriorly, it turns upward to the edge of the hemisphere and there ends in a small incision behind the posterior central gyrus.

The sulcus cinguli—which also bears the names of *sulcus calloso-marginalis, marginal fissure, fissura limbica,* and *fissura splenialis*—consists, properly speaking, of three parts lying one behind the other. Not infrequently these are really separate sulci.

That which lies above and in front of this sulcus cinguli is regarded as belonging to the superior frontal convolution; the convolution lying between it and the corpus callosum is called the *gyrus fornicatus.* A glance at a specimen or the illustration shows that the gyrus fornicatus widens out superiorly in its posterior part and passes directly over the edge of the hemisphere into the lobulus parietalis superior. This widened portion is called the *præcuneus.* Directly in front of the præcuneus lies a part of the cortex which adjoins both central gyri without and connects these with one another. It is called the *paracentral lobule.*

The præcuneus is terminated posteriorly by a deeply-incised fissure,—the *fissura parieto-occipitalis,*—which always extends for some distance over upon the outer surface of the hemisphere. This parieto-occipital fissure frequently passes very far beyond the inner surface and runs out over the hemisphere externally as a deep vertical fissure, the *fissura perpendicularis ext.* This is very frequently the case in the brains of idiots. In almost all simian brains a broad fissure begins in the parieto-occipital fissure (or just behind it, *Ziehen* and *Kükenthal*), which passes downward over the greater part of the lateral surface of the hemisphere and in a very striking manner separates the parietal from the temporal lobe. It is called the simian fissure, or *"Affenspalte."*

The *fissura calcarina* joins the parieto-occipital fissure at an acute angle. This fissure lies exactly in the outer wall of the posterior horn of the lateral ventricle. The wall of the brain infolded by it is indicated within the posterior horn by an elongated prominence known as the *calcar avis.* The triangular cortical area inclosed by the fissura parieto-occipitalis and the fissura calcarina is called the *cuneus.* If the vertex of this triangle is now located, several small annectant gyri, superficially or deeply situated, are found connecting it with the end of the gyrus fornicatus, which passes by in front of the vertex of the cuneus. Notice this comparatively narrow part of the gyrus fornicatus: the *hilus.* It is seen to continue as a rapidly widening convolution to the apex of the temporal lobe, where it ends in a hook-like process: the *uncus,* or *gyrus uncinatus.*

This convolution consequently surrounds the entire margin of the hemisphere. In fact, it is called the marginal convolution; in which case only the anterior portion receives the name of gyrus fornicatus, while the name of *gyrus hippocampi* is given to the part lying posterior and ventral. Posteriorly, as is well seen in the figure, a small, longish convolution of the occipital lobe joins the gyrus hippocampi; it is called the *gyrus lingualis.*

As has previously been shown, the fornix forms the edge of the hemisphere. The first portion of the wall of the brain succeeding this is the above-mentioned *gyrus hippocampi,* which is, therefore, adjacent to the fornix. Externally to it lies the cavity of the ventricle: the inferior horn.

The ventricle is separated at this place from the cranial cavity by a thin, vascular membrane only,—the continuation of the plexus chorioideus,—which is attached to the fornix throughout its entire extent.

The gyrus hippocampi is covered by cortical matter, but the cortex ceases on the side toward the inferior horn; and, close to the ventricle, the white medullary substance, no longer covered by gray matter as on the entire outer surface of the brain, lies exposed. This medullary substance—a long, white stripe, which is directly continuous with the fornix above—is called the *fimbria* (Fig. 133).

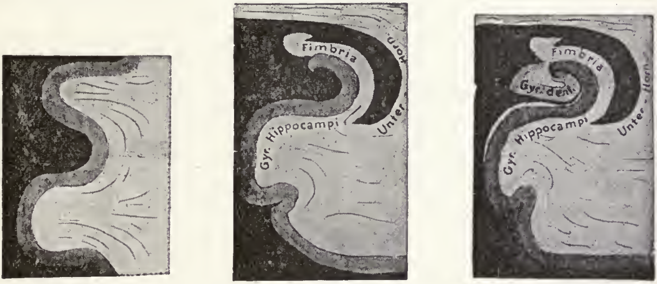

Fig. 134*a*. Fig. 134*b*. Fig. 134*c*.

Fig. 134*a*. Fig. 134*b*. Fig. 134*c*. *Unterhorn,* Inferior horn.

The marginal convolution is pushed by a fissure of its outer surface—the *fissura hippocampi*—into the cavity of the inferior horn. The elevation thus produced along the entire floor of the inferior horn has borne for centuries the name of *cornu Ammonis,* or *pes hippocampi major.*

Owing to the fact that the cortex of the gyrus hippocampi is also infolded by that fissure before the cortex entirely ceases and leaves the medullary substance exposed, there is presented a peculiar, somewhat complicated section, if the gyrus is cut transversely. On other parts of the brain the cortex covers the surface continuously, as is shown in Fig. 134*a*; it ceases, however, close to the ventricle at the marginal infolding, and leaves exposed a white, somewhat curved border, the fimbria. Fig. 134*c* is intended to show this and the infolding which the cortex undergoes before it ends. Between the gyrus hippocampi and the free, medullary edge of the hemisphere (fimbria—fornix), there still lies, however, a small convolution, which has purposely not been mentioned heretofore. It passes downward from the end of the corpus callosum to the apex of the temporal lobe, and therefore takes part in the configuration of the cornu Ammonis also. Locate this narrow gyrus, designated as the *gyrus dentatus* or *fascia dentata*, on the sagittal section previously demonstrated, in order to make its relation to the fornix and the gyrus hippocampi perfectly clear. It lies, as is there seen, just in front of the inrolling of the gyrus hippocampi, produced by the similarly named fissure. A cross-section of the gyrus dentatus is, therefore, not represented by Fig. 134*b*, but more correctly by Fig. 134*c*.

The cornu Ammonis is, therefore, the bulging that arises in the ventricle through the infolding of the gyrus hippocampi by the fissura hippocampi. The complicated appearance of the cornu Ammonis, when seen in transverse section, is due to the fact that the cortex of the gyrus ceases just at this place, and that the fimbria and gyrus dentatus run along over this infolding.

The relation of the gyrus hippocampi to the inferior horn of the lateral ventricle becomes clearest, if their cross-sections are traced in the large sections of the brain reproduced in Figs. 175, 185, 186, and 187.

The gyrus fornicatus and its continuation, the gyrus hippocampi, are formed rather early in the embryo. Dorsal to the margin of the hemisphere (arch of the fornix) there appears in all mammals a fissure which, running parallel with the fornix, passes down with it into the temporal lobe. It is called the *marginal fissure*, or *fissura limbica*, and the gyrus left between it and the fornix, the *marginal convolution*. The fibers of the corpus callosum pass between this gyrus and the fornix in the more anterior region of the brain, and the convolution is there known as the *gyrus fornicatus*. The more posterior portion of the marginal convolution, however, —the portion designated as the *gyrus hippocampi*,—borders almost directly on the fornix. In most mammals the corpus callosum and the gyrus fornicatus are very short.

If the upper surface of the corpus callosum is again examined, a thin, gray, longitudinal line will be seen upon it on each side (Fig. 124, *Lt*). That line—the *stria longitudinalis Lancisi*—is the continuation of the gyrus dentatus: a convolution atrophied even in the cornu Ammonis.

At the posterior end of the corpus callosum a short convolution is sometimes seen passing in a direction toward the fornix, with which it unites. It is the *gyrus callosus*, which occurs in man as a very atrophic structure only, and is not at all constant.

Find the gyrus uncinatus on the fresh brain internal to the apex of the temporal lobe, and from there follow the gyrus hippocampi upward. Then find the arch of the fornix, which is easily done, above the posterior portion of the thalamus, and note that it passes over into the fimbria, which is visible as a white, medullary line almost to the apex of the cornu Ammonis. Finally, make a frontal section, which will show the relation of the structures named to the inferior horn.

On the base of the brain only a few important fissures are found in addition to the fissura hippocampi, which really belongs to the mesial surface. On the under surface of the frontal lobe lie the *sulci orbitales* and *olfactorii.* The convolutions between them, regarded as continuations of the frontal gyri, are designated by the names of those frontal gyri with which they are respectively continuous.

The cortex of the basal surface of the frontal lobe borders on that gray matter at the base of the brain which belongs to the olfactory apparatus. We shall have occasion to consider this gray matter later. Two small elevations situated near the median line and extending out from this gray matter dorsally, the *gyrus rectus* and the *gyrus subcallosus* lying behind this, belong, perhaps, to the olfactory apparatus. At all events, the latter of the two gyri arises from the outfolding produced by a bundle of fibers passing along under it in this situation, which bundle passes from the terminations of the olfactory radiation up over the septum into the fornix. It is that very bundle to which, in the lower vertebrates, I thought it necessary to attribute so great significance for the interpretation of the mesial cortex of the brain. See Figs. 76 and 100: *Tr. cortico-olfactorius septi.*

At the base of the brain the temporal and occipital lobes cannot be separated from one another. Longitudinally-directed fissures, in smaller number, traverse the region common to both lobes, which, in general, is included in the temporal lobe. The middle temporal gyrus extends only a short distance toward the base; that which is visible belongs almost entirely to the inferior, or third, temporal gyrus. This is separated by means of a rather superficial fissure,—which is almost always interrupted several times,—the *sulcus temporalis inferior,* from a long, spindle-shaped convolution, the *gyrus fusiformis,*—a gyrus invariably well defined. This gyrus borders directly on the long gyrus hippocampi. It is separated from the hippocampal gyrus by a long, deep fissure, a fissure appearing very early in embryonic life, the *fissura collateralis.* The collateral fissure extends over the entire under surface of the brain from the occipital lobe to the apex of the temporal lobe.

The fissures of the brain may be very easily fixed in mind by studying them on the developing brain instead of on that of the adult. At the same time, several facts, very interesting from a morphological stand-point, are disclosed as an additional compensation.

If the very young brain is examined, which is shown in Fig. 20, it is seen that a fissure runs along the greater part of the inner edge at the place where the wall of the forebrain passes over into the thin velum interpositum, which consist of epithelium only. The two walls of the fissure are formed just by this epithelial plate. *His* has named it the *fissura chorioidea.* Later in life it is filled up by the vessels growing into it, and it is then no longer demonstrable, because its walls form the covering of the plexus chorioideus.

Even during the second and third months, a second fissure is met with, the *fissura arcuata.* Somewhat dorsal to the fissura chorioidea, which indicates, in a measure, the edge of the hemisphere, it runs in a curved course on the inner side of the brain around this edge, thus separating the fundament of the marginal convolution, or gyrus cinguli. The gyrus fornicatus is formed later from the frontal portion of the marginal gyrus, the gyrus hippocampi from its caudal portion. It will be remembered, when it is here learned how early the marginal gyrus is differentiated from the wall of the brain, that in amphibians and reptiles this same region of the brain was described as that part which possesses phylogenetically the oldest cortical covering.

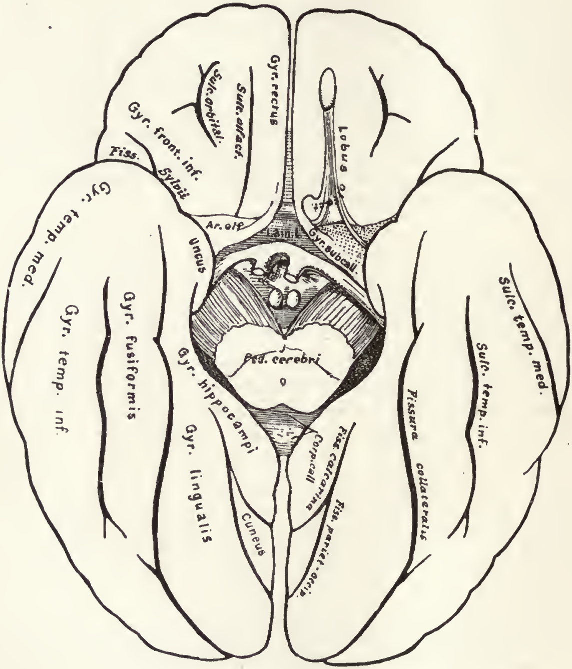

Fig. 135.—The convolutions on the base of the brain (schematic).
The chiasma turned back.

The brain that we are considering is still smooth on the outer surface and just slightly differentiated on the mesial surface by the fissura arcuata. Now, however, about the beginning of the third month, there is presented a beautiful confirmation of the proposition, previously stated, namely: that the fissures of the brain result from the difference in growth between the roof of the skull and the developing fundaments within the brain. Fissures appear only in Primates, the brains of which, as is known, attain the greatest expansion, which fissures are arranged in the form of a fan on the inner and outer side of the brain. They converge toward the base of the skull and, varying in number and formed essentially on the mesial wall, have exactly the direction that would be expected and required if the brain met with compression or pressure during the expansion of its mantle.

Some time during the course of the fourth month, simultaneously with the development of the fibers of the corpus callosum between the hemispheres, these primary fissures disappear, and at the beginning of the fifth month the entire hemisphere is again smooth. These *transitory fissures* have never been found in other mammals, but I may communicate to you the interesting fact that, under certain circumstances, in cases with an abnormal rate of development, fissures having a similar direction cover the surface of the adult brain. Purely mechanical disturbances lead to such radial fissuring, as the example illustrated by Fig. 137 at once shows.

Fig. 136.—Transitory fissures of the brain. Brains of fetuses of the eleventh and thirteenth weeks. (After Cunningham.)

In several of the lower mammals also, as in the Marsupials, such radially placed fissures are here and there found on the brain.

Although the transitory fissures have commonly disappeared by the fifth month, a certain tendency to the development of similar fissures still remains. The fissura parieto-occipitalis develops very early (see Fig. 132) in exactly the course of such a transitory fissure which previously had a similar direction; and on the outer side of the brain there is found—in apes, at least—a continuation probably passing out from it, the *fissura perpendicularis ext.* The fissura calcarina, which is demonstrable very early, also lies in the direction of this old transitory fissure.

Now, however, probably toward the end of the fifth month, there begins the development of those fissures which we have previously become familiar with from the study of the adult brain. The Sylvian fossa, the origin of which was earlier explained, becomes narrower; the wall of the brain around about it grows and soon hangs down over it on all sides. The insula begins to disappear at the bottom of the fissure; the edges of the fossa approach one another more and more, and finally meet toward the end of fœtal life. The fissura Sylvii, with its branches, now alone affords access to the fossa over the insula Reilii, which was at one time wide open.

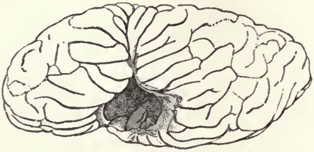

Fig. 137.—Large scar on the outer side of a cerebrum. All the convolutions converge toward the point where the brain could not expand. (After Ziegler.)

By the end of the fifth month the fundament of the central fissure has appeared dorsal to the fissure of Sylvius.

Gradually, in the course of the sixth and seventh months all the other fissures follow the few fissures just mentioned. But they are still so little branched and so simply arranged that a glance at a fetal brain at the end of the seventh month is sufficient in order to survey at once the most important parts of the fissuration of the brain (Fig. 138).

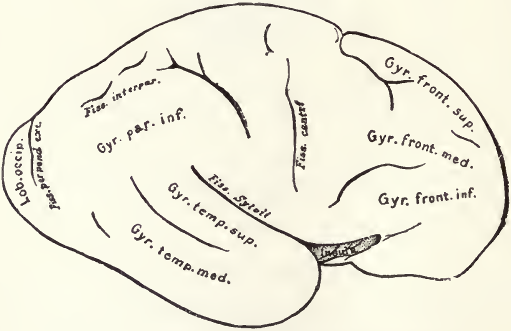

Fig. 138.—Brain at the end of the seventh month.

That which here lies before us resembles a schema of the fissures of the adult brain. The central convolutions in front and behind the central fissure; the three frontal gyri, still incompletely separated from one another; the superior and inferior parts of the parietal lobe, between which the three components of the fissura interparietalis are visible; finally the temporal lobe divided into three parts—these are all prominent, and, when once understood, make their recognition later in the adult brain a very easy matter.

The great interest which is shown in the development and perfection of the brain-fissures is not occasioned purely by morphology. Since the scientific study of the brain has become general, there has been an endeavor to answer the question, whether the intellectual *status* of the individual may somehow be reflected in the expansion of the surface of the cerebrum. *Gall* even believed himself justified in laying down the proposition that men ranking especially high intellectually have larger and more richly convoluted cerebrums than others, and that the frontal lobes are preponderantly better developed.

Here, however, we are dealing with a general impression rather than with the result of exact measurement and comparative observation. Really serious studies in this direction first date from the time when *Rudolph Wagner*, in 1860, presented to the Göttingen Society of Sciences the report of the investigations which he had made on the brain of the celebrated mathematician, Gauss, and on several other brains of philosophers and men of letters. Since then we have come into possession of a very large number of descriptions of convolutions.

There is hardly a fissure, hardly a convolution, that cannot now present a small literature of its own. The typical relations as regards the direction and a certain number of possible variations are well known for all the sulci and gyri. We possess descriptions of the surface of the brain, not only of Europeans, but also of representatives of many foreign peoples. The anthropoid apes have been made the subject of very numerous investigations, and a very zealous study has been devoted to the other apes by many investigators. The development of the convolutions is now exactly known for man, and many apes also. It has become apparent from these studies (*Cunningham*) that the embryonic fissures and convolutions appear by no means simultaneously in all individuals, nor have the same configuration when they are once distinctly present. This fact is, therefore, very important, because it contains the proof that *the cortex of the brain, the organ of the higher intellectual activity, is variously expanded in different individuals, even in the fundament.*

If no mention at all were made of all these numerous investigations while describing the convolutions of the adult human brain, investigations that have made us familiar with the variations to which the individual gyri are subject, it was because these things are, for the present, only to be recorded and as yet are to be brought into no sort of connection with the perfection of the separate intellectual faculties. For investigations of the brain are still wanting entirely which consider, simultaneously with the development of the gyri, the entire intellectual *status* of a single individual. Even now, when numerous careful researches have finally furnished us somewhat of a survey, we are still hardly able to consider such relations. However, the attempt must be made even now to investigate the corresponding cortical development for the faculties known to be localized. It is hoped the time will then come when the convolutions will be no longer described simply as such, but only in connection with the questions which their development always gives rise to in individual cases. Absolutely nothing is known of the possessors of almost all of the brains previously described. Thus a very large part of the data collected seems to me next to worthless, and later will probably be entirely so, for the point in question from which we proceeded, the discovery of relations between the configuration of the brain and the intellectual *status* of the possessor.

Now the attempt has, indeed, been made to decide the question whether greater intelligence may correspond to a larger brain, by weighing. Thousands and thousands of such estimates have been made, but the large amount of material thus obtained contains little that is of any value. First of all, the body-weight has, in many cases, not even been considered. This, however, increases according to factors quite different from those controlling the brain; nevertheless, a certain connection exists between the size of the two. Then, however,—and this appears to me the most important,—*the development of the cerebrum as a whole cannot be used at all as a measure of the sum total of intelligence.* It is an acquisition of the last decade only, *that we have learned that different brains may have a very different development of their various regions.* At present these cortical regions cannot be so separated from one another that they may be compared morphologically or by weight. The brain-weight for the majority of males ranges between 1300 and 1450 grammes; for females it is a little less. Now, uncommonly heavy brains occur at times in individuals who do not rank very high intellectually, and, on the other hand, relatively low weights have been found in men of prominence. We are not accustomed, however, to measure a man's intellectual value in its entirety, which, indeed, is almost never possible, but generally according to some especially prominent characteristic, which gives authority, position, etc., to the individual. *Such peculiarities may very well be traced to the increased development of a single cortical region,* this increase not directly expressing itself in the general relations of the gyri or in the brain-weight. Anyone endowed with enormous visual memory, visual imagery, etc., and with all the intellectual attributes that characterize the great artist, might occupy a position entirely unique, yet the increased development of the occipital lobe would, on weighing, show no essential variation from the average brain-weight if, perhaps, other centres were developed to a less degree. The same may be said of a musician, where, in all probability, we have to do with an increase of the temporal lobe.

One who is a great orator, an energetic man, and an ingenious commander need not necessarily possess a larger brain. These characteristics may well be based upon very small local increases of single cortical areas. Gambetta's brain, for example, the speech-area of which was described as uncommonly developed (see above), weighed hardly more than the average of the smaller brains. At present so little is known regarding the cortical areas that in general hardly more can be said than that especial development of the frontal lobes frequently goes hand in hand with high intellectual qualities, and that insufficient endowment, even idiocy, is found to be comparatively frequent in those with abnormally small frontal lobes. That which is still entirely wanting and is not to be attained at all at the present time, is data of weight for the separate regions of the cortex. From this state of affairs it will be understood why I do not, at the present time, give anything more definite concerning the weight-relations of the central nervous system.

It first occurred to *Perls*, my late friend, that a comparatively large number of men who are intellectually eminent give the impression from their type of face that they may have had an hydrocephalus, which healed in early childhood. He expressed the conjecture that, if a moderate hydrocephalus should recede, a resistance which is proportionally much less would oppose the growth of the brain, on account of the enlarged skull. Since then I have followed this suggestion which he gave me, and have found proofs of its correctness in not a very small number of cases. *Rubinstein's* powerful skull, for example, showed on section, according to newspaper accounts, very clear evidences of an old rachitis; and we even know that *Cuvier*, who had an uncommonly heavy brain, was hydrocephalic in childhood. Whoever carefully examines a good collection of photographs, following the suggestion given by *Perls*, will meet with many faces that are manifestly of an hydrocephalic nature, and precisely in men who rank especially high intellectually. Naturally, all men of high intellectual attainment are not healed hydrocephalics, any more than every healed hydrocephalic must have a better development of the brain as a consequence.

CHAPTER XIV.

THE BRAIN OF MAMMALS AND THE OLFACTORY APPARATUS.

IN the first chapters the relations of the forebrain of mammals could only be touched upon in a very general way. At present, when you are better acquainted with the structure of the human brain, it will pay you to glance at other mammalian brains. Much of that which is known regarding the fiber-systems, etc., has been gained, as you know, not from the human brain, but from a study of that of animals. A great many things that appear hardly intelligible in human brains are met with much better developed in lower vertebrates.

If it is desired clearly to understand the enormous differences in degree of perfection of the mantle of the forebrain which are found in the various mammals, they must be considered in regard to a fact which up to the present time has not been sufficiently recognized. *The mantle is not a unit functionally. It is composed rather of a large number of different parts*—called centers—and numerous physiological experiments have shown that movements which must be acquired, and probably most of the intellectual combinations, are only made possible by the existence of such centers.

The introductory chapters have shown that the real motor and sensory centers are situated low down, from the spinal cord to the midbrain, and that these, even if the forebrain is wanting, are in themselves sufficient for necessary activity. These centers, present in abundance and found at an early period, are connected with one another to form series.

Experimental physiology shows, however, that many of the lower centers are connected with higher centers, located above in the cortex, in such a manner that irritation of the latter produces movement. Of what nature and importance the influence of the higher centers on the lower may be is still a matter of special discussion. For this reason an endeavor has been made to study as exactly as possible the phenomena that appear after the removal of portions of the cortex. Doubtless the importance of the rôle played by the cerebral cortex is different in different vertebrates. While the removal of the entire cerebrum in lower vertebrates does not destroy the ability to perform coarser movements with efficiency, in mammals, after destruction of circumscribed portions of the motor zone, paralyses appear, which are very transitory. In man disease even of relatively small portions of the cortex often leads to permanent paralyses. *Manifestly all motor, and many senso-psychical, functions may be performed by parts of the central nervous system situated lower down. The higher we ascend in the vertebrate series, however, the more is the cortex concerned in the activity of the brain, and the more is consciousness met with as a con-*

comitant. Man has, in this respect, reached a stage where many of the functions concerned can no longer be executed without the participation of the cortex. All the possible transition-stages are observed in mammals. It is true that the separate muscles, etc., can be influenced in mammals through irritation of the cortex, but the parts of the cortex thus involved are not necessary for the movements concerned. In man, however, the greater portion of the surface of the forebrain has become indispensable.

Morphologically, this relation expresses itself in a very different development of the various parts of the brain-mantle. At present the essential parts of the mantle can be distinguished from one another in a few mammals only; yet it is already known that *the development of the cortex is continuous in the mammalian series.* There exists the greatest of variations and the most variable of size-relations; yet even at present the position which a few of the mammals occupy in the entire series can be indicated. Even a superficial consideration of mammalian brains shows that one center especially, the olfactory center, presents most varying size-relations, so considerable, sometimes, that the entire remaining portion of the mantle appears to be a small appendage only of the olfactory lobe.

Fig. 139.—Brain of an armadillo: *Dasypus villosus.* (Side-view.)
The olfactory apparatus is shaded.

The olfactory brain is that part of the cortex which first appears in the animal series; the other cortical regions become only later associated with this. Among many of the lower mammals animals are known which possess rudiments, at first only relatively small, of that portion of the mantle which does not belong to the olfactory apparatus. In such a case, the olfactory lobe, and whatever else belongs to the cortical olfactory apparatus, often forms almost one-half of the entire mass of the forebrain.

What is known regarding the manner of life of such "olfactory" animals agrees well with the structure of their brains. The small armadillo, for example, the brain of which is represented above, spends its entire life burrowing in the soil and creeping about under the foliage of the dense primeval forests. For choosing its food, for finding it, no sensory apparatus will be so important to it as that of smell. The uniformly limited activities of the plump body will need fewer acquired and deliberate acts than the prehensile hand of an ape, perhaps. In the latter, therefore, we should expect a much greated development of the true psychical centers for the upper extremities than in the small creature that lives by wallowing. This, in fact, is what occurs. At present, moreover, we can even occasionally conclude from the development of a definite cortical region the existence of an ability to execute in a certain direction. The elephant, for example, possesses an especially large cortical field in the region of the cortex where the facial area is localized in the higher mammals. This is entirely wanting in the rhinoceros and tapir. If nothing were known of the wonderful ability of the animal to use its trunk in such various ways, it might, however, be conjectured from the presence of the above-mentioned field in the facial area that from this center muscles were innervated which were capable of very special function.

All the investigations on the mantle lead to the conclusion that it is composed of separate areas, which may vary in relative size. One part of these centers stands in relation to motor and sensory processes. Another part, as yet studied in man only, contains, according to the brilliant discovery of *Flechsig*, association-regions alone which are well adapted structurally to form connections with one another and with other centers. According to *Flechsig*, it is probable that the intellectual superiority of the Primates rests upon the high degree of perfection of the "centers of association." In point of fact, the brain-mantle generally increases in such a manner that a larger mantle is found in the more intelligent animals than in those especially deficient mentally and of low rank. It will be the object of continued investigation to show how the individual elements grow. The interest which investigations in the comparative anatomy of the cerebral convolutions really have lies just in this inquiry, rather than in purely morphological considerations.

Very gradually, then, the mantle increases in extent ascending in the vertebrate series. In the apes, belonging to the class of primates, it has attained an expansion which borders closely on the relations found in man. Nevertheless, an important factor, besides more unessential relations, still separates it from the stage reached by man. The frontal lobe, still very small in the lower apes, attains a large size in the higher apes, but always remains very much inferior to that of man. In man, even, this developmental process is in nowise terminated as yet. Differences still plainly occur in the region of the frontal lobe which allow us to infer the possibility of further perfecting. The inferior region of the frontal lobe, which contains the centers of speech, and shows very marked variations in development, is the part more particularly concerned.

When a small mantle is present the fibers issuing from it can naturally be only few in number. In fact, the radiation from the cortex is so meagre in many smaller mammals that a real centrum semiovale is not formed at all—the entire fiber-system more frequently being limited to a relatively thin covering under the cortex. This layer of white matter then borders directly upon the ventricle, and is traversed by the terminal filaments of its epithelium.

Moreover, the principal commissure of that portion of the mantle which does not belong to the olfactory apparatus, the corpus callosum, is also so small that it occupies a relatively small portion only of the mesial surface of the hemisphere. Indeed, in some monotremes and in the marsupials hitherto investigated a corpus callosum is entirely wanting (*Symington, E. Smith*).

Likewise, the fiber-systems passing down from the mantle, especially those to the pons and the spinal cord, the fibers of the pes, are, in all vertebrates very much less developed than in man.

For the most part the olfactory apparatus is much more powerfully developed than in man, but it may also atrophy very enormously, even degenerate to such an extent that it almost disappears, as in the aquatic mammals. Accordingly, mammals have been divided into osmatic and anosmatic. The investigation of a very large series of animal brains shows that the *olfactory apparatus* and the *pallium develop entirely independently of one another phylogenetically*; that the one may atrophy, the other attain a higher degree of perfection; and *vice versâ*. The greater perfection of the olfactory apparatus manifests itself not only in the more powerful development of the olfactory lobe and the olfactory region of the mantle, but also, on the other hand, in a very marked development of definite cell-groups and fibers belonging to this apparatus in other parts of the brain.

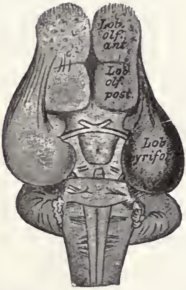

Fig. 140.—Brain of armadillo: *Dasypus villosus.* (Basal view.)

The *olfactory apparatus* will, therefore, be considered, first of all, as a whole. Present in man, as relatively atrophied remnants only, it may be more easily studied in many other mammals.

Illustrations are here presented of the base of the brain of a calf and of an armadillo. A large lobe is here seen which anteriorly is covered as if with a cap by an enlargement, and posteriorly passes over somewhat directly into the convolution of the cornu Ammonis. This is the *olfactory brain.* In the armadillo—and in the dog, rabbit, and many other mammals also—it is much larger than in the calf. It then nearly always occupies the entire base of the brain. This is the same part of the brain which, in reptiles, first made its appearance as a separate region of the mantle. See Chapter XII, pages 170 and 171.

The *fila olfactoria,* cut off unevenly in the specimen, enter the anterior part. The *bulbus olfactorius* is shortly met with. This rests upon the *lobus olfactorius anterior,* the frontal division of the entire apparatus. The lobus olfactorius anterior then passes over into the *lobus olfactorius posterior,* which is particularly well defined in the armadillo (*Dasypus*). In Fig. 141

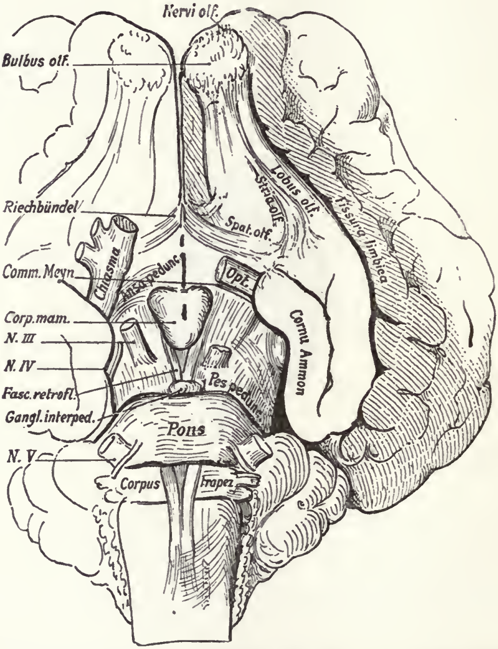

Fig. 141.—The base of a calf's brain. The ventricle purposely opened from below in order to show its recesses: the R. opticus, infundibuli, and mamillaris. *Riechbündel,* olfactory bundle.

it is designated as the *spatium olfactorium* (*olfactory area,* or *espace quadrilatère of Broca*).

To this entire apparatus there is added posteriorly the *cortical area,* or field, of the *olfactory apparatus,* which has been designated, on account of its shape, as the *lobus pyriformis.* Mesially, this pyriform lobe passes directly over into the territory of the *gyrus hippocampi.*

The long *fissura limbica* separates the olfactory brain from the remaining pallium.

The fibers of the *olfactory nerve* dip into the bulbus. A section through the bulbus reveals a distinct separation of the tissues into layers. As would be expected, the fibers of the olfactory nerve lie most externally. Then follows a grayish-white zone, in which, even with the naked eye, there are visible numerous small balls, the *glomeruli olfactorii;* it is known as the layer of the glomeruli. Within this lies the gray layer of ganglionic cells, which then gradually passes, by means of a "granular zone," over into the olfactory medulla. A delicate extension of the lateral ventricle reaches into the bulbus. The ventricular epithelium borders immediately upon the layer of medullated fibers.

Investigations by *Golgi, S.* and *P. Ramón y Cajal,* and those by *Gehuchten and Kölliker* have made us familiar with the elements of these layers, and with the very interesting connection of some of these elements with the fibers of the olfactory nerve.

The fibers of the *olfactory nerve* are no other than the centrally directed terminal processes of the sense-cells of the olfactory mucous membrane. This fact has already been referred to while describing the embryology.

After these fibers have passed the cribriform plate of the ethmoid and arrived at the ventral surface of the bulbus, they undergo repeated decussations, and then sink into the substance of the brain. There each neuraxon immediately breaks up into a delicate terminal arborization. The arborization meets with the thick branches of a dendritic process, which is similarly branched, and both varieties of fibers, which lie in immediate contact with one another, together form a roundish complex: the glomerulus olfactorius.

The dendritic process arises from a ganglionic cell, which gives off similar processes in abundance. Only one of them constantly enters into the described relation with the olfactory nerve-fibers. Each of these cells of the brain is connected with quite a number of olfactory fibers. Such cells, varying in form and size, lie in large numbers in the gray layer under the glomeruli. Each sends its neuraxon centrally; it may be followed as far as the layer of medullated fibers. At times it gives off collaterals on the way. Here is a good example of what was spoken of in the chapter on the combination of the tissues of the central organs. The primary and the secondary olfactory pathways are seen directly before you, and it is recognized that the connection is brought about through the splitting-up of the neuraxon of the primary pathway and its contact with the dendritic processes from the secondary.

A number of other elements (the nervous nature of which is still in doubt) were also found in the cortex of the alfactory bulb. Between the cells mentioned and the layer of medullated fibers, partly within the same also, lie the cells hitherto designated as "granules." I have shown three types of these in the accompanying illustration (*a*, *b*, *c*). Moreover, cells with a very much branched neuraxon are everywhere present (*e*).

The fibrous net-work, which all these elements form, is naturally made much more complicated on account of the fact that the neuroglia-cells lie everywhere within it, and that the processes of the ventricular epithelium extend far into the substance of the bulbus olfactorius. The illustration, combined, in the main, from drawings by *Van Gehuchten*, was kept as simple and diagrammatic as possible. Everything must be imagined much denser and richer in fibers and cells.

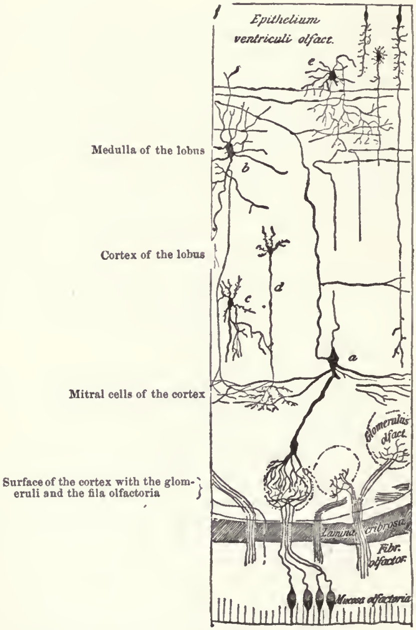

Fig. 142.—Section through the olfactory mucous membrane, the lamina cribrosa, and the bulbus olfactorius. The elements are combined schematically, but the relations, especially the branching and form, are taken from preparations.

The entire formation of the bulbus may be easily traced back to the common cortical type. If Fig. 142 is turned upside down and compared with Fig. 152, that fact is apparent at once. The text to the left of Fig. 142 is intended to simplify the comparison. The entire formation of the *bulbus* is there designated as the cortex of the *lobus.*

The gray mass of the bulbus sends backward the central secondary and tertiary pathways of the olfactory apparatus. First of all, such a pathway extends constantly to the surface of the lobus, where, now splitting up into several, now into fewer, strands, it passes backward. In so doing small fibers continually pass down from this *lateral olfactory radiation* deep into the cortex of the lobus. Yet the tract is not exhausted by this; on the contrary, its fibers, passing over the olfactory area, extend farther backward until in the region of the nucleus amygdalæ. All of these fibers have a large diameter, and have been known for a long time as the *roots* of the *olfactory nerve.*

In the description of the lower vertebrate brain they have been more closely followed, and we have been able to confirm the fact that a part certainly passes into the cortex of the olfactory lobe, just as in the mammals above, and that, in addition to these tractus bulbo-corticales, a tract of fibers is present, which, running in a similar course, soon separates and ends in the epistriatum. This epistriatum has not yet been found in mammals, because only now are we in a position to seek for it, seeing that its existence has been recognized so distinctly in lower brains. Nevertheless, it is very probable that good guides to that still-undiscovered portion of the brain are possessed in those tracts of fibers that extend into the more posterior region: into the lobus pyriformis and into the neighborhood of the nucleus amygdalæ.

From the olfactory radiations from the bulbus there must be distinguished a tract which hitherto has been regarded as part of it, and called the *mesial root* of the olfactory nerve. There develop, namely, from the *medulla* of the *bulbus,* numerous finer nerve-fibers, which pass away *beneath* the cortex into the medulla of the lobus. In it they mix with the medullated fibers of the lobus in such a manner that they are not separable at present. At the posterior end of the lobus, directly in front of the olfactory field, however, a tract, which lies in its continuation, leaves the lobus and passes beneath the thin cortex of the olfactory lobe upon the inner surface of the brain. The cortex is raised up somewhat by this tract. This *mesial olfactory radiation,* passing on the inner side of the brain to the septum pellucidum, extends over this into the fornix, and from there into the cornu Ammonis. It is always less white than the lateral radiation, on account of the thin cortical covering.

A fissure separates the lobus olfactorius posterior from the *lobus hippocampi.* This structure, always uncommonly large in the osmatic animals, contains the inrolling of the cornu Ammonis at its mesial edge. It is hardly to be compared with the small, relatively atrophied convolution of the cornu Ammonis, the gyrus hippocampi, in man. At the base of the brain the gyrus hippocampi follows the entire edge of the hemisphere, passes up posteriorly on to the mesial surface of the brain, and here runs forward some distance. Its subiculum, the cortex, which is not inrolled and lies directly on the base of the brain, then passes immediately over into the *lobus supracallosus—gyrus fornicatus* in man.

In man the hippocampal gyrus does not extend up under the corpus callosum.

Since the lobus supracallosus turns down anteriorly to the base of the brain and appears to reach again the olfactory area with its most anterior end, this entire portion of the cortex forms a kind of arch around the margin of the hemisphere. *Broca,* who first discovered that the various cortical tracts entering it all stand in a direct relation as to size with the development of the olfactory apparatus, has designated the *lobus limbicus*—as he named the entire area—as the olfactory cortex.

It is a question with me whether the gyrus fornicatus belongs to the olfactory apparatus.

The lobus limbicus is always separated from the rest of the brain by a large, distinct fissure: the *fissura limbica.* Its upper, curved portion has already been met with in man as the sulcus cinguli. According to the investigations of *Zuckerkandl,* the gyrus dentatus and its continuation upon the upper surface of the corpus callosum, the stria of *Lancisi,* must also be included in the lobus limbicus. All of these gyri which thus surround the edge of the hemisphere—the lobus olfactorius, the gyrus hippocampi, and the gyrus fornicatus, the stria of Lancisi and the fascia dentata—are very strongly developed in animals having highly perfected olfactory organs. They are somewhat atrophied in those animals which have small olfactory lobes, as is the case with man. In the dolphin, which has no olfactory lobe, they are developed the least of all (*Broca, Zuckerkandl*). These parts of the brain, belonging manifestly to the olfactory apparatus, are included with the lobus olfactorius under the term *rhinencephalon,* suggested by *Turner.* The elements of the rhinencephalon, the sulci and gyri, may be demonstrated in all mammals with a certain constancy of arrangement.

The separate parts of the lobus limbicus of the right and left side are connected with one another by a large commissural system: the *commissura anterior.* Its anterior pedicle arises in the lobus olfactorius of the one side, and, curved in the shape of a horseshoe, passes over at the base of the brain to the lobus of the other side. A posterior pedicle unites the lobi cornuum Ammonis, or at least the regions of the cortex which lie directly without the in-rolling of the cornu Ammonis. Finally, an ascending branch of the anterior commissure is recognized in many mammals. It passes into the capsula externa and is well adapted to connect the dorsal part of the marginal gyrus with parts lying opposite.

The cornua Ammonis themselves possess a distinct communication with one another: an extensive system of fibers extends between them. It is called the *commissure* of the cornu Ammonis, or the *psalterium.*

The cornu Ammonis is connected with the olfactory lobe by the mesial olfactory radiation already mentioned. As the tractus cortico-olfactorius septi, it was first seen to appear in the reptiles; the greatest part of its course is visible in Fig. 144. In the higher mammals and in man the tract is not to be recognized without further study, and by no means as readily as in the brain of the marsupial, shown in Fig. 123. Nevertheless, *Zuckerkandl* has succeeded in demonstrating its existence in an entirely satisfactory manner, and this wholly independently of the more recent, comparative anatomical considerations. He has named it the *olfactory bundle* of the *cornu Ammonis.*

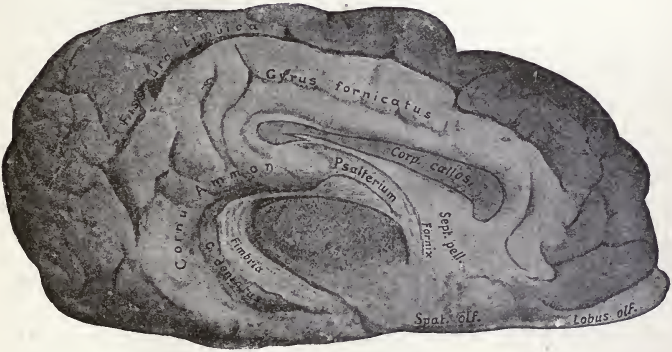

Fig. 143.—Median sagittal section through the brain of a calf. The lobus limbicus is shown somewhat lighter.

The greater portion, at all events, springs from the medulla of the olfactory field. The large tract of fibers arises on the under side of the brain in the cortex of the olfactory area, then turns over this toward the median line (see Figs. 141 and 144) and passes along beneath the gyrus subcallosus (Figs. 133 and 135) dorsally, up to the septum pellucidum. In the septum a part of the fibers cross and another part goes directly backward. Both bundles, reunited, meet with the fornix at the posterior margin of the septum and run farther backward in it as far as the medulla of the cornu Ammonis.

For that which follows, compare especially Fig. 144.

The olfactory lobe and the olfactory field have, in the main, received the afferent tracts, the olfactory-nerve pathways of the second order, from the bulbus olfactorius. It has been learned in earlier chapters that both of these brain-parts are everywhere present, from the fishes on upward.

The lobus pyriformis and the cornu Ammonis are, indeed, parts which are connected with the olfactory apparatus; nevertheless, they are characterized by their structure as immense separate territories which are able of themselves to bring about the most manifold associations, etc.

They are most probably the *cortical areas of smell*; their very large development also argues in favor of this.

Let us now examine more closely what tracts they receive and what others they give origin to.

The cortical area of smell receives its tracts, on the one hand, through the olfactory bundle; on the other, through the fibers running superficially in the layer of tangential fibers. But what tracts does it send out? These collect at its mesial edge as the *fimbria* (Fig. 143), and then pass toward the anterior. It is soon recognized that they belong to at least two different systems. A large part separates at the anterior end of the gyrus hippocampi, and even somewhat farther posteriorly also, and passes over to the cornu Ammonis of the other side. These connecting fibers, in their entirety, are called the *psalterium.* These are the mesially-lying fibers. From the more lateral fibers, however, another bundle is collected. Tracts, directed for the most part longitudinally, here pass forward and run for a short distance next to the olfactory bundle, entering at this point, but soon leave it again to pass backward in a downward-directed course. These are the *fornix.* It ends near the base of the brain in the corpus mamillare and also in the opposite thalamus. *The fornix is consequently that part of the medulla of the gyrus hippocampi which, not used for commissures, connects this medulla with the interbrain.* With the "descending fornix," as that part is called in contradistinction to the bundle running longitudinally forward from the cornu Ammonis—the "ascending fornix"—there is associated, however, another tract of fibers which arises from that part of the marginal gyrus that is not inrolled to form the cornu Ammonis, the gyrus limbicus. In order to reach down to the fornix its tracts must pass through the corpus callosum, which always covers over the ventricle in mammals. The bundle is called the *fornix longus.* Its fibers always lie just under the corpus callosum and anteriorly, forming the most mesial bundles of the pillar of the fornix; they pass down with this to the bottom of the interbrain.

It is very probable that the descending fornix, as well as the fornix longus, receives in its course fibers from the opposite olfactory cortex by way of the psalterium.

In the smaller mammals the relations of the fimbria and the psalterium, as well as of the fornix, are better known than in man. This is because, on the one hand, they are relatively much larger structures in the osmatic animals investigated than

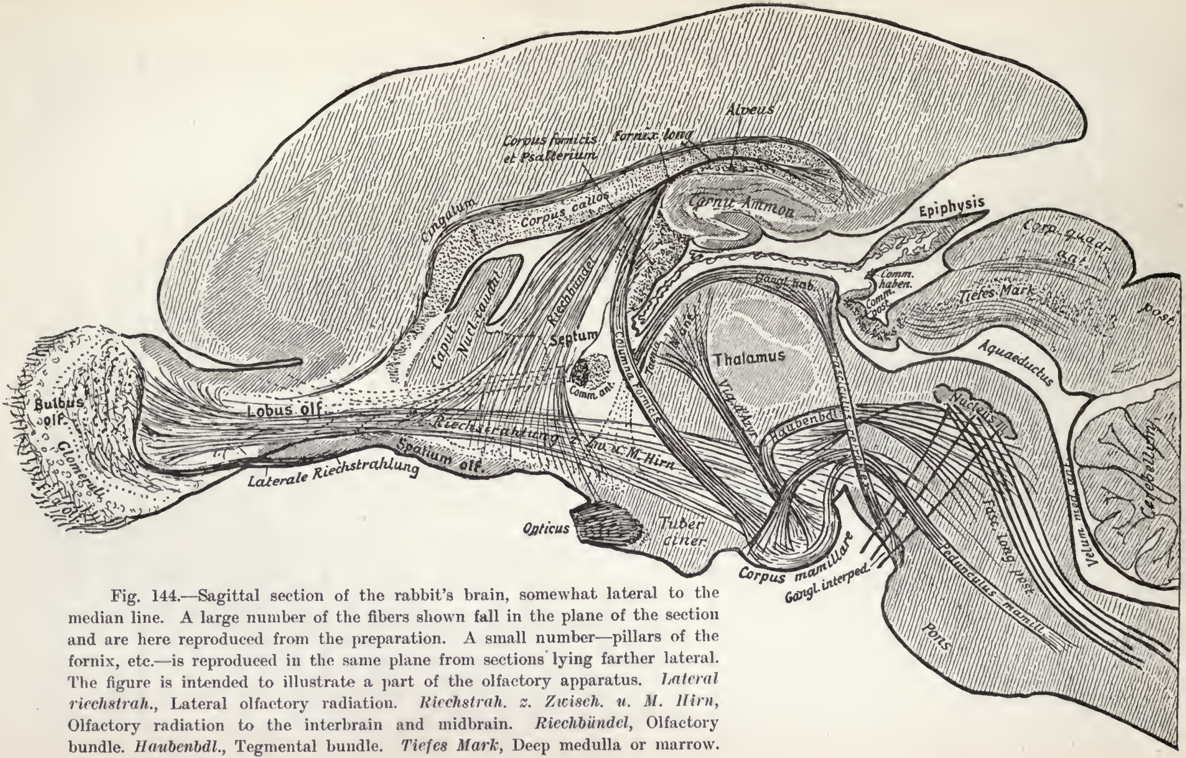

Fig. 144.—Sagittal section of the rabbit's brain, somewhat lateral to the median line. A large number of the fibers shown fall in the plane of the section and are here reproduced from the preparation. A small number—pillars of the fornix, etc.—is reproduced in the same plane from sections lying farther lateral. The figure is intended to illustrate a part of the olfactory apparatus. *Lateral riechstrah.*, Lateral olfactory radiation. *Riechstrah. z. Zwisch. u. M. Hirn*, Olfactory radiation to the interbrain and midbrain. *Riechbündel*, Olfactory bundle. *Haubenbdl.*, Tegmental bundle. *Tiefes Mark*, Deep medulla or marrow.

in man; on the other, because *Gudden*, with a masterly hand for experimentation, was able to throw abundant light on this very region of the anatomy of the fornix by experiments on animals.

The fornix longus has been demonstrated in man only recently by *Kölliker.*

In many of the smaller animals the fibers of the psalterium, the decussations in it, the decussation of the fornices longi, and the crura fornicis at their turning-point into the depths of the central gray matter, together form a single thick mass, which has been designated as the *corpus fornicis.*

The olfactory lobe and the hippocampal lobe possess, in addition to those mentioned, a number of tracts that are fitted to connect them with one another or with other regions. Thus there runs dorsally on each side of the median line of the corpus callosum along its entire length a delicate bundle of large fibers, the *stria longitudinalis medialis*, which, arising in the dorsal regions of the hippocampal cortex, curves down anteriorly over the corpus callosum and radiates into the septum pellucidum. Then it is known that a long bundle, the cingulum, running in the gyrus fornicatus sends tracts into the olfactory cortex, as well as into the other parts of the marginal gyrus.

All these tracts belong to the cortical centers of the olfactory apparatus. There are, however, connections between the olfactory apparatus and the interbrain which must be very important, because they are well developed in all animals, even in those without a cerebral cortex, and are everywhere demonstrable. In order to understand them, we must return again to the medulla of the lobus olfactorius. It is known that this arises, for the most part, from the bulbus. Posteriorly it continues directly into the medulla of the olfactory field. We have already become acquainted with one connecting tract of this *"deep olfactory medulla"*: the *olfactory bundle* to the *cornu Ammonis.*

The olfactory medulla possesses at least two other connections. One of these tracts, consisting essentially of fine fibers, runs backward and can be followed as far as into the region of the corpus mamillare. In its course it must pass through the most ventral regions of the corpus striatum; but it receives no fibers from this—as has been supposed.

Certain of these fibers proceed still farther posteriorly, as far as into the region of the ganglion interpedunculare; perhaps into the fillet also.

A second tract, originating essentially from the lateral parts of the medulla of the olfactory area and passing through the forepart of the thalamus, rises to the inner surface of the ventricle, and passes along this, backward to the ganglion habenulæ. It is the *tænia thalami.*

In a dog's brain, in which the entire cerebral cortex had been removed eighteen months before death and the entire radiation from the mantle was wanting as a

consequence, the cortex of the olfactory area alone remained intact. From this, the olfactory radiation could be traced backward very clearly and distinctly to the corpus mamillare and upward as the tænia thalami to the ganglion habenulæ. The fibers must have their origin in the olfactory field itself, for the tænia was not degenerated, although the fibers had accidentally been badly injured just in front of the ganglion habenulæ on both sides during the operation.

The olfactory fibers have thus been followed, on the one hand, as far as into the cerebral cortex, and, on the other hand, as far as into the ganglion habenulæ and into (?) the corpus mamillare. It will be seen, later, that still other ganglia of the midbrain and interbrain stand in intimate connection with these ganglia.

In mammals (*Lotheissen*) fibers from the fornix also mix with those of the tænia thalami, exactly as in reptiles (see above).

The entire olfactory apparatus thus appears as a huge complex of ganglia and bundles running through the greater part of the brain. In the subsequent chapters its separate parts will be constantly met with.

It has been seen that a not inconsiderable portion of the surface of the brain owes its perfection essentially to the development of the olfactory apparatus. All the gyri and tracts belonging to this are constantly demonstrable in the same place and in a similar relation.

The development of the remaining portion of the mantle and the fissures running in it is much less constant. You will remember that the development of the brain is limited by other factors than those of the cranium, that the presence and the course of the fissuration is determined by the resultant of at least two different developmental tendencies, as has been explained in the preceding chapter.

Fissures that are deep and long in man may be entirely wanting in closely related animals; others, only suggested in man, are at times well developed in animals.

In some mammals, the fissura Sylvii, for example, one of the fissures most frequently present, is not present at all or indicated by a shallow sulcus only. The other sulci may assume the most various directions. In general, however, it may be recognized that there are essentially three principal directions: fissures running parallel with the longitudinal fissure, *sagittal*; fissures curving around the Sylvian fissure, *fissuræ arcuatæ*; fissures, finally, of a more or less *vertically* ascending type, *fissuræ coronales*. In the human brain the central sulcus is a good example of the last; sagittal sulci traverse the frontal lobe, and arcuate sulci surround the Sylvian fissure in the temporal and parietal lobes. It is precisely the vertical fissures which are in most cases but feebly developed in animals. On the bear's brain (Fig. 145) the central fissure is certainly relatively long. Make use of this well-known fissure, in order to facilitate the comparison with the human brain. The frontal lobe, lying in front of it, is seen to be very much less developed than in Fig. 130. It is difficult to homologize the frontal sulci. The central fissure runs more vertically, probably on account of the imperfect development of the frontal lobe; likewise all the parts lying behind it are, in a measure, pushed upward, the fissura Sylvii standing almost vertically. Arcuate fissures surround the fissura Sylvii, on which, upon comparison with Fig. 130, a similar arrangement is readily recognized after a moment's consideration: how these pass over into the temporal sulci and the interparietal fissure.

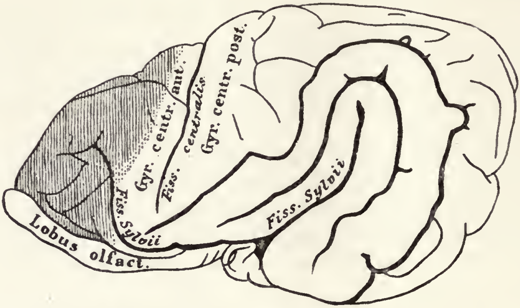

Fig. 145.—Brain of a bear. The frontal lobe is shaded. (After Turner.)

Fig. 146.—Brain of the narwhal: *Monodon monoceros.* (After Turner.)

The Sylvian fissure is more vertical in all animal brains than in that of man; it is more horizontal the more the frontal lobe is developed. It is commonly relatively short.

In the vertebrate series arcuate fissures occur more frequently than any other. On the richly convoluted brain of the narwhal they form the type of the entire fissuration (Fig. 146).

They are numbered, counting from the Sylvian fissure out, as the first, second, etc., arcuate fissure, or they are also named as: fissura ectosylvia, fissura suprasylvia, etc. On the brain of the dog, which here follows, a number of these fissures are again recognized from the form and the location. At the posterior boundary of the frontal lobe a short sulcus passes downward in a vertical course: the fissura cruciata. It probably corresponds to the fissura centralis; yet the identity of the two fissures is not undisputed. As was mentioned in the second chapter, the brains of many animals are entirely smooth. On others there are found only slight indications of sulci. On many brains—for example, those of the horse and the cow—the arcuate type is only distinct in the territories lying next to the Sylvian fissure—toward the edge of the brain the fissures have a more sagittal course. It would be too much of a digression to mention what is at present known concerning the direction of the sulci in the various classes of animals. The examples given are only intended to illustrate certain types and to serve as an introduction to studies of your own.

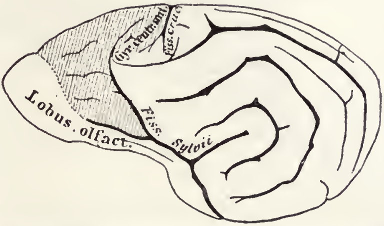

Fig. 147.—Brain of a dog. The frontal lobe is shaded.

Our knowledge of the course of the convolutions of the brain comes from the investigations of *Burdach* (median surface), *Leuret, Gratiolet, Meynert* (comparative anatomy), *Bischoff, Ecker,* and *Pansch* (growing and adult brain). Moreover, there exist numerous investigations on separate regions of the brain: on the gyri running near the margin of the brain by *Broca* and *Zuckerkandl*; on the frontal gyri by *Eberstaller* and by *Hervé*; on the insula by *Guldberg*; further, accurate studies on the development and course of single fissures by *Rüdinger, Cunningham,* and others. Besides this we possess very many monographs on the brain-surface of various mammals; on anthropoid apes by *Bischoff, Waldeyer,* and others; on lemurs by *Flower* and *Gervais*; on whales by *Guldberg, Ziehen,* and *Kükenthal*; on ungulates by *Krueg, Ellenberger, Tenchini,* and *Negrini*; on carnivorous animals by *Meynert,* *Spitzka*, and others. For recent compilations, criticisms, and comparisons, we are especially indebted to *Turner*, then to *Ziehen* and *Kükenthal*. The numerous variations from the type described, whether they may exist normally or on account of malformations, have received consideration from most of the above-mentioned authors, but particularly from *Richter*, *Sernow*, and others.

For the olfactory apparatus, the older investigations of *Meynert*, *Ganser*, *Bevan Lewis*, and others, are the foremost. The description given in the text follows personal investigations made in common with *Dr. Flatow*. More recent important researches come from *Kölliker* and from *Löwenthal* ("degeneration" experiments). Finally it must be emphasized at this point that, as the excellent investigations of *Elliott Smith* show, the brains of the marsupials and the monotremes present especially clear and simple relations for the central olfactory apparatus.

A perusal of the work of this investigator is particularly recommended.

It does not lie within the scope of this text-book to impart the rich store of facts concerning the functions of the separate parts of the brain which pathology has ascertained. The study of the function of the cerebral cortex is still entirely in its infancy, and is in nowise concluded. It may be said, in general, that more is positively known about man than about animals concerning the phenomena occurring after injury to the cortex. The following comprehends a short summary only of these symptoms:—

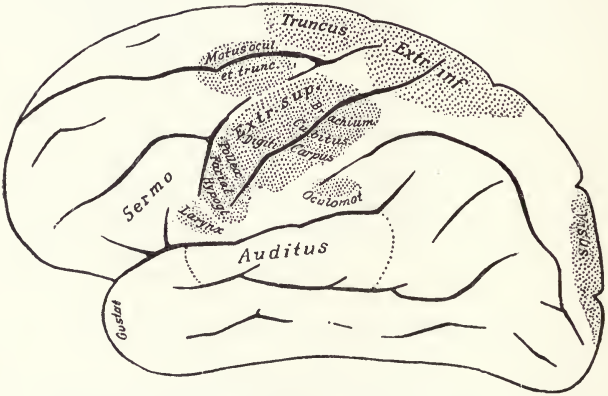

Fig. 148.—The projection areas of the cortex at present known.

Injuries that involve the normal structure and the normal function of the cerebral cortex produce, in man, different symptoms, according to the place where they are located. Up to the present time, several hundred carefully observed cases of disease of the cerebral cortex have been known, and, by comparing these with one another, the following conclusions may be arrived at:—

Motor symptoms of irritation (from the twitching of a single muscle up to epilepsy) may arise from any point of the cerebral cortex. There exists a zone of the brain, embracing the two central gyri, after disease or injury of which disturbances in motility almost always appear on the opposite side of the body. These disturbances are divided into phenomena of irritation and phenomena of degeneration. The symptoms of irritation are expressed by spasms or convulsive movements; the symptoms of degeneration by a more or less high degree of inability to set the muscles in motion at will, oftentimes only in a sense of weakness, or by awkwardness in executing complicated movements.

From an accurate analysis of the known cases of disease, it may be stated that, in disease of the upper part of both central gyri and of the paracentral lobule, the motor disturbances manifest themselves preponderantly in the legs; that, if the inferior end of the central gyri is involved, the regions of the facialis and the hypoglossus are affected, and that motor disturbances in the upper extremity especially may be produced by disease of about the middle, and a portion of the upper, third of these gyri. The separation of the "centers" from one another is not a distinct one.

Complete destruction of separate parts of the central gyri may lead, in man, to permanent paralysis of the muscles connected with those parts. The paralyzed muscles almost always fall into a state of contracture.

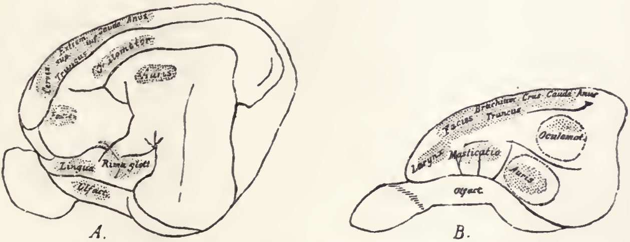

Fig. 149.—The cortical areas, as far as they are demonstrable by irritation. *A*, Cat. *B*, Rabbit. (After Mann.)

Diseases or injuries that involve the cortex of the left inferior frontal gyrus or the left insula generally lead to a more or less complete loss of speech, although the vocal organs may still be normally innervated and the patient may often perfectly understand all that is said. It appears that the ability to understand whatever is said even in a loud voice is lost if the superior temporal gyrus is affected. The ability to comprehend reading has been repeatedly seen to be lost after lesions of the cortex situated between the apex of the occipital lobe and the posterior end of the Sylvian fissure. Perhaps deep tracts are here involved, and it is not a question of cortical localization.

Lesions in the region of the occipital lobe may lead to disturbance of vision, manifested as a dimness of vision or blindness on the outer side of the eye on the affected side and on the inner side of the other eye (see below).

The preservation of the cuneus appears to be especially important for the comprehension of what is seen.

Sensibility may also suffer from affections of the cerebral cortex. Feelings of numbness, heaviness, and marked disturbances of the muscular sense are frequently observed. As a rule, the sense of touch at first appears to be blunted so far as the judgment of what is felt comes in question, but very slight stimuli may be recognized as tactile irritants if they are of a very simple nature (as touching with a downy feather, needle-point, etc.). Areas of the cerebral cortex from which disturbances of sensibility arise more frequently than from lesion of others are not definitely known. At all events, such disturbances may appear after lesions situated in the territory of the central gyri and their neighborhood. It is very probable that lesions of the cornu Ammonis, perhaps of the remaining parts of the marginal gyrus also, may produce disturbances in the sense of smell.

The paralyses that arise from affections of the cerebral cortex alone are never so complete as those produced by the destruction of the peripheral nerves or their proximal ends in the spinal cord. In animals it is generally impossible to obtain permanent paralyses by the removal of the cortex in the motor zone, or the removal of the entire portion of the brain that contains this zone. Nevertheless, upon irritation of circumscribed areas of the cerebral cortex in these same animals the same muscles may nearly always be made to contract from the same cortical area.

And now, having become acquainted with the location of the cortical centers in man, let us cast a glance at the illustrations shown in Fig. 149. They show, according to the experiments of *Mann*, what parts of the surface of the mammalian brain are at present known to have a definite function.

This leads us back to what was said in the twelfth chapter respecting the *significance of the mantle as a collection of individual centers and areas of association.* It is immediately recognized that much that is found in the brain of Primates is not present at all in the lower mammals, or is so small as not to be demonstrable.

For a better understanding of the physiological *status* of the mantle of the brain, consider again what was presented on page 173, and, moreover, recollect the experiments of *Ewald*, mentioned on page 44. These show that many things are necessary for the orderly execution of the acquired movements, and that, where lesions exist, one factor or another may occasionally compensate for what was lost.

It may truly be said that the mantle of the brain increases in mass as, ascending in the vertebrate series, new centers are established in it: cortical areas that are concerned in the execution of movements for the inhibition, recognition, and interpretation of sensory impressions, and, probably in a large measure, for association also.

CHAPTER XV.

THE CORTEX OF THE FOREBRAIN AND THE MEDULLA OF THE HEMISPHERES; THE COMMISSURES AND THE CORONA RADIATA.

A GENERAL survey has now been attained of the outer form-relations of the brain. The present chapter is intended to familiarize you with the structure of the cerebral cortex and to give an insight into the mode of connection of the cortical regions with one another and with the deeper-lying structures.

The finer structure of the cortex is known in its elements only. Knowledge of the combinations of these elements with one another is still wanting, and therewith, unfortunately, a proper understanding of the anatomical basis of the great organ of the mind. There is hardly a doubt but that the cerebral cortex, as a whole, may be regarded as the place where most of those cerebral processes take place which arise in consciousness, that it is the seat of memory, and that the voluntary acts proceed from it.

The entire hemisphere is covered by the cortex. This has not, however, exactly the same structure everywhere on the convexity. Even if a sort of fundamental type exists, greater or lesser differences in the layers, in which the ganglion-cells and nerve-fibers are arranged, may, nevertheless, be found, depending on the region of the brain investigated. One cortical type never passes abruptly over into another. Inasmuch as the significance of these anatomical variations is not understood, one region only, the frontal lobe, will be considered at present.

A dense net-work of fine, medullated fibers, mostly running parallel with the surface, lies close under the pia, but is separated from it by a thicker layer of neuroglia. It is the *layer of tangential fibers* (Fig. 150). Cells are distributed in it in relatively-small quantity. Directly beneath it, however, begins the layer of the *pyramidal cells*—cells distinctly typical of the cortex. They appear first as a layer of numerous smaller elements (2, Fig. 150), which passes over into the *layer of* the *large pyramids* (3, Fig. 150). All of these cells send their dendrites toward the surface of the cortex and in various other directions, as the apical process, lateral processes, etc., and, for the most part, send their neuraxons deep down into the medullary layer. The layer of the large pyramidal cells in the frontal and parietal lobes is the broadest in section of any of the cortical layers of these lobes. The in-

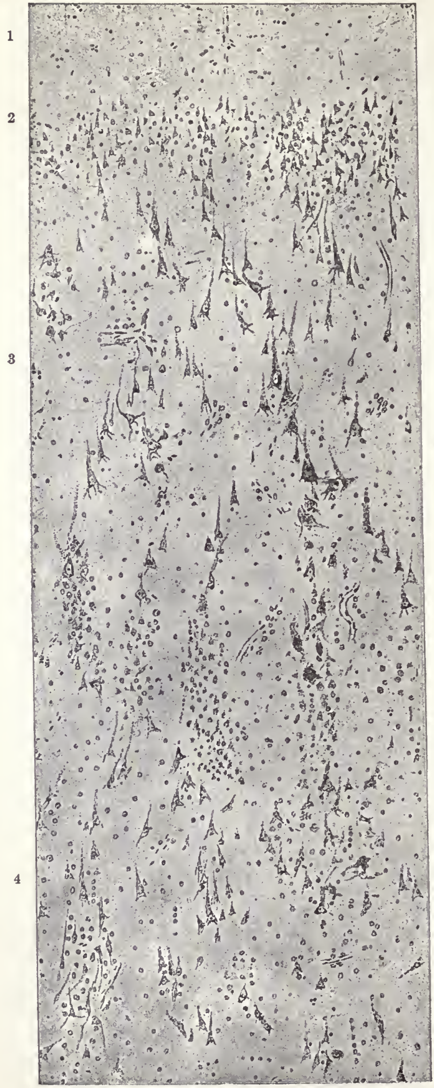

Fig. 150.—Section through the cortex in the middle of the right superior frontal gyrus. From a man 20 years old. (After Nissl.)

dividual cells are larger and their apical processes longer, the farther the cells lie from the surface. The fourth layer of cells, lying beneath the large pyramids, consists again of smaller cells, not uniformly distributed. They are wedged in between the radiating masses of medullated fibers passing into the cortex.

Besides the pyramidal cells mentioned, there is scattered in all layers of the cortex a large quantity of smaller, polygonal cells, the neuraxons of which split up completely very soon after leaving the cell.

In Fig. 150 these cells appear as numerous, clear, polygonal structures lying everywhere in the neighborhood of the pyramids.

In order to become acquainted with the histology of the cortex, it is necessary to employ several methods. Each shows a different picture, and only by combining these is there obtained an accurate conception of it as a whole. Since a small part only of the cells is visible in Fig. 151 (left side), a section is here shown in Fig. 150 accurately reproduced by *Nissl* from an alcoholic preparation. It may be of good use to you in practical work.

The medullary rays separate, on reaching the cortex, into numerous fine tracts, and these become gradually lost in the more superficial layers of the cortex; that is to say, become connected with the neuraxons of the cells. Besides these tracts, numerous other medullated nerve-fibers are seen in the cortex. Until recently the origin and destination of these fibers were entirely unknown. Lately, however, the investigations by *Golgi*, *Martinotti*, and especially by *S. Ramón y Cajal*, have acquainted us with a great number of new relations in the cerebral cortex; so that it now appears possible to consider the separate elements in their various combinations. It is true, most of the facts have been recognized on the cerebral cortex of small mammals, and a few only have been confirmed for man. Thus, much work still remains to be done. What is known, however, takes us such a good step forward that I must impart it to you. In order that I might make my description brief, I have represented the most important discoveries combined in a single drawing (Fig. 152).

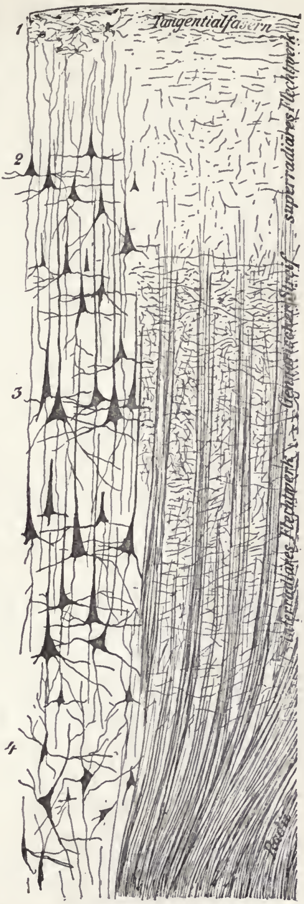

Fig. 151.—Section through the cortex of a frontal gyrus. The right half is reproduced from a preparation stained with *Weigert's* hæmatoxylin, the left half from preparations made by *Golgi's* sublimate method. On the right the fibers only are to be seen; on the left the cells only. More cells are present than are shown in the drawing. Since the spaces around the cells and their processes are filled by *Golgi's* method, these appear to be larger than they really are. *Tangentialfasern*, Tangential fibers. *Superradiäres Flechtwerk*, Superradial net-work. *Gennarischer Streif*, Line of *Gennari*. *Interradiäres Flechtwerk*, Interradial net-work.

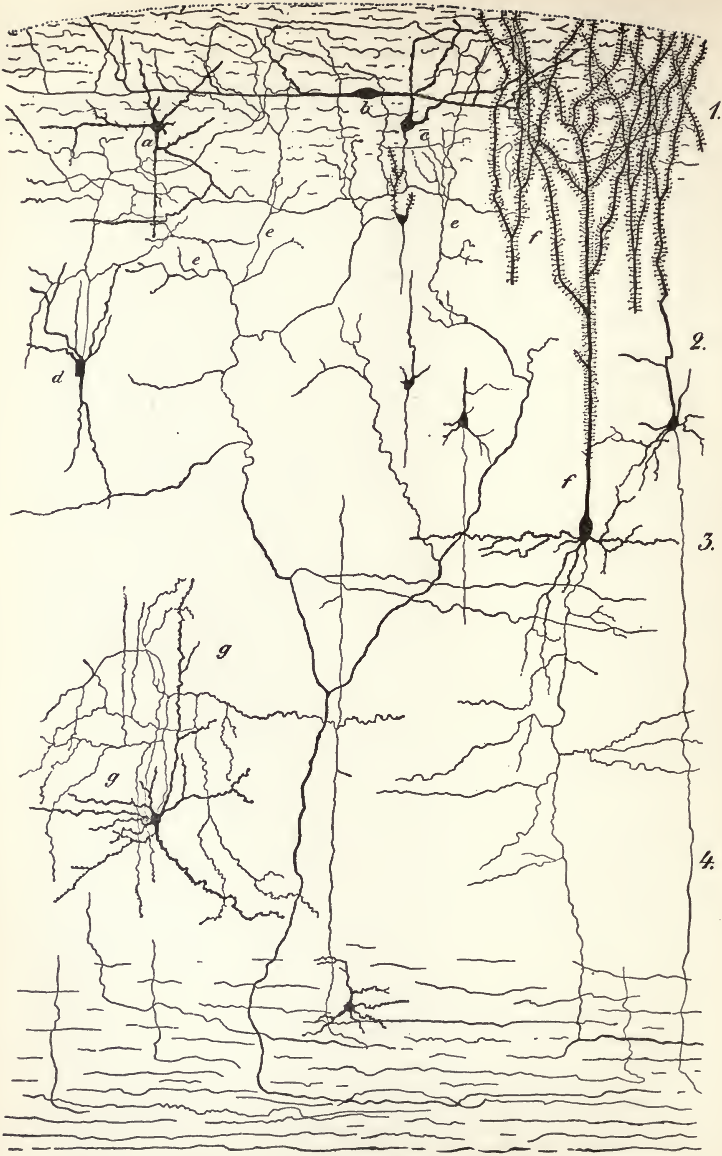

Fig. 152.—Section through the cerebral cortex of a mammal. (Combined from preparations by S. Ramón y Cajal.)

The outermost layer contains numerous nerve-fibers running, for the most part, in a tangential direction. These arise from ganglionic cells (*a*, *b*, and *c*), all of which possess several neuraxons, and from small fusiform cells (*d*) of a deeper layer. Two kinds of elements enter this outermost zone. Large fibers (*e*), mostly medullated, which pass into the cortex from the medullary layer, are traced in their outermost ramifications into this layer. They must originate from ganglionic cells that lie in other parts of the brain. The caliber of the fibers speaks especially for a distant origin. Then the dendrites of the more deeply situated pyramidal cells (*f*) end in this layer in dense, profuse ramifications. Numerous fine secondary twigs, terminating in little knobs, project from each of the small branches. The ramification is so dense that exceedingly abundant opportunity is afforded for the contact of the dendrites of deep cells with similar dendrites and the neuraxons of cells lying in this locality. Even the most daring phantasy of speculative psychologists has hardly allowed itself to imagine such an abundance of possible combinations as has here been revealed of the dendrites with neuraxons of cells which have very different locations.

And, moreover, every cell is, and remains, an independent individual, not here only, but everywhere else in the cortex. Direct union is nowhere recognized; connection by contact alone is observed throughout.

The layer of small pyramidal cells lies under the layer of tangential fibers. It passes very gradually over into the layer of the large pyramids (3). The neuraxons of all these cells pass in a direction toward the medullary layer; they give off numerous collaterals. Many neuraxons divide near the medullary layer into a horizontal and a descending branch. From these fibers arise the tracts which connect the cerebral cortex with deeper-lying centers and which connect distant cortical centers with one another.

The dendrites extend a greater or less distance out toward the periphery, and some of them end only under the pia.

Near the medullary layer, below the well-defined pyramids, lie numerous irregularly triangular, also small pyramidal, cells. As regards the course of their neuraxons, as well as their dendrites, they are analogous to the pyramids, but they present more irregular forms and a less dense ramification. In this deepest layer are found numerous multipolar cells (*g*), the neuraxons of which may run in the most various directions: horizontal, ascending, descending, etc. The neuraxon is always characterized by the fact that, after a short course, it breaks up into a wide, complicated arborization, the terminal fibrils of which all end freely. Moreover, such cells are also present in almost all of the other layers of the cortex. With their extensive ramification, they are well adapted to connect other cell-groups with one another physiologically.

The innumerable neuraxons with their collaterals and the numerous fibers passing into the cortex from other parts of the brain together form, as would be expected, an extraordinarily dense net-work. It was only possible to untangle this complex through the happy circumstance that the method of *Golgi* always impregnates, at the most, relatively few cells in any one section. The same net-works of fibers, as shown in Fig. 151 by the myelin-staining method, may be demonstrated with the staining of the cells, but in the latter case they are much more compact and solid. It appears that the neuraxons of most of the cells in the cortex, and the collaterals, also, which arise from the neuraxons of the pyramids, possess a medullary sheath.

So long as we are unable correctly to name all of these fibers according to their function, it will be advantageous, for the sake of clearness,—*e.g.*, in investigations in pathology,—to introduce *provisional names* for them.

Let us distinguish (1) the radii, medullary rays; (2) the interradial net-work, consisting mostly of fibers running parallel with the surface; (3) the superradial net-work, and (4) the tangential fibers. Along the boundary between the superradial and the interradial net-works, the latter becomes greatly thickened. This layer, everywhere visible to the naked eye as a white line, is so much thicker in the region of the cuneus that it is there very easily recognized. It is designated as the *line* of *Gennari*, or after its later describers as the *line* of *Baillarger*, or the *line* of *Vicq d'Azyr* (in the cuneus particularly). In the occipital lobe, however, the line lies somewhat

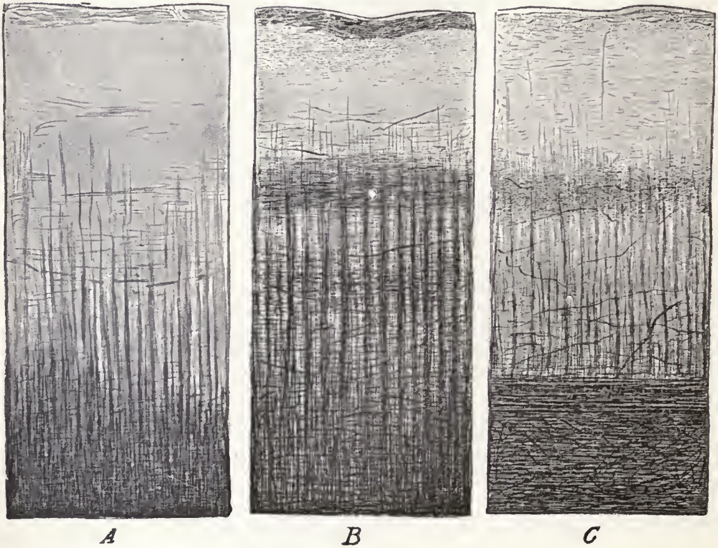

Fig. 153.—Three sections through the cortex of the anterior central gyrus. *A*, From a child $1\,^1/_4$ years old. *B*, From a man 36 years old. *C*, From a man of 53 years. Myelin staining. Controls have shown that the differences are essentially occasioned by the age. Yet the possibility that a different amount of use of the cortical region under discussion may have added in some degree to the difference cannot be overlooked. (After Kaes.)

deeper in the third layer, nearer to the fourth, and not so high up as is shown for the frontal lobe in Fig. 151.

The medullated fibers in the superradial net-work probably come, for the most part, from fibers radiating into the cortex from without. It is very questionable whether the cells with the short, branched neuraxons have medullated processes. The line of *Gennari* is formed entirely by the collaterals of the neuraxons from the pyramidal cells. The interradial network consists likewise of the collaterals from the neuraxons of the pyramidal cells, and perhaps also of the arborization formed by the cells with the short, branched neuraxons.

It must not be expected that these lines, etc., will be found uniformly well developed. Disregarding the fact that they are variously well defined, according to the zone of the cortex, developmental investigations also show that very considerable differences may exist according to the age. Probably it will be proved, when we at last recognize a fixed type for all the parts of the cortex and all ages of life, that definite relations exist between the intelligence of the individual and the number of fibers in his cortex.

The discoveries of *Kaes* along these lines are promising much. He was able to show by means of numerous accurate measurements that *the cerebral cortex increases in richness of fibers for a long time, even to the fortieth year and longer.* Tracts come particularly under consideration that pass along within the basal portion of the medullary rays in a direction parallel with the surface, fibræ arcuatæ intracorticales, and then tracts of fibers which, lying within the superradial net-work, follow closely on the layer of tangential fibers. Medullation occurs here very late in some portions of the cortex; so that a very great part of the cortex below the layer of tangential fibers is gradually traversed by delicate fibers. According to *Kaes,* still larger medullated fibers are added to these, which, in the course of years, are seen to extend very gradually toward the surface of the cortex from the layers lying next to the medulla. It is probably the fibers of this plexus, some very large, which *Bechterew* has described and by which he saw formed a distinct line lying just beneath the layer of tangential fibers: *Bechterew's line.* Fig. 153, which I owe to the kindness of *Dr. Kaes,* illustrates well the different types of cortex and at different times of life.

As far as can be seen at present, these are all *new association-pathways,* or at least pathways which, only called into use late in life, become medullated at a late period. It is possible, also, that we are concerned with collaterals, which, with the greater demand consequent upon increased associations, now attain their complete development: the formation of the medullary sheath. It is known that in other tissues also an acceleration of growth may occur, owing to an increased demand made upon the elements. Thus, the similar process in the cerebral cortex should present nothing that deviates from the known phenomena. It may well be imagined that man creates new pathways for himself by cerebral activity, in the sense that the new formation, or the strengthening of pathways already present, may, as the anatomical basis, correspond to the increased ability for execution which exercising of the brain produces.

As has been previously mentioned, the cerebral cortex is not similarly constructed at all points of the surface. The *cortex in the neighborhood of the fissura calcarina*, for example, is characterized by a preponderance of the small polygonal cells (most of which are clearer) and by a relative poverty of the large pyramidal cells, in addition to the line of *Gennari*.

The conformation of the cornu Ammonis deserves special consideration. Near the median line at the base of the brain, the cortex first turns outward, then directly inward again, and then curves outward again for a short distance (see Fig. 154). The pyramidal cells of the gyrus hippocampi, however, do not, as a consequence, pass over immediately into those of the gyrus dentatus. They end, rather, by being irregularly grouped together (at *a* in Fig. 154), and this irregular mass is then surrounded by the semicircle of regularly arranged cells of the gyrus dentatus. We are now able, without difficulty, to trace the layers of the cornu Ammonis back to the typical layers of the cortex (*Meynert* and especially *Schaffer*). Nevertheless, they present,. in their entirety, so many peculiarities that names which they received earlier are still used in describing them.

In the accompanying illustration let us first follow the cortex from below upward.

That part of the hippocampal lobe upon which the part that is rolled up rests is designated as the *subiculum cornus Ammonis*.

It is covered by an uncommonly well developed layer of tangential fibers, the reticulated arrangement of which is apparent even in the fresh brain. Many of these fibers, traversing the entire thickness of the cortex, appear to extend into the medullary layer of the convolution. At the place where the inrolling begins the layer of tangential fibers becomes thinner, but it accompanies the entire gyrus hippocampi farther and lies, as a glance at the figure must show, directly upon the cortex of the gyrus dentatus. This also possesses a layer of tangential fibers. In man it is difficult to separate the tangential fibers of the gyrus hippocampi from those of the gyrus dentatus; they form together a single layer. The dendrites of the cortical cells extend into this layer exactly as is shown in Fig. 152 for the rest of the cortex: on one side, the dendrites from the cortex of the dentatus; on the other, the dendrites from the cortex of the cornu Ammonis. A second large layer of medullated fibers lies beneath the layer of tangential fibers in the region of the gyrus hippocampi. This curved plate of fibers, the *lamina medullaris circumvoluta*, is a system of association-fibers which arises in the cornu Ammonis and terminates at the place where this is surrounded by the gyrus dentatus.

The fibers must belong to the cortex itself, and not simply penetrate thither, for in a dog in which a single gyrus hippocampi only remained of the entire cerebral cortex, this system was shown to be entirely preserved.

Fig. 154.—Section through the base of the brain and the gyrus hippocampi lying under it. (After a preparation stained with hæmatoxylin-copper-lake.) The plexus chorioideus is drawn somewhat simpler than it is in the adult. Notice that it separates the ventricle from the cavity of the skull, and the manner in which it is done. *Tangentialfasern,* Tangential fibers.

The lamina medullaris circumvoluta lies in the region of the long dendrites, which the cells of the gyrus hippocampi give off. The directing of so many long dendrites outward gives to this stratum a slightly striated appearance on section. It has therefore been designated as the *stratum radiatum.* The cells, themselves, in the hardened preparations, appear to lie in large cavities. Thus, their long curved course appears as a clear layer, and has received the name of *stratum lucidum.* Besides their dendrites, they send a part of their neuraxons also out to the layer of tangential fibers, exactly as in the rest of the cortex. The greater part of the neuraxons, however, pass ventrally, and these, with other fibers, then form a true medullary layer, the *alveus,* which lies directly underneath the ventricular epithelium. The small space between the stratum lucidum and the alveus is filled by numerous fibers passing into the cornu Ammonis and by fibers leaving it. It contains innumerable fiber-branchings and a number of very remarkable association-cells, which we have only recently become acquainted with through *Ramón y Cajal.* They are adapted in consequence of their much-branched neuraxon, which penetrates into the cell-layer of the stratum lucidum, to connect well together the pyramidal cells of the gyrus hippocampi (see Fig. 9). The entire layer is designated as the *stratum oriens.*

All investigations on the cortex of the cornu Ammonis show that there exists here an abundance of cells and a multiplicity of fiber-relations which, so far as is known, has no counterpart in all the remaining cortex.

If what is typical in the structure of the cerebral cortex be once comprehended, it is not difficult to recognize the type in regions where it is less distinct. The *bulbus olfactorius,* for example, formerly was not understood at all. If Fig. 142 is inverted and compared with Fig. 152, the similarity strikes the eye at once. We are here concerned with a cortex in the molecular layer of which the olfactory-nerve fibers enter, and terminate by splitting up into an arborization. But the entire cortex is more condensed. The entrance, also, of the olfactory-nerve fibers into the layer of tangential fibers of the surface, and the different manner in which the dendrites of the cortical pyramids divide and terminate, occasioned by the former, give to the whole an appearance that has hitherto rendered difficult of perception the fact that we are here dealing with nothing other than a common cortical formation.

The surface of the cerebral cortex is covered in man (*Weigert*) by a dense net-work of neuroglia, from which numerous, but somewhat widely separated, prolongations radiate down into the region of the smaller pyramids. Then the net-work of neuroglia constantly becomes thinner, and in the deepest layers of the cortex it is almost entirely wanting. Within the radii separate fibrils only are perceptible. In the medullary layer there again lies a relatively-dense accumulation of neuroglia, which everywhere surrounds the medullated fibers.

If the nervous elements of the cerebrum are destroyed—*e.g.*, in paralyses—there appears in their place an hypertrophy of neuroglia which is characterized not only by its appearance in an abnormal place, but also by the thickness of its fibers, which by far exceed the otherwise normal fibers. Only in extreme age, where—probably in consequence of the senile cachexia—there is somewhat more neuroglia in the cerebral cortex, do such fibers occur. Where many of the glia-platelets cross, there arise the astrocytes and "cells" of *Deiter*, which are very frequently met with, therefore, in paralyses.

As exact a knowledge as is possible of the cerebral cortex is justly striven for in all directions. Psychiatry can boast pleasing results which have come from studies in this field. I will only mention the discovery of *Tuczeck*, who demonstrated that in the progressive paralyses of the insane the net-work of nerve-fibers in the first layer was the first to degenerate, and that the fibers in the deeper layers then successively disappear as far as into the fourth. A similar process has later been proved for other psychoses, and more recent discoveries have shown that in the deeper parts of the brain also a degeneration of fine fibers occurs in paralyses. This is here and there occasioned, as the course of its spreading allows us to infer, through the secondary degeneration of fibers interrupted in the cortex.

The nerve-fibers in the cerebral cortex become medullated only very late. Medullation occurs in the ninth month of fetal life first of all in the superior parietal lobule and in the posterior central gyrus; in the first month of extra-uterine life single fibers in the anterior central gyrus are added to these; later, in the second and third months, the process begins in the occipital lobe of the cortex. It is probable that these events stand in relation to the time at which man begins to store up impressions in the separate regions of the brain; that, for example, with the acquisition of visual perception, the optical centers of the cortex first begin their development.

In later life more extended regions are constantly becoming medullated (see page 231).

The *white medulla* of the *hemisphere* lies beneath the cortex. This homogeneous white substance, revealed to the naked eye by a section through the centrum semiovale, is resolved by the microscope into a large number of fibers crossing one another in various directions, but the separate fibers are traced only with difficulty. Let us endeavor, so far as at present possible, to become acquainted with these fibers.

If sections are made through the fresh brain of a newborn child, it will be seen that there lies almost everywhere beneath the cortex a peculiar grayish-red, transparent mass, in which white nerve-fibers are to be found at one small spot only: beneath the upper portion of the posterior central gyrus and in its neighborhood. In the course of the first months of life other nerve-tracts become medullated: first of all those tracts mostly which pass downward from the cortex; soon, however, tracts also that connect separate cortical regions with one another.

The latter, the *fibræ propriæ of the cortex,* are exceedingly numerous in the adult brain; they everywhere extend from gyrus to gyrus, connecting distant gyri and those adjacent to one another. They also connect entire lobes. Apparently these "association-fibers" arise only in consequence of the association of two cortical regions in a common action; in other words, these fibers are developed as distinct medullated tracts from the indifferent mass of nerve-fibers whenever they are brought into use more frequently than other tracts. These association-fibers lie for the great part close beneath the cortex, another part in the medullary layer of the hemispheres. Such a system is, as you see, thoroughly adapted to bringing all parts of the brain in communication with one another. The manifold processes of association in thought, in motion, and in sensation, for which the brain serves, may possibly find their anatomical basis in the fibers.

It is not improbable that these fibers play an important rôle in the spreading of the epileptic seizures. It is possible, in animals, to call forth, first, contractions in the muscles by irritating the region of the cortex with which they are respectively connected, and, second, convulsions of the entire affected side by increasing the irritation. The sequence of these convulsions corresponds to the arrangement of the affected centers in the cerebral cortex. As this impulse spreads a neighboring motor center is never skipped over. The convulsions, when they have completely spread over one-half of the body, involve the other half under certain conditions (intensity of the irritation, disposition of the animal experimented on). Extirpation of the single motor centers occasions an omission of the groups of muscles involved from the general convulsive seizure.

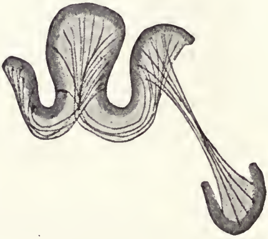

Fig. 155.—Schema of the fibræ propriæ of the cortex.

It is not necessary that the cortical point from which such a convulsive seizure starts belong directly to the motor region. The convulsions thus produced have the greatest similarity to the symptoms of partial or general epilepsy in man. Since the writings of *Hughlings Jackson*, especially, forms of epilepsy have been recognized that begin with contractions or convulsions in one limb and at times spread over the other limbs or the entire body. In the latter case they present a typical picture of an epileptic seizure. Consciousness almost never disappears entirely so long as the attack remains partial. After the attack paralyses sometimes remain, which are mostly localized in the parts first attacked. This partial, or cortical, epilepsy is not to be separated from the classical epilepsy. The latter probably represents a form in which the initial symptoms follow one another in more rapid succession.

It is not necessary, however, that the spreading of an impulse from one point of the cortex to another or over the entire brain occur precisely by way of the fibræ propriæ. Many other ways are presented, as, for instance, the fine net-work of nerve-fibers on the surface of the cortex; then, too, the entire cortex may be influenced simultaneously by a variation in the volume of blood in its vessels.

The tracing of the fibræ propriæ between two neighboring cortical regions is not extremely difficult if the teasing method is employed. The demonstration of connections between regions lying farther apart from one another is much more difficult and leads very easily to artefacts, which correspond in part to the actual direction of the fibers. A few tracts only are to be followed with some degree of certainty. Such are the *fasciculus uncinatus*, the *fasciculus arcuatus*, the *fasciculus longitudinalis inferior*, the *cingulum*, and a few others.

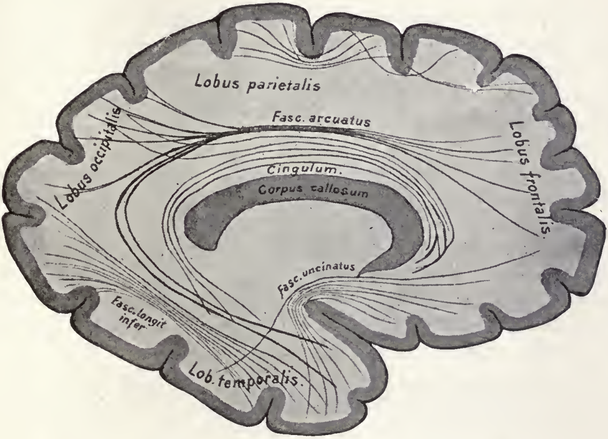

Fig. 156.—Diagram of the course of the long association-pathways.

The *fasciculus uncinatus* arises from the cortex of the temporal lobe, passes forward close to the ventral margin of the insula, and becomes lost in the most ventral regions of the frontal lobe (Figs. 170 to 172). The *fasciculus arcuatus* passes along over the dorsal part of the insula from the more posterior portion of the temporal lobe to the cortex of the parietal and frontal lobes. Fibers accompany it (doubtful) which arise in the frontal lobe and terminate in the cortex of the occipital lobe (see Figs. 169 to 172).

The *cingulum* is a long tract that runs in the marginal gyrus—the gyrus fornicatus—from the cortex of the cornu Ammonis to the most ventral region of the frontal lobe, and perhaps to the olfactory lobe also (dog and rabbit). It probably consists (*Beevor*) of several separate parts, and does not entirely degenerate after section (see Figs. 169 to 172).

The *fasciculus longitudinalis inferior,* a very large tract of fibers, connects the temporal lobe with the occipital lobe (see Figs. 186 to 188).

Déjèrine, who has studied this bundle very thoroughly in its relations to many other parts of the fiber-systems of the brain, observed that it was degenerated in a case of pure word-blindness. This fact and the course of the tract make it very probable that essentially it serves to carry optical impressions to other parts of the brain. It exists in other Primates also. *Flechsig* has lately felt compelled, as a result of embryological studies, to exclude this bundle entirely from the system of association-pathways. It is said not to terminate in the temporal lobe, but to curve up near the apex of the same, into the thalamus; so that it would consequently be a part of the radiatio occipito-thalamica.

Sachs justly emphasizes the fact that the temporal lobe is really connected with all the remaining parts of the brain by means of long tracts only. There is localized in it, as the researches of pathology show, the auditory imagery of speech. The very abundant possibilities of communication may correspond to the importance which such auditory factors have in human thought.

In Fig. 156 the long association-pathways above mentioned are combined diagrammatically. One tract only is not included there, because until recently it was very questionable whether or not it represented a long association-pathway. It is the *fasciculus fronto-occipitalis.* Arising from the medullary covering of the posterior and lateral horns of the ventricle, its fibers pass forward as a well-defined bundle external to the lateral ventricle. They always keep close beneath the corpus callosum and on the dorsal edge of the nucleus caudatus (see Figs. 170 to 172).

It is the same tract that I designated earlier as the association-bundle of the caudate nucleus (Fig. 168). Investigations by *Déjèrine, Rietz,* and *Muratow* have shown, however, that we are here really concerned, as *Forel* and *Onufrowicz* had conjectured, with an association-bundle between the medulla of the occipital lobe and that of the frontal pole. Consequently, the bundle will be found designated as the fasciculus fronto-occipitalis in the large frontal sections through the entire brain, to be shown later. Moreover, the smaller part only of this tract of fibers is, like all longer association-bundles, composed of fibers of very great length; a far greater part consists of fibers that connect together single sections of its long course.

It is perfectly proper to designate all of these long tracts as *interlobular association-bundles,* and to distinguish them from those that connect with one another separate points within this or that lobe. These *intralobular tracts* have been little studied hitherto. They are best known for the occipital lobe, where pathways have been demonstrated by *Sachs, Wernicke, Viault,* and others, which are adapted to connect with one another various regions and layers of this lobe in all directions.

Besides these fibers, which connect parts of the same hemisphere with each other, there are also fibers that connect one half of the cerebrum with the other. Almost all of these fibers run in the *corpus callosum* and in the *anterior commissure,* thus passing transversely through both hemispheres from one to the other.

Inasmuch as I presuppose that the macroscopic relations of the corpus callosum are known to you—at least its general form, where it is distinct from the other brain-mass—little remains to be said by way of explanation of the accompanying illustration (Fig. 157).

It must be borne in mind that just as the fibers of the corpus callosum are seen passing transversely from side to side in this section (which is made about through the chiasma), so they are to be seen in the whole region of the brain over the lateral ventricles.

Fig. 157.—Frontal section through the forebrain. Diagram of the course of the corpus callosum and the commissura anterior.

From the frontal lobe, also, the corpus callosum receives on each side a large afferent bundle that grows to it anteriorly over the roof of the lateral ventricle, on its lateral side. The fibers of the corpus callosum from the occipital lobe closely surround the posterior horn like a cap. Their radiation is known as the *forceps major.* The portion of the corpus callosum passing into the temporal lobe on the lateral side of the inferior horn is called the *forceps minor.* The inner side of the posterior horn and that of the inferior horn are covered by a layer of white, medullated fibers, the *tapetum.* (Compare the sections through the fibers of the corpus callosum which are shown in Figs. 169 to 174 and 185 to 188.)

The simple methods of sectioning formerly employed made this entire layer originate like the fibers of the corpus callosum,—made it appear, in a measure, as the most mesial radiation of the fibers of the forceps. Lately, however, the investigations of the authors cited above, in connection with the fasciculus fronto-occipitalis, make it probable that the tapetum does not radiate into the corpus callosum; rather that it is the most posterior radiation of that long association-tract. The radiation of the fasciculus fronto-occipitalis lies directly beneath the epithelium of the ventricle, next to the cavity, and only outside of it lie the posterior radiations of the corpus callosum.

For all that, it appears to me that numerous fibers of the corpus callosum are mixed with these. At least, the relatively small medullated bundles that form the fasciculus fronto-occipitalis in the dog do not cover all the numerous fibers of the tapetum. The fact that the tapetum has been observed to be present in cases where the corpus callosum was wanting, and the fact that it does not degenerate after section of the corpus callosum, appear to be the most important reasons for permitting it to be separated from the corpus callosum.

In the osmatic mammals, where the cornu Ammonis extends upward as far as the under surface of the corpus callosum, it is recognized more clearly than in man that the posterior end of the corpus callosum curves forward again. In this manner it forms a distinct layer of fibers dorsal to the psalterium, which, in sections, is to be distinguished from the fibers arising from the cornu Ammonis by the smaller diameter of its fibers only. This portion of the corpus callosum, as well as the dorsal portion, is penetrated by the bundles of the fornix longus (Fig. 144).

The accompanying illustration (Fig. 158) represents the fibers of the corpus callosum when exposed from the inner surface of the brain. With its help, an accurate idea may be easily formed of the radiation of the corpus callosum.

The commissura anterior has already been described in connection with the description of the olfactory apparatus. In man it passes as a large bundle of fibers, close to the floor of the ventricle, in front of the pillars of the fornix. It cannot be followed in a transverse section in the manner intimated in the semidiagrammatic figure here. On each side its fiber-mass, while it passes through the corpus striatum, curves much more, downward and backward, in a semicircle and is lost in the most posterior portion of the medulla of the lobus temporalis. In Fig. 127 this curved portion is cut on both the right and left sides below and external to the nucleus lentiformis.

The greatest part of the anterior commissure in man contains only fibers that can be traced backward until in the region lateral to the cornu Ammonis (compare Fig. 154). A small bundle only of the commissure of the olfactory lobe is shown,—it is seen passing downward in Fig. 157.

Numerous fibers arise from all parts of the cortex of the forebrain, which connect the forebrain with the deeper-lying parts of the central nervous system. A great many pass into the interbrain; others may be traced as far as the gray masses of the midbrain and as far as into the nerve-nuclei of the pons, in which they appear soon to terminate. Some of them pass down through the internal capsule, the crus cerebri, the pons and the medulla oblongata, into the spinal cord, where the fibers enter the gray substance at various levels.

Taken together, these fibers passing downward from the cortex are designated as the *corona radiata*. You will not form a wrong idea of this if the thalamus is imagined as placed free under the overarching dome of the cerebral cortex, and it is then assumed that nerve-fibers pass to it from all parts of the cortex. Tracts of fibers enter it from the cortex of the frontal, parietal, temporal, and occipital lobes—perhaps tracts of fibers from the cortex at the entrance to the fossa Sylvii and from the cornu Ammonis

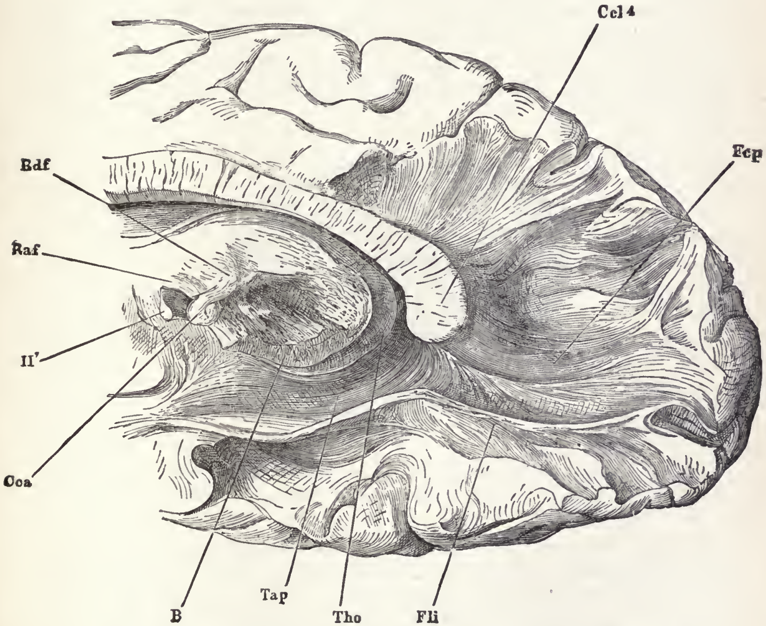

Fig. 158.—Posterior portion of the right hemisphere seen from the inner surface. By teasing out with forceps, the radiation of fibers from the posterior end of the corpus callosum (*Splenium, Ccl*^{4}) is shown. The mass under the corpus callosum is the *thalamus opticus* (*Tho*). On the wall of the ventricle surrounding it, the *tapetum* (*Tap*). A part of the *fasciculus longitudinalis inferior* (*Fli*) is also to be seen in the illustration. The thalamus has under it the pes pedunculi (*B*). The other letters refer to structures that will be mentioned in the text later on: *Rdf*, Vicq d'Azyr's bundle; *Raf*, Fornix; *Cca*, Corpus candicans; *II'*, Nervus opticus; *Fcp*, Forceps.

also (the latter running in the fornix). Others of the tracts of the corona radiata, however, do not go to the thalamus, but pass on farther downward, in front of, to the outside of, and back of it, to terminate in centers that lie deeper.

The corona radiata is therefore composed of fibers that go to the thalamus and of fibers that go to deeper lying parts.

1. Fibers pass *to the thalamus* from almost the entire surface of the cortex, and by no means so few bundles as the diagram before you would indicate. These fibers unite, in part, close to the thalamus to form thicker bundles, which are called the *pedicles of the thalamus.*

Monakow has been able to show, by means of numerous cases of secondary degeneration, that a very definite cortical zone sends its fibers to each of the thalamic nuclei. We shall have occasion to consider these in more detail later on. At present we will mention only some of the most important tracts of this group, known as the *tractus cortico-thalamici.* First, there is the *cortical tract of the fillet.* It arises from the region posterior to the anterior central gyrus and terminates in the most ventral thalamic nuclei. The fibers of the fillet also pass thither from the spinal cord and medulla oblongata. For this reason, we may regard the tract mentioned as the continuation of a considerable part of the *sensory radiation to the cortex.* In the posterior region of the thalamus there lies a part of the primary terminations of the *optic nerve.* The afferent tracts from the cortex to these are also well known. They pass forward, after leaving the medulla of the occipital lobe, in an almost horizontal direction, and end in the groups of ganglia of the posterior region of the thalamus. In Fig. 160 this *"optic*

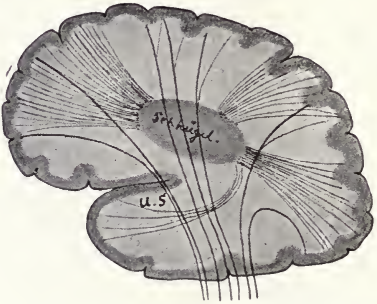

Fig. 159.—Diagram of the fibers of the corona radiata, especially the fibers to the thalamus. *U. S.*, Inferior pedicle; *Sehhügel*, Thalamus.

radiation" is reproduced from a horizontal section through the brain of a child 9 weeks old.

In man its destruction leads to homonymous hemianopsia (see below). In animals it does not appear to be of so great importance, for the occipital cortex may be destroyed on both sides without producing permanent actual blindness. The real centers for the sense of sight, consequently, lie deeper. Sight may be retained if these alone are preserved; it is impaired, however, when the connection between these centers and the cortex is destroyed. This connection, probably serving for psychical processes, is most important in man; apparently of lesser importance in the other mammals, it is wanting entirely in lower animals,—*e.g.*, the fish. These, at least the Teleostei, see without possessing, in general, anything more than a thin epithelial vesicle in place of a cerebrum.

2. Cortical tracts extend into the *midbrain*, partly from the occipital lobe by way of the above-mentioned optic radiation, partly from the temporal lobe to the terminations of the secondary *radiation* of the *auditory nerve.* The fibers arising from the end-nuclei of the acusticus extend upward as far as into the ganglia of the midbrain. There they soon end, but the cortical tracts begin at the place where they terminate.

3. In the region ventral to the thalamus a tract is soon lost to further observation which *Flechsig* has named the *tegmental radiation.* From the cortex of the superior parietal lobule (and from the posterior central gyrus?), perhaps from cortical regions, also, lying still farther posterior, its fibers extend into the internal capsule and pass, in part, below the thalamus, toward the spinal cord; in part, they sink into the lenticular nucleus. They pass through the two inner divisions of the lenticular nucleus, then unite again close to the base of the brain to form a more compact bundle, the course of which we shall become familiar with later. These fibers are the first to become medullated in the cerebrum. They alone are to be recognized in fetuses of the eighth to ninth month as thin, white tracts in the internal capsule, which at this time appears gray (Fig. 2).

But this is not the end of the cortical radiation. Its most caudal portions pass into the pons, the medulla oblongata, and the spinal cord.

4. The cortical tracts to the pons, *tractus corticis ad pontem*, are divided, after *Flechsig*, into the frontal system from the frontal lobe, and the posterior, from the occipital and temporal lobes. The fibers end in the pons in large ganglia, from which originate the peduncles of the cerebellum.

5. The *speech-tract*, the tractus cortico-bulbaris, runs to the nuclei, in the oblongata, of the nerves that are necessary for speech. Its origin in the cortex of the inferior frontal gyrus, its course through the medullary layer external to the tail of the nucleus caudatus and its termination in the above-mentioned nuclei, all have been inferred from clinical cases that have been carefully observed and verified by autopsies. It has not as yet been demon-

strated by actual anatomical investigation. The speech-tract, where it passes over the anterior part of the nucleus lentiformis, lies very near to *the central hypoglossal tract.* In it lie, also, most probably, the small tracts that serve to bring about voluntary movement of the vocal cords.

6. The cortical tracts to the spinal cord, *tractus cortico-spinales,* arise from the cortex of the central gyri and the paracentral lobule only. They pass down into the lateral and anterior columns of the cord, and are known as the *pyramidal tracts.*

There doubtless still exists a large number of other systems belonging to the corona radiata.

Brains with recent apoplectic lesions form excellent material for investigations that are directed toward the finding of such systems. About three weeks after the appearance of such an attack, upon application of Marchi's osmium method, tracts of fibers will always be found undergoing a descending degeneration, which extends far down from the point of lesion (*Hoche*).

The brains of children of the first years of life are also very instructive. The fibers become medullated at different periods, and, so far as is known at present, the entire corona radiata has become medullated by the end of the second year.

As a result of such investigations, *Flechsig* has now advanced the very interesting conclusion that the fibers of the corona radiata pass out from by no means all parts of the cerebral cortex; that, on the other hand, there are regions which form their white medullary substance essentially of association-tracts. *Accordingly, the mantle region may be divided into two grand divisions which differ as to structure.* The first contains, besides the bundles of the corona radiata mentioned above—among which the tractus cortico-thalamici are the largest—association-fibers and fibers of the corpus callosum in abundance. From here originate the sensory systems of fibers, and those fibers also for the innervation of the muscles and organs of speech. *Flechsig* calls the entire region the sensory centers. It includes the optic center in the area of the cuneus, the auditory center in the most posterior part of the first temporal gyrus, the olfactory center in the gyrus hippocampi and the ventral part of the frontal lobe, and, finally, that large field which includes the posterior portions of all the frontal gyri and the central gyri, the same cortical area from which proceed the tractus cortico-spinales and the cortical pathway to the termination of the fillet. All of the fibers belonging to these areas become medullated earlier than those parts of the cortex which, in general, contain association-fibers only. *Flechsig* calls these *association-centers.* They include four large regions: the anterior portion of the frontal lobe, the greater part of the temporal lobe, the posterior portion of the parietal lobe, and the insula Reilii. Numerous association systems connect these parts with two, and even more, neighboring sensory centers. The speech-centers appear, as a whole, to lie in the common boundary region of the sensory and association centers.

One sees that even the short description, which the author was able to give here, of the tracts running in the white medullary substance shows this to be a very complicated structure. In fact, sections made at any place whatsoever, never, or almost never, show one of the systems alone; at least, decussating fibers are almost always present, originating from the association-bundles, or from the corpus callosum also, or from the other systems of commissures. Perhaps the collaterals, the exit of which from the fibers of the corona radiata is easily demonstrable in the mouse by means of the Golgi method, here play an important rôle in complicating matters. However, one recognizes even now the cardinal feature of brain-structure when one sees that *from particular cortical areas definite fasciculi pass to definite termini.*

Numerous investigators have turned their attention to the histology of the cerebral cortex and the finer anatomical relations of its structure. Hitherto the more it was investigated, the more difficult the solution of the problem appeared to be. New and more complicated relations were constantly becoming known. *Baillarger, Bevan Lewis, Clarke, Meynert, Golgi, Bellonci, S. Ramón y Cajal, Kölliker,* and many others have attempted to throw light upon the most important points. The cortex of the cornu Ammonis was specially investigated by *Meynert, Kölliker, Henle, Duval, Schaffer, Golgi, Sala,* and *Ramón y Cajal.* Much was learned concerning the system of fibers in the white matter of the hemisphere by *F. Arnold, Reil,* and *Burdach,* even by means of the teasing method, while the microscopic investigations by *Meynert, Sachs, Brissaud,* and *Déjèrine,* more particularly the embryological studies of *Flechsig,* and the numerous experimental researches of *Gudden, Löwenthal, Monakow,* and others, have advanced our knowledge of the subject wonderfully. The advantages that have accrued to the study of the anatomy of this portion of the brain from investigations on pathological brains are not to be undervalued. *Wernicke, Charcot, Féré, Pitres, Friedmann, Sioli, Monakow, Richter, Zacher, Déjèrine* and others have made such investigations.

CHAPTER XVI.

THE CAPSULA INTERNA, THE CORPUS STRIATUM, AND THE GANGLIA OF THE INTERBRAIN.

ON their way downward the fibers of the corona radiata enter into important relations with the corpus striatum and the thalamus opticus. They converge accordingly and so arrive in the region outside of the thalamus.

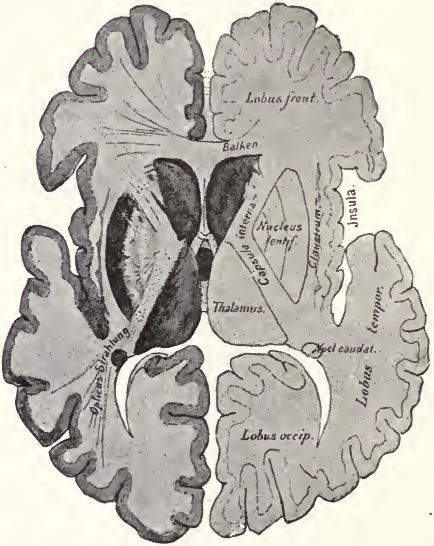

Fig. 160.—Horizontal section through the brain, trending downward somewhat toward the sides. *Balken*, Corpus callosum. *Opticus Strahlung*, Optic radiation.

In order to pass thither the fibers from the anterior parts of the brain must penetrate the corpus striatum. This will be made clear by the accompanying section, made horizontally through the cerebrum.

This section is made about a finger's breadth below the section shown in Fig. 124. You must understand that the two hemispheres are in part removed, and bear in mind that their coronal fibers passed downward from above into the knee-shaped, white line of the *internal capsule.* The portions of the capsule formed by fibers coming from the frontal and occipital lobes lie in part in the plane of the section. A few words now in explanation of this section.

The frontal, occipital, and temporal lobes are recognized immediately. The temporal lobe lies over the island of Reil, and thus partly conceals it. As in Fig. 125, you see the corpus callosum in front cut transversely, and adjoining it the septum pellucidum, at the posterior end of which the pillars of the fornix ascend.

Anteriorly, external to the septum, lies the head of the nucleus caudatus, which is cut into in this section. Its tail, which was seen passing along the side of the thalamus in Fig. 125, is not visible. It is contained in the part of the brain removed. Only a small portion of it is still to be seen, posteriorly and externally, near to the cornu Ammonis. The above sketch, which represents a nucleus caudatus dissected out, shows how this condition is brought about.

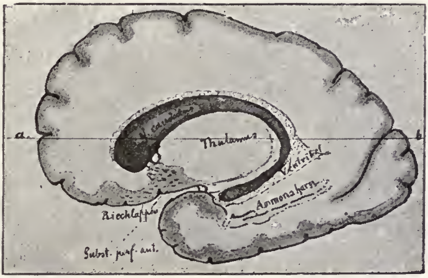

Fig. 161.—Nucleus caudatus exposed along its entire length (diagrammatic). *Ammonshorn,* Cornu Ammonis. *Riechlappen,* Olfactory lobe. *Ventrikel,* Ventricle.

The tail of the nucleus caudatus bends around the brain-stem in a gentle curve, and is to be traced almost to the apex of the inferior horn of the lateral ventricle. The entire nucleus must consequently be cut twice in every horizontal section made through the deeper planes of the brain. This is shown by the line *a b* in Fig. 161.

Thick tracts of fibers are seen external to the head of the nucleus caudatus. They come from the cortex of the frontal lobe, and contain the corresponding fibers of the corona radiata passing to the thalamus, and the frontal fibers passing to the pons.

In order to pass into the thalamus and the pons, this mass of fibers must cut through the ganglion of the corpus striatum, which lies in the way (Fig. 160). The part which lies nearer the median line is the aforesaid *nucleus caudatus*; the part that comes to lie more external is the *nucleus lentiformis*. Nevertheless, they are not absolutely separated from one another by the fibers from the frontal lobes; numerous connecting fibers pass between them. The above-mentioned fibers of the corona radiata to the thalamus, the fibers from the frontal lobe to the pons, the bundles between the head of the nucleus caudatus and the nucleus lentiformis, and, finally, other fibers from the nucleus caudatus to the thalamus and to the nucleus lentiformis, all of these fibers together constitute the white, fiber-mass of the *capsula interna*, met with in the horizontal section shown in Fig. 160.

The frontal section reproduced in Fig. 162 is intended to complete the idea of these relations shown in the horizontal section. Situated very far forward, it strikes, principally, the ganglia of the corpus striatum, and likewise distinctly shows the fibers of the capsula interna separating them.

The form and location of the nucleus caudatus will probably be clear to you now; but it will be more difficult to form an idea of the peculiar, wedge-shaped figure of the nucleus lentiformis. A study of the horizontal section and of the frontal section (Fig. 162) will be of benefit in this connection. Internally, two other, somewhat lighter-gray, ganglionic masses are associated with this ganglion, which are intimately attached to it by fibers. We commonly speak, therefore, of a threefold division of the lenticular nucleus, whereas the broad, darker, outer division alone, the *putamen*, probably is morphologically equivalent to the *nucleus caudatus*. This nucleus caudatus sends its fibers, as was mentioned above, through the anterior limb, or segment, of the internal capsule to the two inner divisions of the lenticular nucleus, and on through them farther downward. The fibers of the putamen run an exactly similar course.

External to the corpus striatum lies the cortex of the island of Reil. In the narrow strip of white substance which lies between the cortex and the ganglion, the *capsula externa*, there is situated an accumulation of ganglionic cells, known as the *claustrum*. Anatomically, this is somewhat different from the neighboring cortex, and it extends ventrally as far as into the olfactory field.

Behind the nucleus caudatus, the horizontal section shown in Fig. 160 passes through the thalamus, the interbrain. In front of this the pillars of the fornix ascend from below. The *commissura media*, a thin band of gray matter, extends from one thalamus to the other. External to the thalamus lies the *posterior limb of the internal capsule*. The point where both limbs meet has been named the *genu* (*knee*) *of the internal capsule.* Impress this peculiar angular form of the capsula interna well upon your memory. The relation of the separate parts of the corona radiata to the two limbs, or segments, is probably approximately constant, and therefore exceedingly important clinically. In the posterior limb, for the most part near the genu, lie the fibers running from the motor zone to the extremities (pyramidal tract). Just in front of them are the tracts which stand in relation with the nuclei of the facialis and hypoglossus, and which arise from the lower end of the anterior central convolution.

Fig. 162.—Frontal section through the forebrain, close behind the pillars of the fornix.

Behind the pyramidal tract the tracts designated as the tegmental radiation are met with in about the last third of the posterior limb, or somewhat more anteriorly. Adjoining these posteriorly lies the tract from the occipital lobe to the origin of the opticus. According to clinical facts, there must also be fibers in this region which pass from the cortex of the temporal lobe to the nucleus of the acusticus, and also fibers which stand in some relation to the sense of smell. Thus there meet, in the posterior third of the posterior limb of the internal capsule, all the sensory fibers and the fibers connected with the nerves of special sense. Besides these, moreover, there are here found coronal fibers to the thalamus from the cortex of the temporal and occipital lobes, and the temporo-occipital tract to the pons. The following figure shows diagrammatically the relative positions of the separate tracts composing the internal capsule.

All of these fiber-masses, therefore, converge from the cortex toward the region lying lateral to the thalamus. A part of them enters the thalamus (corona radiata of the thalamus); another part—and that the larger—passes under the thalamus, where it ends in ganglia or passes on farther down to the spinal cord. Lesions that lie in the centrum semiovale must, therefore, involve part of the fibers of the corona radiata. But by no means always do they produce symptoms which lead us to suspect an interruption in the conducting pathway from the cortex to the periphery. This is probably on account of the fact that the coarser lesion-symptoms which may be detected by our present means of diagnosis arise only whenever the entire tract involved is destroyed. It appears that small remnants are sufficient to conduct voluntary impulses from the cortex to the deeper parts, or to convey sensory impressions from the periphery to the cortex.

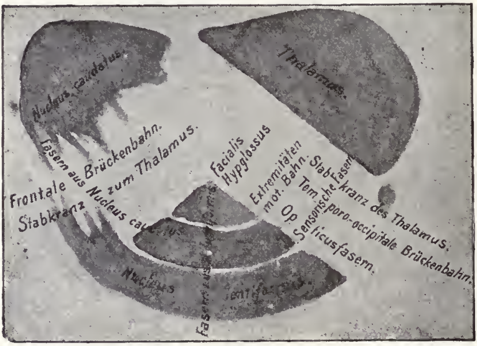

Fig. 163.—Diagram of the internal capsule, in which the location of most of the tracts of fibers which compose it is indicated by their respective names. *Extremitäten mot. Bahn,* Motor tract to the extremities. *Fasern aus Nucleus Caudatus,* Fibers from nucleus caudatus. *Fasern aus N. Lentiformis,* Fibers from nucleus lentiformis. *Frontale Brückenbahn,* Frontal cortical tract to the pons. *Opticusfasern,* Optic fibers. *Sensorische Fasern,* Sensory fibers. *Stabkranz des Thalamus,* Corona radiata of the thalamus. *Stabkranz zum Thalamus,* Coronal fibers to the thalamus. *Temporo-occipitale Brückenbahn,* Temporo-occipital cortical tract to the pons.

Lesions, in particular, that do not lie in the medullary substance under the central convolutions—that is to say, lesions which involve the cortical tracts to the pons and the tegmental radiation—often fail to give rise to symptoms. Focal lesions, on the other hand, that involve the pyramidal tract produce paralysis of the opposite half of the body. Disease of the medullary substance under the cortex of the inferior frontal convolution often leads to aphasia. Moreover, cases are known which make it extremely probable that interruption of the tegmental radiation may lead to a unilateral loss of sensibility. Two cases recently observed by the author show that the pains which appear after apoplexies may at times be explained through the proximity of the lesion and the tegmental radiation.

It appears fairly-well established that diseases which involve the region posterior to the knee of the internal capsule—that is, diseases which make the fibers running in this region incapable of conduction—suspend the motility of the entire opposite half of the body; that lesions situated in the terminal two-thirds of the posterior limb destroy the sensibility of the opposite half of the body, or at least diminish it very much. In most cases the sense of sight suffers also, and probably hearing at times. The disturbance of sight appears in the form of hemiopia.

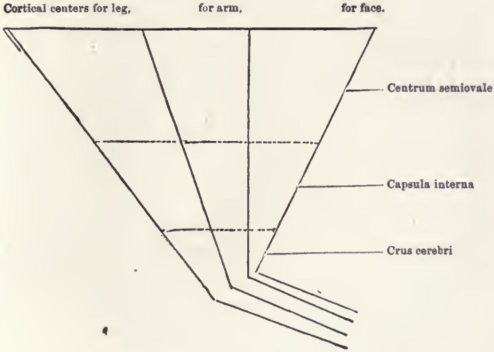

Fig. 164.

If you bear in mind what has been repeatedly stated: that all the fibers converge from the cortex toward the internal capsule, it will be easily understood that small lesions in the internal capsule may produce the same symptoms as larger ones in the centrum semiovale, or still more extensive lesions in the cortex. In the internal capsule fibers lie close together which higher up are spread out over a greater space. For example, a very extensive cortical territory (one including both central convolutions and the parts of the frontal and parietal convolutions closely bordering on them) must be destroyed if complete crossed hemiplegia is to be produced. A smaller lesion in the medullary substance of the centrum semiovale under the central gyri might have the same effect. In the internal capsule, on the other hand, the destruction of a small portion alone of the posterior limb suffices to call forth the combination of symptoms. In cases of hemiplegia, therefore, we will always think, first of all, of lesions which are in the neighborhood of the internal capsule or are situated in it, if additional symptoms do not point directly to other regions of the brain.

Hemiplegias from cortical lesions are very rare. Hemiplegias that proceed from the midbrain or from deeper-lying points are still more rare, and are mostly associated with symptoms involving the cranial nerves, which indicate the seat of the lesion.

On the other hand, both anatomical considerations and clinical experience teach us that cerebral affections involving single parts of the body—for example, a hand—are only very rarely produced by lesions in the internal capsule. This is, indeed, because the fibers are so closely crowded together there that a lesion can hardly involve separate bundles of fibers alone without involving those near by. Monoplegias and monospasms not infrequently arise from cortical lesions, however. There a lesion may even be of relatively large size before it involves a neighboring center. The accompanying diagram (Fig. 164) will serve to elucidate what has been said. It shows why monoplegias proceed more frequently from the cortex and hemiplegias more frequently from deeper-lying parts of the brain; for it is at once seen that a lesion of given extent located in the cortex may easily involve *one* center alone, whereas a similar lesion situated farther below will involve the fibers of *many* centers.

It has not as yet been learned what symptoms appear when fibers of association-bundles alone are involved, on account of the proximity of these fibers to the corona radiata.

Probably certain forms of disturbances of speech, reading, and hearing belong in this category. Furthermore, little is known concerning the symptoms appearing after a loss of function (*Functionsausfall*) of the corpus callosum. It appears that under certain conditions it may be entirely destroyed without the appearance of disturbances of motility, of co-ordination, of sensibility, of the reflexes, of the special senses, or of speech, and without the manifestation of any considerable disturbance of the intellect. Uncertain gait, without actual vertigo or ataxia, was once observed in a case of disease of the corpus callosum.

The fibers of the corona radiata terminate, in great part, therefore, in the interbrain, in the thalamus opticus. The other fibers pass on farther downward and backward in the internal capsule. They thus come to lie free, for the most part, on the under surface of the brain, behind the thalamus. These thick, white bundles there emerging from the brain-mass are designated as the *foot* of the *crus cerebri, pes pedunculi*, or *crusta* (Fig. 165, below and to left).

As is seen in the accompanying frontal section, this free part of the internal capsule, the fibers of which curve caudad as the crus cerebri, lies ventral to the thalamus. Into this *foot,* the pes pedunculi of the crus cerebri, pass the bundles of the frontal tract to the pons, those of the temporal tract to the pons, and those of the pyramidal tract. The coronal fibers of the opticus and the tegmental radiation do not enter the pes. Farther caudad, in the region of the corpora quadrigemina, the nerve-fibers which come from the thalamus and from other brain-parts, also those from the tegmental radiation, lie dorsal to the pes in a position corresponding to that of the thalamus. The fibers from the forebrain, the interbrain, and the midbrain are there divided into a ventral part, the *foot, pes,* or *crusta,*—and a dorsal part, the *tegmentum.*

A very instructive section may be made which gives an idea of the origin of the fibers found in the pes. Take a fresh brain and cut into the crus cerebri perpendicularly until the substantia nigra is met with. Then turn the knife and cut horizontally through both hemispheres in a direction obliquely upward and forward. The section upon which is based the illustration shown in Fig. 258 is made in a similar manner. For the passing of the fibers from the internal capsule into the pes, see Fig. 175.

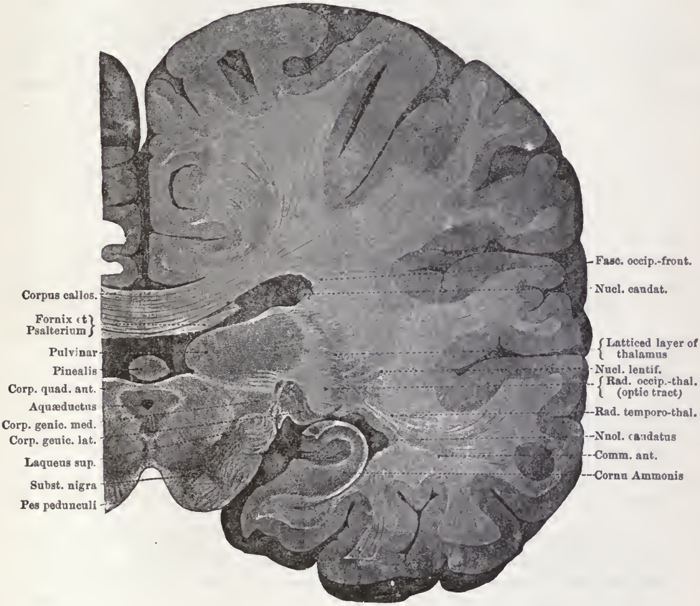

Fig. 165.—Frontal section through the forebrain and interbrain close to the place where the fibers of the capsula interna become fibers of the pes pedunculi.

The tracts from the cortex form the chief mass of the pes. Dorsally there is added to them a small tract which, coming from the corpus striatum, terminates in a ganglion situated dorsal to the pes, in the substantia nigra. It is the *stratum intermedium pedunculi.*

We will now turn our attention to the *corpus striatum* and the fiber-systems arising from it.

This large ganglion, situated at the base of the forebrain, is divided by the fibers of the internal capsule arising in the cortex into the nucleus lentiformis, located laterally, and the nucleus caudatus, which lies dorsally and mesially. The nucleus lentiformis consists of an outer division, the *putamen,* and two or more inner divisions, the *globus pallidus.* From the *putamen* and from the *nucleus caudatus* arises the fiber-system of the corpus striatum. Moreover, the corpus striatum is traversed by a system of fibers originating in the cortex: the tegmental radiation.

The fiber-system of the corpus striatum itself connects the same with the ganglia of the interbrain. It passes, in part, in the anterior limb of the internal capsule, in part—so far as it comes from the putamen—under the internal capsule at the base of the brain, to the interbrain. Thus the latter portion of fibers must surround the fibers of the internal capsule at the place where they come to lie free at the base of the brain as the pes pedunculi. This part is designated as the loop of the lenticular nucleus, or *ansa lentiformis.* It contains essentially the fibers from the putamen.

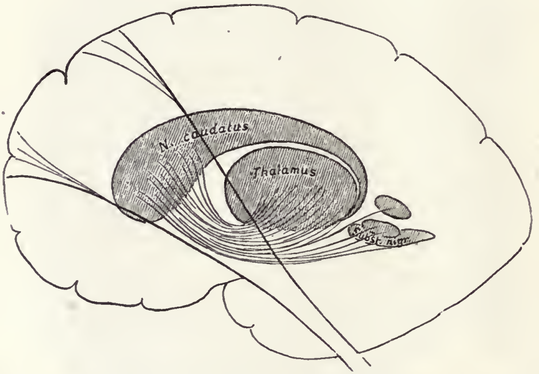

Fig. 166.—The fiber-system which arises from the nucleus caudatus and passes to the ganglia of the interbrain and midbrain (Radiatio strio-thalamica). The fiber-system of the lenticular nucleus is not represented. It would run from the observer toward the thalamus.

We are here concerned with a very old fiber-system, one very important for the entire mechanism of the brain. For in all vertebrates, from fishes up to mammals, there may be demonstrated a well-defined bundle of fibers, which arises in the corpus striatum and in part terminates in a nucleus of the interbrain, in part passes on farther down. In man it is to be found with difficulty, because so many tracts from the mantle region are associated with it. Yet I have recognized this *basal bundle* of the *forebrain* in young embryos, and it is probably the fibers of this bundle which *Wernicke* and *Flechsig* have described as arising from the corpus striatum. The latter has also recognized the connection with the thalamus. It has already been described in the chapters on comparative anatomy and there designated as the *tractus strio-thalamicus.*

Recently, however, I have succeeded in fully establishing the course of the tracts arising from the corpus striatum in the brain of a dog from which the cortex had been completely removed. In this animal experimented upon, all of the fibers of the corona radiata coming from the cortex were secondarily degenerated and had almost disappeared. It was there recognized with all certainty that very large fiber-masses developed from the head of the nucleus caudatus and from the putamen, which passed toward the base and at the same time somewhat posteriorly in the anterior division of the internal capsule. The greatest part of this fiber-mass turned inwardly at once and was lost in the thalamic ganglia. The part that extended farther downward gradually passed toward the median line to disappear in the ganglia in the region below and behind the thalamus. In the region posterior to the corpora quadrigemina, the entire fiber-system, anteriorly so large, had passed over into the ganglia. Its last tracts were taken up by the substantia nigra. The researches by *Mahaim* and by *Monakow* upon the secondary degenerations appearing after disease in the neighborhood of the corpus striatum show that in man also the fiber-system arising there has the relations represented in the diagram opposite.

The radiatio strio-thalamica forms, therefore, a large and important connecting pathway between the corpus striatum and the ganglia of the interbrain and midbrain.

The fibers of the tegmental radiation, from the cortex, pass between the divisions of the globus pallidus. They pass through this as white lines, and collect at the base of the lenticular nucleus to form a definite bundle of fibers, which is dorsal to the ansa lentiformis and passes mesially exactly like this. It later extends into the medulla oblongata.

Most of the fibers of the tegmental radiation pass mesially into the region which lies under the thalamus opticus and is named the *regio subthalamica.*

The accompanying illustration, a section through the brain of a fetus of 8 months, shows the relation of the tegmental fibers to the lenticular nucleus. Excepting the fibers represented, there are no other medullated fibers present in the entire cerebrum at this embryonic stage. The fibers, in particular, which arise in the nucleus caudatus and the putamen are still entirely wanting. Only after the investigation of the fetal brain was it possible to explain with certainty the relation of the lenticular nucleus and the tegmental radiation to one another.

In mammals there exists a small fiber-tract which passes laterally along the entire extent of the nucleus caudatus. It begins in front of the head of this ganglion as a few fibers which appear to come out of the head itself. The tract increases more and more in size posteriorly, but becomes smaller in consequence of the slenderness of the tail of the nucleus, and is to be traced no farther than the nucleus itself. The bundle lies in the angle between the surface of the nucleus caudatus and the roof of the ventricle; the fibers of the corpus callosum radiate directly over it. The fibers of the bundle appear to me to come from the nucleus caudatus itself, and to return into it again. It is called the *association-bundle* of the *nucleus caudatus* (*Sachs*); but I cannot sharply separate it from the fronto-occipital association-bundle, which lies close to it.

You have now become acquainted with the origin and the proximal part of a large number of the fibers which go to make up the forebrain.

Fig. 167.—Frontal section through the brain of a fetus of about thirty-two weeks. *All* medullated nerve-fibers stained black by hæmatoxylin. Tegmental radiation (above), ansa lentiformis (below), and anterior commissure (below and external) are medullated. No medullated fibers are as yet seen in the putamen and the nucleus caudatus.

Let us now turn to the regions where the majority of the medullated tracts of the cerebrum terminate.

Back of the cerebrum lies the *interbrain*. Its lateral walls are the *thalami optici*. These consist of several gray nuclei, which are not sharply separated from one another. White medullated fibers, the *stratum zonale*, cover the thalamus. They may be traced, on the one hand, in a direction toward the base of the brain into the optic nerves; on the other hand, they appear to arise from the posterior parts of the capsula interna, perhaps from the optic radiation. All pass into the depths of the thalamus, where they collect into bundles between the thalamic ganglia, and thus apparently separate these from one another. Microscopic investigation shows that they penetrate into the fine net-work of nerve-fibers which pervades these ganglia. There may be distinguished in each thalamus: a *mesial* (*inner*) *nucleus*, which projects into the ventricle; a *lateral* (*outer*) *nucleus*; and, between these, the *anterior nucleus*. The lateral nucleus is the largest. The anterior nucleus, with its blunt end directed anteriorly, appears as a wedge driven in between the other two. This anterior, thicker end, which is visible anteriorly as an elevation on the surface of the thalamus, has been met with earlier under the name of *tuberculum anterius.*

The *pulvinar* borders on the mesial nucleus, and is not easily separable from it in man. It is a huge "cushion" (*Polster*) which, occupying the entire posterior division of the thalamus, projects like a tumor (*Wulst*) into the ventricle. On the median border of the inner nucleus lies the *ganglion habenulæ,* previously mentioned.

Monakow, who has recently studied the thalamic nuclei more thoroughly, proposes, on account of the structure and the entering radiations, to separate the ventral region of the lateral nucleus and designate it, along with several other small nuclei-groups which are also situated ventrally, as the *ventral nucleus* of the thalamus. On the thalamus posteriorly there lies, ventral and external to the pulvinar, a ganglion of a peculiar grayish appearance: the *corpus geniculatum laterale.* It projects far into the substance of the thalamus, and gives origin to a large number of fibers of the *tractus opticus.*

Externally, the optic thalamus borders on the internal capsule (Fig. 160). Numerous tracts, the *corona radiata of the thalamus,* pass from the capsule into the thalamus. They come from various directions and cross one another as they converge into the thalamus. Masses of gray matter are found within the net-work of crossing fibers. The outer zone, containing these crossed fibers, is, from its appearance, designated as the *"latticed" layer* (*Gitterschicht*). Since most of the medullated fibers converge into the lateral nucleus, this thus appears lighter than the other thalamic nuclei.

The thalamic ganglia atrophy, to a large extent, if the cortical region from which they receive their converging fibers degenerates or is removed. The investigations by *Monakow*, especially directed toward these relations, show that the most anterior and mesial divisions of the thalamus are connected with the convolution-groups of the frontal lobe, the lateral nuclear groups with the parietal convolutions, and the ventral nuclei with the operculum. At present not the least is known concerning the physiological significance of these pathways. Some of the other thalamic radiations are now better understood. First of all, there are the fibers from the parietal region to the ventral nucleus. They must contain, as I have previously stated, that portion of the sensory fiber-system which passes to the cortex from this nucleus, where a part of the fillet terminates. Then we know that the greatest part of the fibers converging into the posterior divisions of the thalamus, especially into the pulvinar and the corpus geniculatum laterale, arises from the occipital lobe, and represents the secondary pathway from the primary optic terminals to the cortex.

The inner side of the thalamus is separated from the ventricle by a uniform layer of gray matter. This is called the *central gray matter* of the middle (third) ventricle, and consists of a tissue rich in cells and traversed in all directions by numerous fine, medullated nerve-fibers.

Schütz, who has made this gray matter a subject of especial study in man, found that it contains afferent tracts from almost all of the ganglia surrounding the third ventricle, and, what is particularly interesting, that it degenerates like the fibers of the cerebral cortex in progressive paralyses. A tract of fine, medullated fibers, which may be traced in the gray matter from the third ventricle down as far as the nuclei of the hypoglossus, has been named by him the *dorsal longitudinal bundle* of the central gray matter. It is, for the most part, especially well defined, and constantly lies close under the epithelium of the ventricle.

In the median line of the brain the central gray matter forms the floor of the ventricle. There here run across in it from one side of the brain to the other several slender tracts of fibers. One of these, *Meynert's commissure,* is better defined than the others. Its origin and destination are not sufficiently well known. It was retained in the dog after complete destruction of the cortex. *Gudden's commissure,* lying anterior and ventral to it, we will become better acquainted with later. In reptiles, Meynert's commissure arises from the giant-celled nucleus of the central gray matter.

The central gray matter on the mesial surface of the thalamus unites with that of the opposite side for a distance of about three-fourths of a centimeter to form the *commissura mollis,* or *media.*

In man few medullated fibers run in it. Whether a commissure which is present in lower vertebrates in an analogous location, and which is much richer in fibers, is identical with the commissura media still remains to be determined (see Fig. 82).

Nissl has shown for the rabbit that each of the thalamic nuclei is again divided into from three to four subnuclei, which are easily distinguishable from one another by the behavior of their cells toward stains. Moreover, he has described in this animal: a nucleus of the "latticed" layer and, anterior to the ganglion habenulæ, the nucleus of the median line. To these, then, there might still be added the small nucleus magno-cellularis, found in the most anterior planes of the thalamus. *Monakow* has shown that the corpus geniculatum laterale is divided into five nuclei: a dorsal and a ventral nucleus which are each subdivided into two, and a latero-ventral nucleus. Of these nuclei, the posterior division of the dorsal nucleus belongs to the retinal fiber-system, while the remaining nuclei receive afferent tracts from the cortex to the primary optic terminals. Each of these latter nuclei stands in relation with a definite portion of the visual system.

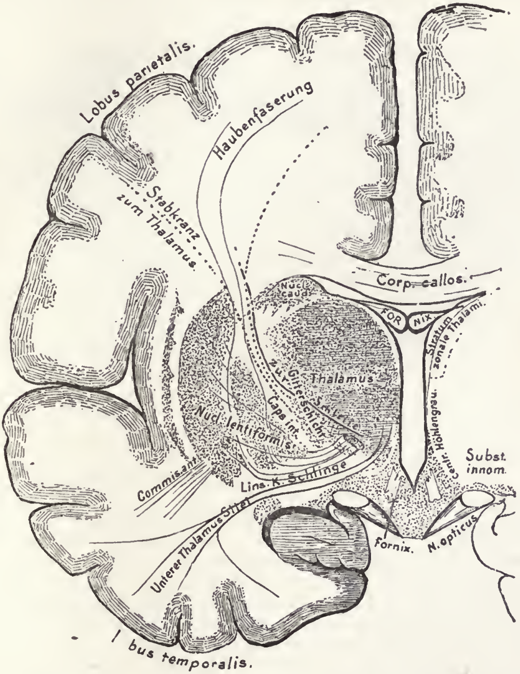

Fig. 168.—Frontal section through the brain just behind the chiasma. Diagrammatic. *Centr. Höhlengrau,* Central gray matter of the ventricle. *Gitterschicht,* Latticed layer. *Haubenfaserung,* Tegmental fiber-system. *Lins. K. Schlinge,* Ansa lentiformis. *Stabkranz zum Thalamus,* Corona radiata to the thalamus. *Unterer Thalamus Stiel,* Inferior pedicle of the thalamus. *Zur Schleife,* To the fillet.

The thalamus is essentially a "receiving-station": on the one hand, for the fibers from the cerebral cortex—the corona radiata of the thalamus; on the other hand, for the fibers from the corpus striatum—radiatio strio-thalamica, *ansa lentiformis, etc. In proportion to its enormous mass, the thalamus sends only a few fibers downward.*

The tracts arising from the ganglia run, for the greater part, in two, white, transverse lamina, passing through their mass: the *lamina medullaris externa* and *interna.* The thalamic fibers extend farther downward only to a very limited extent. Essentially but a single bundle, the superior fillet, com-

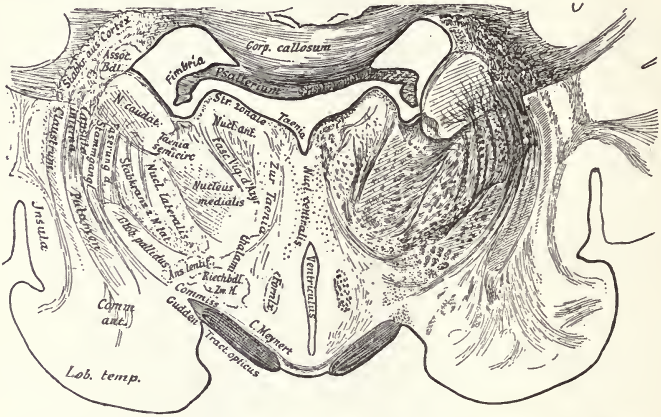

Fig. 169.—(From the dog.) Frontal section which passes approximately through the anterior third of the thalamus. Like the following sections, it requires only a few words by way of supplementary explanation, since all the parts are lettered. To the right and above, the fibers from the mantle pass down into the internal capsule, lateral to the corpus striatum. They there meet with the large fiber-system from the nucleus caudatus, penetrate it, and converge, in part, as the corona radiata into the lateral thalamic ganglion. Most of the fibers, however, remain in the position named, and pass backward. This part must be surrounded by the fiber-system of the corpus striatum, when the same passes inward to its terminal in the ganglia of the interbrain. To the tracts thus embracing the fibers there are added—close to the base—the tracts from the putamen, which form with those the ansa lentiformis. Mesial to the bundle of the ansa, already met with here, lies the slender radiation passing from the olfactory field to the corpus mamillare. From the olfactory radiation there is given off at this level, and farther posteriorly, the bundle of the tænia thalami, which ascends dorsally. This is seen to pass as far as the surface of the thalamus and then to turn backward to the ganglion habenulæ. The bundle of Vicq d'Azyr probably belongs to the olfactory apparatus also; it develops from the medullary capsule of the anterior thalamic nucleus, which is here cut in the section. *Faserung d. Stammgangl.*, Fiber-system of the corpus striatum. *Riechbdl Zw. H.*, Olfactory bundle, interbrain. *Stabkranz aus Cortex*, Corona radiata from cortex. *Stabkranz z. N. lat.*, Corona radiata to nucleus lateralis.

ing from the stria medullaris externa and particularly from the ventral nucleus, may be traced as far as the end of the oblongata, perhaps into the lateral columns of the spinal cord also. The stria medullaris interna is not traceable beyond the midbrain. From the most posterior thalamic region arises the *radiatio thalami ventralis,* the termination of which is entirely unknown (oblongata—lateral columns of cord).

On the accompanying very diagrammatic illustration (Fig. 168) is to be studied the relation of the thalamus to the base of the brain, to the central ventricular gray matter, to the capsula interna, and to the nucleus lentiformis.

You will observe something in this section that until now could merely be mentioned cursorily. It is the region internal to the lenticular nucleus and ventral to the thalamus. There are collected here several fiber-strands, running somewhat parallel with one another, which, in part, cross the inferior portion of the capsula interna at an angle, in part pass on over it. Those fibers which are superior belong to the lenticular fiber-system; they form the *ansa lentiformis,* previously mentioned. The inferior fibers are the coronal fibers to the thalamus, which come from the occipital and temporal lobes; they are designated as the *inferior pedicle of the thalamus* (*u. s.,* Fig. 159). The entire mass of fibers met with in section in Fig. 168 ventral to the nucleus lentiformis is called the *substantia innominata.* Just behind the substantia innominata the fibers of the capsule, which become the pes pedunculi, or crusta, emerge at the base of the brain. The substantia innominata bounds the crus cerebri at the anterior end. It resembles a loop laid over the peduncle in front, and is therefore designated as the *ansa peduncularis.*

The diagram (Fig. 159), moreover, departs so far from the real appearance that it will be advantageous to give some attention to the opposite illustration of an actual section through the thalamus of a dog (Fig. 169).

From this and the following illustrations you will obtain a better idea of the structure of the interbrain than I could give you heretofore. They contain somewhat more details (pedicles of the thalamic nuclei, etc.) than were mentioned in the text, because they are intended to afford an opportunity to study actual sections more closely. I beg to make use of these illustrations again at the end of this and the next chapter.

In the preceding two chapters it was necessary to describe so many brain-structures by themselves that I fear I can hardly have succeeded in giving you a correct idea of the relation of these parts as a whole and to one another. Such a conception must be thoroughly acquired, however, because even a better knowledge than I have been able to give you of the fiber-systems and ganglia will be of little value when you come to study a brain topographically. The time has arrived, then, when I must demonstrate to you a series of frontal sections through an adult brain. They may serve as a guide in your own investigations.

For topographical study I advise you to place an entire, uncut brain in 10-per-cent. formol solution (*Blum*), and, after from four to eight days, to cut it up with a razor into sections about one centimeter in thickness. The illustrations which I here present to you are made from sections prepared in this manner. Here and there an examination in water with the lens will prove advantageous.

The first section that I make (not shown here) passes a few centimeters behind the frontal pole of the brain. Surrounded by the convolutions, which are here small, it contains an homogeneous white mass constituted essentially as follows: Just under the cortex it is composed of short association-bundles; beneath these of the coronal fibers to the thalamus and to the pons (which begin to pass downward even here); and, finally, of the frontal ends of the longer association-systems.

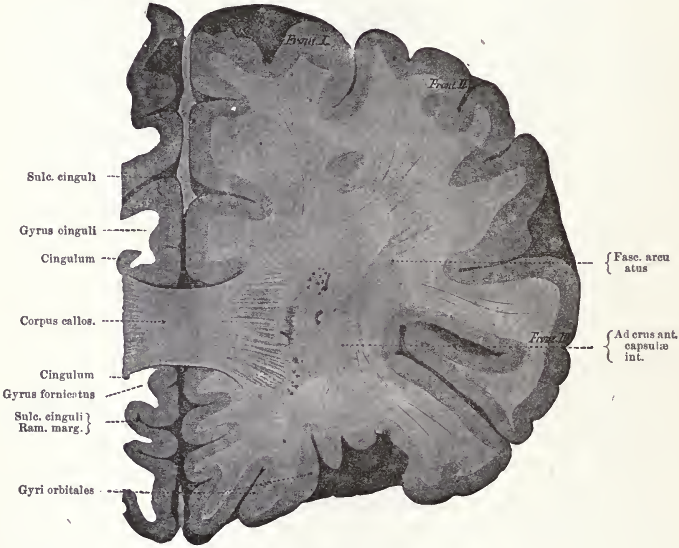

Fig. 170.

The second section (Fig. 170) is made a few millimeters behind the beginning of the corpus callosum. It just cuts through the genu of the corpus callosum, the most anterior fibers connecting both hemispheres. A great part of these fibers is cut away laterally; it is those fibers which turn anteriorly in a gentle curve, and thus naturally are chiefly contained in the portion of brain removed. Directly lateral to the fibers of the corpus callosum there is cut the gray substance which surrounds the lateral ventricle; that is to say, its anterior horn. Indeed, at several points, the ventricle itself has been opened.

The *white, medullary substance* lateral to the ectoventricular gray substance is formed, first of all, by the tracts from the frontal lobe to the anterior limb of the internal capsule. It is approximately the region which is designated "*Ad crus ant.*" This bundle, cut transversely, is then surrounded ventrally, and in part split up and interlaced, by fibers of the corpus callosum and by long association-fibers, which belong to the fasciculus uncinatus.

Dorsal to it lies the region (indicated by light shading in the illustration) in which the fasciculus arcuatus spreads out. In addition to this there are next, close under the cortex, the curved tracts of the short association-pathways. Over the entire area there are disposed numerous fibers, which pass, in part, to the thalamus; in part, have an unknown course. There is probably quite a number of association-pathways here also. Even in the plane of this section, in specimens hardened in chrome-salts, the cingulum may be met with, cut transversely, just above and below the corpus callosum; and, dorso-mesial to the fibers of the corona radiata passing to the internal capsule, is also met the anterior radiation of the fronto-occipital association-bundle.

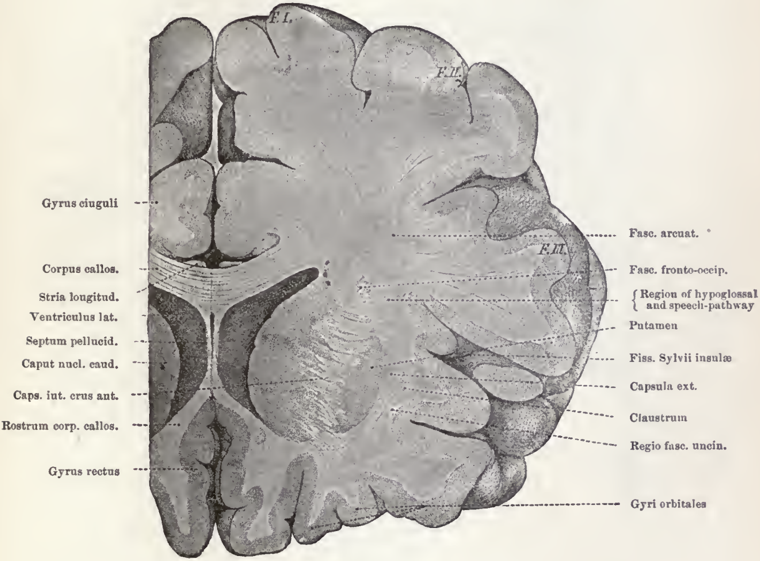

Fig. 171.

The next section (Fig. 171) is made just behind the genu of the corpus callosum. Dorsally, it passes through the body of the corpus callosum, ventrally it cuts the most posterior portion of the inferior limb of the corpus callosum, the rostrum. Between these two parts lies the inner wall of the hemisphere, the ventral portion of which is designated as the area Brocæ, the more dorsal part as the septum pellucidum. The ventriculus septi is visible between the two walls of the septum. The anterior horn of the ventricle is now widely opened, and the head of the nucleus caudatus is cut through its greatest expanse. Lateral to this the fibers of the internal capsule pass down from the frontal pole, with which there is associated in exactly this region the large fiber-system passing from the nucleus caudatus to the thalamus, the radiatio strio-thalamica.

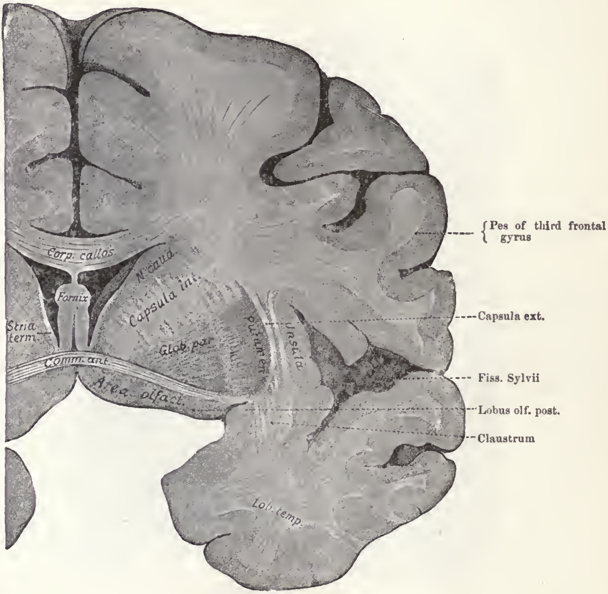

Fig. 172.

Externally to the internal capsule, here still interrupted by many bands of gray matter, lies the most anterior part of the putamen. Then follows laterally the capsula externa, the claustrum, and the medulla and cortex of the insula. The fasciculus uncinatus is lost in the first. This section already strikes the anterior end of the Sylvian fissure.

The entire dorsal half of the section is occupied by the medullary masses that here arise from the three frontal convolutions.

They consist, for the most part, of association-fibers that connect the regions of the hemisphere with one another, more especially such fibers as belong to the frontal lobe itself, but there are some longer fibers also, as the fasciculus arcuatus and the fronto-occipital association-bundle. Besides these, the entire white medullary substance is here traversed by fibers of the corpus callosum. Only a few white fibers pass from this region into the capsula interna. Of the tracts that are important clinically there are essentially only the coronal fibers from the facialis and hypoglossus centers, and the speech-pathway, the transverse section of which is to be assumed as lying somewhat lateral to the fasciculus fronto-occipitalis. The ventral, cortical region belongs to the gyri orbitales, over which the olfactory lobe passes.

A section made only a little farther back passes through the most posterior part of the septum pellucidum, and now cuts the pillars of the fornix, which ascend there. I demonstrate such a transverse section (Fig. 172), because it is also well adapted to show the course of the commissura anterior, the decrease in size of the head of the nucleus caudatus, and the increase in that of the lenticular nucleus.

The triangular, gray mass between the commissure and the caudate nucleus by this time belongs to the central gray matter which covers over the thalamus. The white fiber-tract that covers this mass and projects free into the ventricle is the stria terminalis, especially that part of the same which arises from the anterior commissure.

Just posteriorly there lie in the same relation, and having a similar course, the tracts of the tænia thalami. Ventrally, the olfactory area begins to appear.

A section made exactly where the olfactory lobe becomes intimately connected with the base of the brain (Fig. 173) strikes, farther dorsally, the posterior portion of the septum, where are found the posterior pillars of the fornix. These have reached their present position from the postero-ventral region of the brain. Their transverse sections will be met with in all the succeeding illustrations until here in front, where they turn toward the base of the brain and pass ventrally into the central gray matter of the ventricle. Their oval frontal sections lie in the gray matter directly in front of the transverse fibers of the commissura anterior.

The lateral ventricle, here only a fissure, lies lateral to the pillars of the fornix; into it projects the most anterior portion of the thalamus, the nucleus anterior. This is covered over by white fibers, which penetrate into its interior, and here separate it from the nucleus lateralis thalami. The thalamus here receives fibers at its lateral and at its ventral surfaces. The lateral fibers come from the capsula interna and belong, the same as the ventral fibers, to the fiber-systems coming from the cortex, as well as from the corpus striatum. Those fiber-tracts, especially, which enter at the ventral end are plainly formed by the inferior pedicle from the temporal lobe and the lenticular loop from the corpus striatum.

In the plane of this section the fibers from the anterior central gyrus have in large part become mingled with those of the internal capsule. This now contains at least the coronal fibers for sight, the motor speech-pathway, the hypoglossus and a part of the pyramidal fiber-system for the arm and hand. Fibers from the caudate nucleus, which run ventro-posteriorly, pass through its tracts arising from the mantle. The white medullary substance is still formed essentially as in the previous sections.

Lateral to the capsula interna there is now met with the greatest expanse of the corpus striatum: the putamen and the two divisions of the globus pallidus.

Numerous medullary radiations arise in the first; they pass, in large part, into the lenticular loop (ansa lentiformis). Ventral to the corpus striatum the transverse section of the commissura anterior is recognized. It lies just over the olfactory formation, the cortex and medulla of which may here, indeed, be separated from one another. The entrance of the olfactory radiation into this is to be recognized. From this region the tænia thalami rises dorsally and enters the layer of white matter covering the mesial side of the thalamus. Yet its entire course is not to be seen in this section.

The fifth section (Fig. 174) is made directly anterior to the chiasma. This is not divided, however, but is turned ventrally. The narrow, fissure-like ventricle is lengthened ventrally to form the infundibulum. In its inferior third it is crossed by the commissura media. The thalami, covered by the stratum zonale and the tænia, project into it, and it is closed above by the columns of the fornix, over which lies the corpus callosum. The lateral end of each column is directly continuous, as Fig. 173 shows, with the plexus chorioideus of the lateral ventricle. Close by the side of the commissura mollis the descending columns of the fornix are seen, cut transversely, in the central gray matter. Traversing the gray matter of the infundibulum, they here turn posteriorly and ventrally to the corpus mamillare.

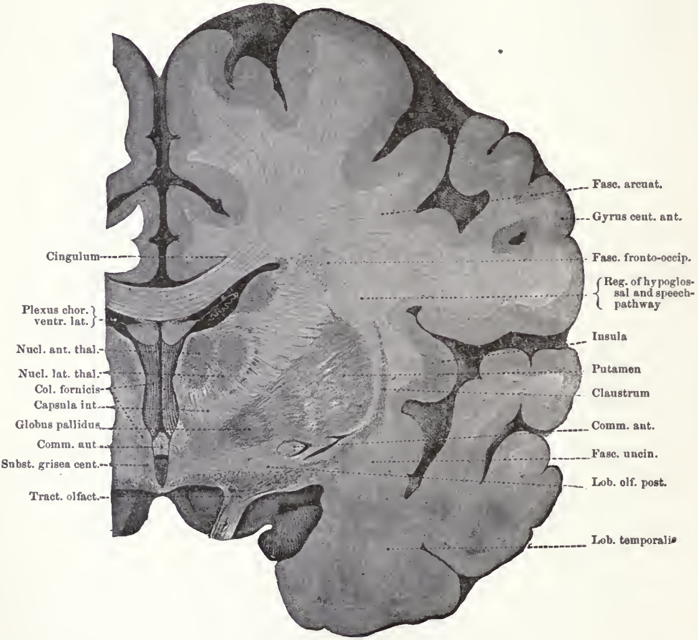

Fig. 173.

Of the thalamus there is now visible the nucleus anterior, the nucleus medialis, and the nucleus lateralis—also the latticed layer. From the first there develops the tractus thalamo-mamillaris, the bundle of Vicq d'Azyr. The fibers from which it originates and fibers from the stratum zonale, as well as fibers of a still unknown origin, together form a proper medullary capsule around the nucleus anterior. The lateral part of this capsule, and a portion of the ventral, may be traced far backward as the lamina medullaris interna thalami.

The tail of the nucleus caudatus of the corpus striatum is visible dorsally and ventrally. On its mesial side it has the tract of the stria terminalis. Besides this part of the corpus striatum there is visible the lenticular nucleus with its three divisions, from which the fibers of the ansa lentiformis are seen to develop at precisely this level.

These fibers pass to the basal part of the capsula interna, which they cross to enter the thalamic ganglia from below. For almost this entire distance they lie upon the fiber-system, which likewise passes into the thalamus, as the inferior thalamic pedicle, from the temporal lobe.

The internal capsule here contains nearly the entire motor fiber-system. Moreover, it contains the pathways from the frontal lobe to the pons. Many coronal fibers pass from it into the thalamus. The motor speech-pathway still lies in the same place as in the preceding figure. Ventral to the lenticular nucleus lies the commissura anterior, and under this we see the nucleus amygdalæ.

Fig. 174.

The optic thalami everywhere lie so close upon the internal capsule that diseases only rarely come under observation in which the thalami alone are involved. Even in these it often remains doubtful how many of the phenomena which appear are to be referred to the thalami, since the function of the neighboring fibers of the capsula interna was impaired indirectly. For this reason it has not yet been possible accurately to determine the symptoms that are produced by disease of the optic thalamus. According to *Meynert,* the innervation sensations of the upper extremities are thereby disturbed. In this manner are said to arise the delusive ideas concerning the position of these members, and from these ideas, again, the forced positions. Motor paralysis is probably not produced by destruction of the thalamus; just as little, sensory paralysis. Disturbances of sight in the form of homonymous lateral hemianopsia, perhaps of crossed amblyopia also, were repeatedly observed.

Likewise in disease of the optic thalami, the symptoms of hemichorea, of athetosis, and of unilateral tremor were observed not very infrequently. These have also been observed following lesions of other parts of the brain, yet were commonly concerned with fiber-systems connected with the thalamus.

The same difficulty presents itself when an attempt is made to determine the symptoms of disease of the corpus striatum. What was for a long time described as such (hemiplegia, for example) may arise just as well through the involvement of the neighboring capsula interna. A case is known of the destruction of both putamina which terminated without a symptom referable thereto.

CHAPTER XVII.

METATHALAMUS AND HYPOTHALAMUS.

THE REGIO SUBTHALAMICA AND THE STRUCTURES AT THE BASE OF THE BRAIN.

At the end of the last chapter we had approached a region of the brain which, extraordinarily complicated in structure, hitherto belonged to the parts of the brain that were least understood and explained. I now purpose to bring before you the most important structures of this *regio subthalamica.*

If you examine Fig. 173 or Fig. 174 it is apparent that the thalamus lies upon the internal capsule. Farther posteriorly this relation ceases. Several small, gray ganglionic masses shift between it and the internal capsule, into which masses converge numerous fiber-tracts from the nucleus lentiformis, from the capsula interna, and from the thalamus itself. The posterior, basal region of the interbrain where this occurs has received the name of *regio subthalamica.* The *metathalamus* has become more thoroughly understood only through the investigations of *Luys, Forel, Flechsig, Wernicke, Monakow,* and *Kölliker.* Yet we are still far distant from an understanding of the complicated relations which are presented in this small region, a region where fibers of very different origin meet with one another,

Fig. 175.—Section through the regio subthalamica.

intermingle, and decussate, a region containing gray masses which are themselves again filled, in part, by a fine net-work of small decussating, medullated fibers.

Fig. 175 shows some of the details of a section through this region. Below the thalamus is a roundish ganglion, the *nucleus tegmenti*, the *red nucleus* of the *tegmentum*; external to this there has appeared the *corpus subthalamicum* (*nucleus* of *Luys*), which has a somewhat lenticular form. Posteriorly, the nucleus tegmenti will appear much larger in the transverse sections. It is the point of origin of a large bundle, the peduncle, or Tr. tegmento-cerebellaris, which passes to the opposite half of the cerebellum. Ventral to it, and mesial to the corpus subthalamicum, there is found a third ganglion, the *substantia nigra Sömeringi*, an accumulation of nerve-cells which are mostly pigmented with gray. This is also better developed in the more posterior planes. It lies directly over the fiber-systems from the internal capsule, which now become the pes.

From the regio subthalamica on down as far as the end of the midbrain this dark-grayish ganglion may always be demonstrated above the pes.

There terminates in the substantia nigra, designated as the *stratum intermedium pedunculi*, the last remnant of the fiber-system from the corpus striatum.

Between the ventral nucleus of the thalamus and the ganglia mentioned there pass a great many convergent white fibers. They arise from several sources, and also have an approximately stratified disposition; so that the individual layers may be separated somewhat. Nevertheless, "degeneration" preparations were the only ones on which the discrimination could be clearly made. Farthest lateral lie the tracts of the *tegmental pathway* destined for the ventral, thalamic nucleus. It has long been believed that some of them turned directly downward to the afterbrain, and this part was designated as the *superior*, or *cortical*, *fillet*. Even now this view is maintained on some sides (see my older Fig. 168, also). But in the last few years it has been successfully shown that the fiber-tract from the cortex terminates in the thalamus, that, however, a new pathway arises from this, the *tractus thalamo-bulbaris*, the *superior fillet*, which may be followed downward as far as into the nuclei of the posterior columns. *This is a portion of the sensory pathway, of which we now know two parts*: *the cortico-thalamic and the thalamo-oblongatal parts.* Ending extraordinarily near to one another, both must be in intimate contact within the ventral thalamic nucleus (*Monakow*, *Mahaim*, *Bielschofsky*).

The superior, or upper, fillet is found, on the sections illustrated, ventral to the thalamus and near to the nucleus tegmenti. But it is separated from this by means of a thick medullated bundle, the *tractus cortico-tegmentalis*, the coronal bundle of the tegmental nucleus (Déjèrine). Laterally the superior fillet and the coronal bundle form a true medullary capsule around the nucleus tegmenti: the *lamina medullaris nuclei tegmenti*.

The radiations to the tegmental nucleus and to the superior fillet do not form, however, the only elements of the medulla of the regio subthalamica. In the section from the dog, shown in Fig. 176, which falls somewhat farther frontally than Fig. 175, and also subsequently in Fig. 178, you see large

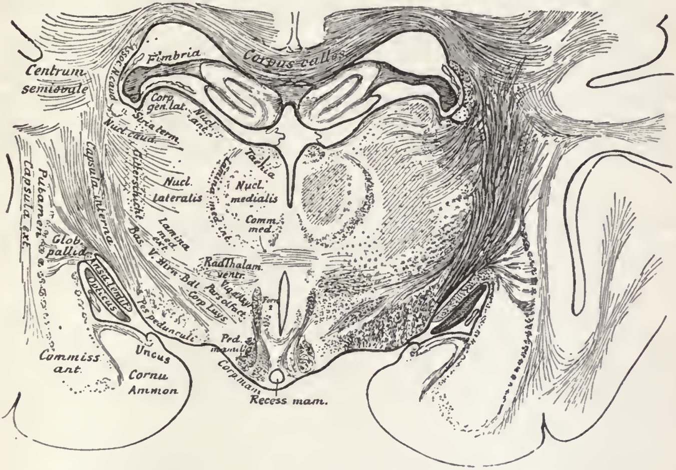

Fig. 176.—From the dog. Frontal section through about the middle of the thalamus. Beneath the corpus callosum lie the frontal ends of both cornua Ammonis, which are connected by means of the psalterium, and send out the immense fimbria on each side. In the thalamus: the nucleus medialis and lateralis in their greatest expanse, separated from one another by the lamina medullaris interna, cut transversely; bounded dorsally by the tænia thalami, into which fibers pass from the stratum zonale, bounded by the posterior part of the nucleus anterior and the dorso-frontal ganglion of the ganglion habenulæ. Lateral and dorsal, the tail of the nucleus caudatus and its association-bundle. From the capsula interna enters the corona radiata of the nucleus lateralis and of the nucleus anterior; between the nucleus lateralis and the capsula interna there develops from the first the lamina medullaris externa. At the base, the corpus mamillare, in which, at the level of this section, the bundle of Vicq d'Azyr from the nucleus anterior and the tegmental bundle enter united. Laterally there develops the pedunculus mamillaris; dorsally, directly beneath the ventricle, the decussatio subthalamica anterior. The capsula interna lies exposed on the under surface as the pes pedunculi; its most mesial fibers here arise from the forebrain-bundle and end in the corpus Luys. Dorsal to the corpus Luys the fibers of the deep olfactory medulla, and, lying close to these, the radiatio thalami ventralis. Lateral to the capsula interna, the lenticular nucleus, from which the ansa lentiformis applies itself closely to the pes. Between the ansa and the ventral part of the cornu Ammonis, the nervus opticus.

Bas. V. Hirn Bdl., basal forebrain-bundle. *Gitterschicht*, latticed layer.

fiber-masses, arranged in several bundles, converge toward this region. They all originate from the corpus striatum, and terminate, so far as at present known, in the nuclei of the stratum intermedium (*Zwischenschicht*), especially in the substantia nigra and in the corpus subthalamicum, or at least in its neighborhood, where there are found several other small ganglionic accumulations: the *ganglia of the stratum intermedium.*

This radiation is no other than the posterior end of the tractus striothalamici, which we have met with so frequently from the fishes on up to man. It arises from the ansa lentiformis, comes to view at the mesial border of the corpus striatum, crosses over the capsule, and, coming from the side, streams thus into the separate ganglia of the stratum intermedium.

That these fiber-bundles, designated as separate *strata* of the stratum intermedium, arise, at least in great part, from the corpus striatum, I conclude from the preparations from the dog without forebrain, which hâve been repeatedly referred to here.

The region ventral to the thalamic ganglia and to the ansa peduncularis (Fig. 169) is traversed by fine longitudinal fibers, which, arising from the olfactory lobe, pass to this region in a straight line. We will designate them as the *olfactory bundles* of the *interbrain.* They may be traced as far as into the region of a ganglion-complex which, situated at the base of the interbrain, there projects as a small hemisphere on the base of the skull.

It is called the *corpus mamillare,* and is very much larger in the osmatic vertebrates than in the Primates (compare Fig. 141). In Figs. 176 and 178 it falls exactly in the plane of section.

Down toward the corpus mamillare there passes through the central ventricular gray matter the bundle of the pillar of the fornix from the cornu Ammonis and the marginal convolution. The bundle appears to end in it partly on the same side, partly on the opposite. The small decussation dorsal to the corpus mamillare, which contains, in part at least, fornix fibers, is called the *anterior decussation* of the regio subthalamica. In Figs. 133 and 134 trace the course of the fornix from the cornu Ammonis on down as far as the region just described. Frequently consult these figures, also, for the following description:—

The corpus candicans consists, as *Gudden's* experiments showed, of three nuclei. The most lateral nucleus sends its pedicle (*pedunculus corporis mamillaris*) far down into the oblongata; from the posterior of the two mesial nuclei arises a thick bundle which ascends into the thalamus and is lost in its tuberculum anterius. This *tractus thalamo-mamillaris* (bundle of Vicq d'Azyr) is entirely visible in Fig. 144, and, for a part of its course, in Fig. 174. Close beside this, coming from the more anterior nucleus, or ganglion, there ascends a small fiber-strand toward the thalamus.

It soon separates, however, from its companion and, bending down posteriorly at an angle, extends into the tegmentum, posterior to the region of the corpora quadrigemina, where it may be traced until into the ganglia that lie beneath the aquæductus Sylvii. This is the *tegmental bundle* of the *corpus mamillare.*

S. Ramón y Cajal and *Köllikcr* have recently stated that only a single bundle arises from the corpus mamillare, which passes dorsally. The axis-cylinders of this bundle divide at some distance from their point of origin. The anterior branches, or divisions, ended as the tractus thalamo-mamillaris in the nucleus anterior, the posterior as the tegmental bundle in a nucleus of the frontal tegmentum. *Kölliker*

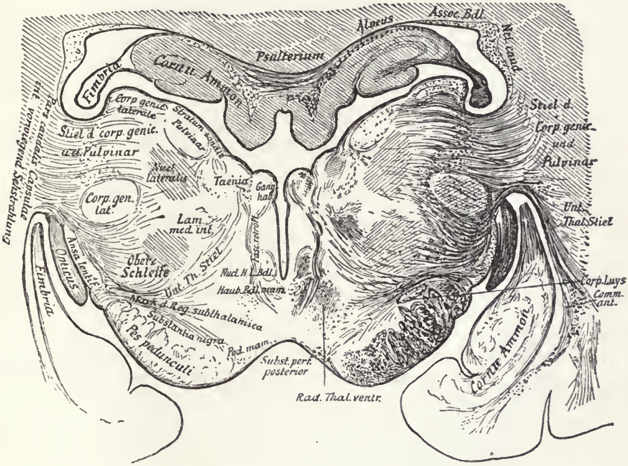

Fig. 177.—From the dog. Frontal section through the interbrain in the region of the posterior third of the thalamus. For the explanation of the greater part of the figure, see Fig. 169. In comparison with that of Fig. 169 there is to be noted in this section: the ganglion habenulæ, in which the tænia disappears; the inferior thalamic pedicle; the radiation of the ansa lentiformis into the medulla of the regio subthalamica; the corpus Luys; and the separation of the superior fillet from the medullary masses lateral and ventral to the thalamus. The pulvinar appears mesial to the corpus geniculatum laterale. *Haub. Bd. Mam.,* Tegmental mamillary bundle. *Mark d. Reg. subthalamica,* Medulla of the regio subthalamica. *Nucl. H. L. Bdl.,* Nucleus of posterior longitudinal bundle. *Obere Schleife,* Superior fillet. *Pars caudalis Capsulæ,* etc., Posterior portion of the capsula interna, principally optic radiation. *Stiel d. Corp. genic. u. Pulvinar,* Pedicle of the corpus geniculatum and pulvinar. *Unt. Thal. Stiel,* Inferior thalamic pedicle.

does not regard the fornix as terminating in the corpus mamillare, but thinks that after crossing through the same it goes, *via* the decussatio hypothalamica, into the opposite thalamus, where it is said to end within the ventral nuclear groups.

By means of the substantia nigra, the fiber-systems which pass downward from the forebrain and interbrain are divided into two parts, which differ as to their physiological significance, the *pes,* or *crusta,* and the *tegmentum.*

Now let us briefly consider the *glandula pinealis* (*conarium*), or *epiphysis,* which, with its pedicles running on the inner side of the thalamus, represents a portion of the roof of the interbrain (see Figs. 20 and 21). It consists essentially of solid epithelial tubules, which have originated through proliferation of the primary evagination.

The conarium contains, in addition to the tubules and an abundant blood-supply, the *brain-sand*: small concretions of a stratified structure, which consist principally of calcium-salts and of a small organic basis.

The position of the glandula pinealis, at the posterior end of the thalamus and between the corpora quadrigemina, is shown in Fig. 125.

I would like to remind you again of what was said on page 127 about the significance of the conarium in reptiles.

Fibers appear to extend as far as the conarium from the tracts of the tænia thalami. The tænia rises anteriorly by the side of the fornix from the depth of the olfactory field and, after it has received an afferent tract from the fornix, ends in the *ganglion habenulæ* after it has passed along the mesial edge of the thalamus. The ganglion is located just in front of the epiphysis (see Fig. 177). The posterior portion of the bundles of the tænia is also designated as the *pedunculi conarii.* Between the two pedunculi conarii runs the delicate *commissura habenularis,* probably a decussating tract from the tæniæ habenulæ (very clearly shown in transverse section in Fig. 144). It is also to be noted in Fig. 144 how the glandula pinealis, almost massive in man, appears in the rabbit to be an evagination of the roof of the forebrain and passes over into the plexus chorioideus.

Precisely as in the lower vertebrates, so in mammals, a large tract passes down to the base of the midbrain from the ganglion habenulæ. It is the *tractus habenulopeduncularis.*

I will now take up again the demonstration of the brain-sections that was interrupted at the close of the last chapter. They are intended to assist you in reviewing and studying what has just been presented, and to serve as a means of orientation. The section shown in Fig. 178 follows directly upon that of Fig. 174.

Located just behind the chiasma, the section shows, on the one hand, the thalamus in its greatest breadth; on the other, as an important factor, the emerging of the fiber-systems of the internal capsule at the base of the brain as the *fundament* of the *pes,* or *crusta.* Between the pes and the thalamus is situated the regio subthalamica, and new ganglia lie in this. Note the "ganglion of the zona incerta," the corpus subthalamicum (Luys), and ventrally the group of ganglia of the corpus mamillare. The latter is surrounded by its medullary capsule, in which the fornix has now disappeared, and it sends away above the tegmental bundle (the tractus mamillo-tegmentalis), and the tractus thalamo-mamillaris (the bundle of Vicq d'Azyr), which at first pass along united.

The nucleus lateralis and medialis thalami allow the posterior end of the nucleus anterior to extend between them dorsally; ventrally they flow together. Here begins the region of the nucleus ventralis. The more posterior portion of the ansa lentiformis streams in here, and other fibers from the corpus striatum go to the gray nuclei of the regio subthalamica. The lamina medullaris interna thalami has become much richer in fibers, and between the latticed layer and the lateral nucleus there develop the tracts of the lamina medullaris externa thalami. The stratum zonale is very perceptibly diminished, and the tænia is to be seen more clearly. The lenticular nucleus, the claustrum, the capsulæ, and the cortex of the insula, with the exception of somewhat altered forms, present nothing that differs essentially from the sections previously shown. In the white medullary substance the long association-tracts may still be sought for in the same situations where they lay in the section shown in Fig. 174.

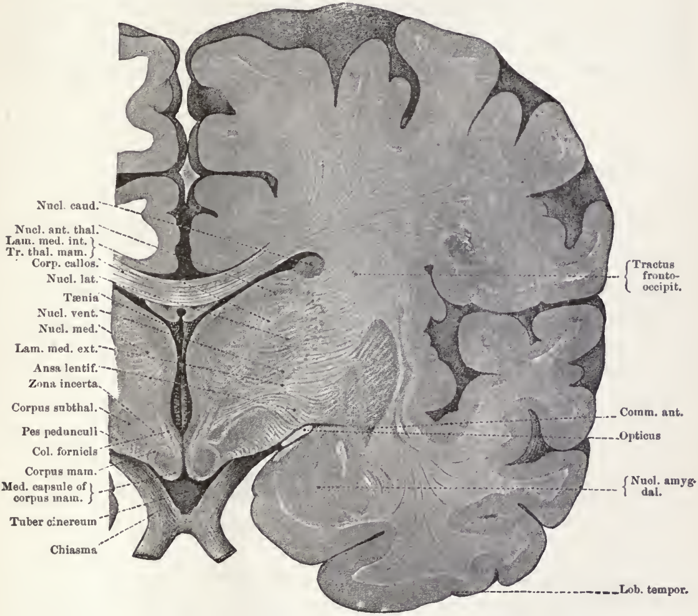

Fig. 178.

Posterior to the region of the previous section, the separate elements found in the regio subthalamica and in the tegmentum, which is here increasing, lie so closely upon one another that, for the most part, they are not separable without staining and magnification. In the illustrations found farther front in the text, much will, therefore, be clearer than in Fig. 179; see especially the figures from the dog.

The thalamic ganglia are almost entirely blended together. Only the form of the cells and degenerative changes now allow the separation of special nuclei. The nucleus lateralis and the nucleus ventralis have gained the most in expanse; the mesial and the anterior nucleus have entirely disappeared. Here, close to the entrance into the aqueduct, the layer of central, ventricular gray matter increases in thickness also. Just outside of it appear the "sagittal nuclei of the interbrain": the *nuclei of the posterior longitudinal bundle.* Then follows laterally the red, tegmental nucleus, and, in the place where the corpus subthalamicum was situated in the last section, the substantia nigra. The first-named ganglion has dwindled to a small remnant which lies farther laterally. In the clear field ventral to the thalamus there are gathered: fibers from the most posterior territory of the fiber-systems of the corpus striatum, forming a capsule around the red nucleus and entering into it in part; then fibers of the tracts of the lamina medullaris externa; and, separated from this by gray matter, in the most ventral thalamic nucleus, the fibers of the superior fillet. The internal capsule contains, in this situation, substantially the tegmental radiation to the thalamus and tracts from the posterior region of the temporal lobe to the thalamus, also tracts from the same source to the pes pedunculi—that is, to its lateral portion.

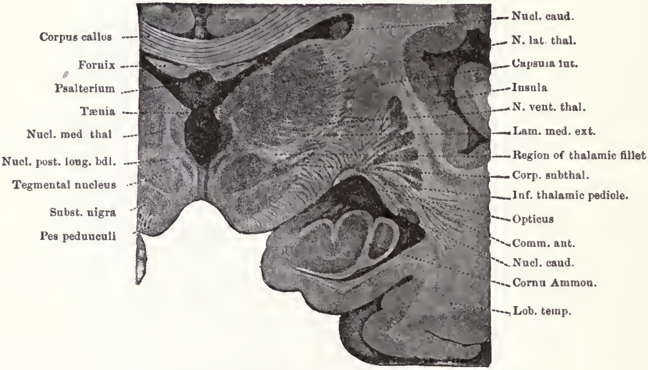

Fig. 179.—Section through the regio subthalamica.

Ventral to the putamen, here considerably diminished, there is recognized the radiation of the commissura anterior in the neighborhood of the inferior horn. Into the inferior horn itself the most *anterior part of the cornu Ammonis* is now seen to infold and project. The roof of the inferior horn here also contains the tail of the nucleus caudatus, which is curved downward, and then, naturally, the fiber-system from the temporal lobe to the thalamus. Outside the ventricle, and separated from this by the plexus chorioideus, lies the tractus opticus. The pes pedunculi is separated from that of the opposite side by the substantia perforata posterior.

The two columns of the fornix are united, and form a short, thin plate already in relation with the psalterium.

CHAPTER XVIII.

THE BASE OF THE BRAIN. THE OPTIC NERVE AND ITS ORIGIN. THE CORPORA QUADRIGEMINA.

WE have hitherto taken no occasion to examine the base of the brain more thoroughly. Now, when the origin of several of the structures found there is known to us, it may be time gently to free a brain, with the base turned upward, from the pia and blood-vessels, and to study the preparation so made.

The illustration that follows may serve as a guide. First of all, the crura cerebri are seen to emerge from out the mass of the cerebrum. Just in front of them, in the space here concealed for the greater part by the optic nerve, lies the substantia innominata, which contains the ansa lentiformis and the inferior thalamic pedicle (see Fig. 174 also). Frontal sections, previously demonstrated, have taught you that the white mass here visible, the *pes*, is the direct continuation of the fibers of the internal capsule. After a short course the crus cerebri is covered by thick masses of fibers, which appear to pass transversely across it from one-half of the cerebellum to the other. These fibers are designated as the *pontal fibers*, or *fibræ pontis*. On the other side of the pons a part of the fibers contained in the pes pedunculi can again be seen as the *pyramids*, another part has terminated in the ganglia that are scattered in between the fibers of the pons.

The gray matter between the crura cerebri is called the *substantia perforata posterior*. It borders internally on the regio subthalamica. In front of it lie the *corpora mamillaria*, those two roundish ganglia that we have previously met with in transverse section: the same ganglia to which the bundle of Vicq d'Azyr passes from the thalamus, the ganglia in which the fornix ends.

In front of the corpora mamillaria the floor of the middle ventricle, which is here designated as the *tuber cinereum*, bends, or bulges, downward and forward—so that a funnel arises, the lumen of which is nothing but the continuation of the ventricle. At the lower, pointed end of this funnel, the *infundibulum*, the *hypophysis* is attached (see Fig. 162).

The hypophysis—an appendix to the base of the brain, about the size of a cherry—consists first of all of the continuation of the ventricular floor, the lobus infundibuli, or lobus posterior, which is not positively known to be of a nervous nature. In front of this lies the anterior lobe, a tuft of epithelial tubules, which has grown firmly to the lobus infundibuli, and which, as you know, arises from the mucous membrane of the pharynx. Recent investigations (*Flesch, Dostojewsky*) make possible the recognition of two kinds of cells in it: smaller, clear cells, and larger, granular, and cloudy cells. Since, as is known, exactly similar elements are found in several very active glands, it is thus probable that the hypophysis also performs some physiological function. The hyperplasia of the epithelial part hitherto established in several cases of myxœdema points directly thereto. Between the pharyngeal and the cerebral lobes of the hypophysis there is found a number of other epithelial tubules, the lumina of which, as far as I can ascertain, are not con-

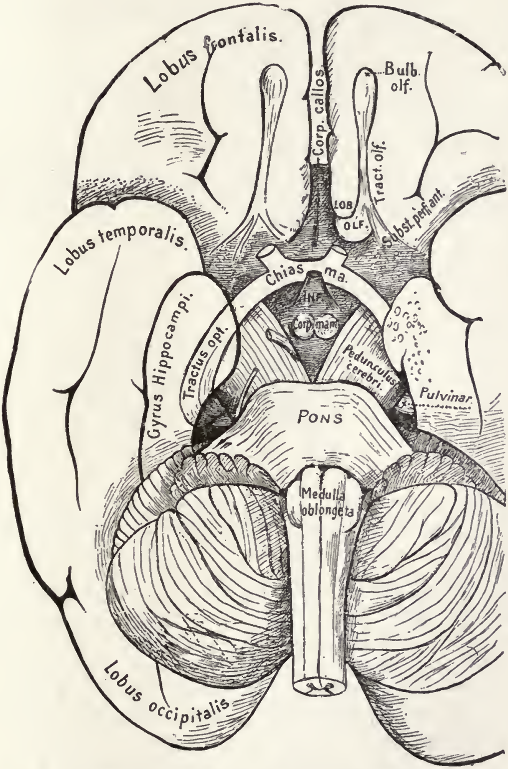

Fig. 180.—The base of the brain; the left lobus temporalis is, in part, represented as transparent in order that the entire course of the tractus opticus might be seen.

nected with either the one or the other part of the hypophysis. The accompanying sagittal section through the hypophysis of a human embryo of four months shows all three parts very plainly.

The *optic tracts* pass in a broad curve around the infundibulum and over the peduncles in a direction toward the pulvinar of the thalamus. Concealed on both sides by the lobus temporalis, they curve upward and outward around the origin of the peduncles, the crura cerebri, to attain the corpus geniculatum laterale and the pulvinar.

Anteriorly, in front of the infundibulum, the tracts unite to form the *chiasma*, from which, after the decussation of a part of their bundles, the *optic nerves* proceed.

In front of the optic tract and lateral to the chiasma there lies, just under (above, when examining the brain from the base) the anterior part of the corpus striatum, the *substantia perforata anterior*, a gray mass that is pierced by numerous vessels from the pia. The region of the *lobus olfactorius* begins in front of it.

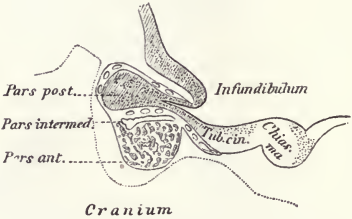

Fig. 181.—Sagittal section through the brain-floor and the hypophysis of a human embryo of four months. Combined from three consecutive sections.

The substantia perforata anterior is nothing else but the olfactory field, or area, which has become greatly atrophied in man. In Primates the lobus olfactorius is also atrophied along with the entire olfactory apparatus. In man only the most posterior part of it has been retained with its cortical structure (Figs. 172 and 173); the anterior part has diminished to an insignificant, gray cord, the *tractus olfactorius*, on which anteriorly is found the small bulbus olfactorius. From the bulbus, however, there still arise, precisely as in the other vertebrates, the large fiber-tracts of the olfactory radiation. Since these pass backward to the cortex of the lobulus olfactorius and the region of the gyrus hippocampi, they must pass over the tractus olfactorius, giving a white appearance to its under side. After reaching the olfactory field (the substantia perforata anterior) the tracts, which here, to be sure, are essentially thinner, split up exactly as they do in the osmatic vertebrates, and pass away as white strands—earlier named olfactory roots—over the gray substance. A lateral tract, often divided into two, may commonly be separated from a mesial. The former gradually turns inward near to the gyrus hippocampi. At times a thin, light-colored cross-band may be seen to pass over the substantia perforata anterior from without inward and upward. It is nothing other than the atrophied remnant of the olfactory bundle to the cornu Ammonis, which is to be seen in so high perfection in this situation in the osmatic vertebrates. Before leaving the consideration of the base of the brain, turn once more to Fig. 144, because in the osmatic brain there shown so many relations appear clearer; and the structures are better developed. The olfactory apparatus, especially, will then be clearer to you.

On the mesial edge of the substantia perforata anterior the fibers of the corpus callosum dip down as far as the base of the brain. The elevation they here produce on the inner, mesial cortex of the hemisphere, extending nearly to the base of the brain, is designated as the *gyrus subcallosus.* Between the two gyri subcallosi there lies a gray plate, which may be traced upward as far as the genu of the corpus callosum. It is the *lamina terminalis.* In it we must recognize a remnant of the embryonic closing plate —that wall which once closed in the primary forebrain, the same wall from which the hemispheres, now of such enormous size, grew and arched over the other parts of the brain. Now, this is only a small gray area of little importance, which lies at the most anterior point of the base of the brain (Fig. 133).

If an affection involves only the base of the brain in front of the pons, the symptoms that are produced by irritation or paralysis of the nerves lying there will be, by far, the most important for diagnosis. Moreover, disturbances of motility and sensibility may also appear in the extremities if the crura cerebri are involved with the rest. A careful analysis of the symptoms with the aid of an illustration of the base of the brain often leads to a surprisingly accurate diagnosis of the location of the lesion.

The optic tracts curve around the crura cerebri and disappear farther dorsally in the region of the *corpora quadrigemina,* particularly in a small ganglion lying adjacent to this laterally, the *corpus geniculatum laterale.* If you now wish to become better acquainted with the actual termination of the optic nerves, you must first of all give your attention to those parts of the midbrain just mentioned.

The following illustration shows the corpora quadrigemina when seen from above. They lie upon the peduncles, somewhat crowded in between the thalami. Behind them, on each side, a large fiber-tract comes from beneath them and sinks into the cerebellum. It is the *anterior cerebellar* *peduncle.* It arises from the nucleus ruber tegmenti, which lies in the tegmentum beneath the thalamus and the corpora quadrigemina.

We distinguish anterior and posterior corpora quadrigemina, but this distinction is easy to the naked eye in many mammals alone. In all other vertebrates the anterior are so large that the posterior corpora quadrigemina disappear as small ganglia in the region under them. From the anterior corpora quadrigemina arises a part of the optic nerves. The anterior cor-

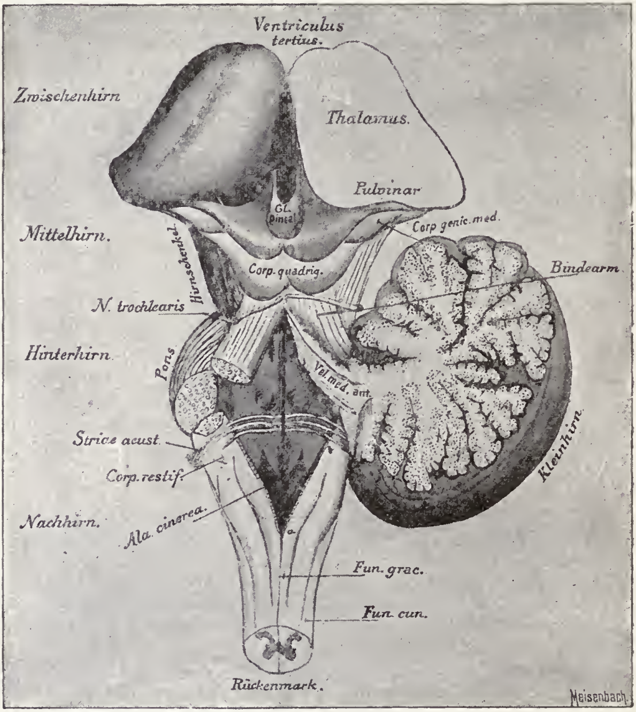

Fig. 182.—The brain-structures from the thalamus to the spinal cord (the "brain-stem"). The cerebellum divided, and removed on the left. ***Bindearm,*** Peduncle. ***Hinterhirn,*** Hindbrain. ***Hirnschenkel,*** Crus Cerebri. ***Kleinhirn,*** Cerebellum. ***Mittelhirn,*** Midbrain. ***Nachhirn,*** After-brain. ***Rückenmark,*** Spinal cord. ***Zwischenhirn,*** Interbrain.

pora, like the thalami, receive fibers from the territory of the occipital lobe, which run to the internal capsule in the optic radiation, and from there ascend to the corpora as the *brachia* of the anterior corpora quadrigemina. Fibers to the optic tract itself also run downward in this very brachium, or arm.

The brachium of the anterior corpus quadrigeminum, which is composed, therefore, of fibers *from* the cortex and fibers passing *to* the optic tract, sends its cortical fibers alone into the corpus quadrigeminum; its optic-nerve fibers spread out over the gray surface of the quadrigeminal body, thus forming the stratum zonale, and there sink below.

The posterior corpus quadrigeminum appears, at first sight, it is true, to stand in some relation with the optic tract, but it is *very* improbable that it contains fibers which are used in the visual act. Its brachium arises from the corpus geniculatum mediale and also from the *commissura inferior* (*Gudden's* commissure), not previously mentioned, which passes along with the optic tract to the posterior angle of the chiasma.

The posterior quadrigeminal body receives its coronal fibers (*Monakow*) from the lobus temporalis. The extraordinary development of the posterior corpus quadrigeminum in whales, and the huge tracts which, in these vertebrates, pass from there to the acusticus nucleus of the opposite side make it probable (*Spitzka*) that this ganglion stands in some relation with the auditory nerve. The results of experimental investigations, directed thereto, are in accord with this view. After destruction of the auditory-nerve nuclei, the secondary fiber-systems of the same atrophy as far as the posterior corpora quadrigemina (*Baginsky*, *Bumm*).

When seen from the side, the relations of the quadrigeminal brachia to the ganglia and the tractus opticus are very clear; likewise the relations of the corpora geniculata: the *corpus geniculatum mediale*, lying adjacent to the posterior brachium; the *corpus geniculatum laterale*, appearing to be thrust in between the pulvinar and the tractus opticus, of which mention was made when the thalamus was described.

The *tractus opticus* receives fibers from the latter ganglion, in addition to fibers from the pulvinar thalami and its stratum zonale.

The opticus fibers from the anterior corpora quadrigemina were mentioned previously. They probably run, for the greater part, in the brachium of the anterior corpus quadrigeminum.

In the lower vertebrates the optic nerve arises mostly from the anterior corpora quadrigemina; the other centers of origin, on the other hand, are very insignificant. The greater the development of the occipital cortex, however,—the cortex which sends its fiber-systems principally into the other centers, or terminals, and only supplies the anterior corpora quadrigemina with a relatively insignificant afferent tract,—the more do the fibers of the optic nerves arise from these terminals, and the less from the anterior quadrigeminal bodies. This still continues in the mammalian series. The portion of the opticus arising from the anterior corpus quadrigeminum, still very large in the rabbit, is considerably atrophied in man. On the other hand, the principal part of the optic nerve arises in man from the corpus geniculatum laterale.

It may be expressed as follows: Vertebrates which are dependent entirely, or almost entirely, for vision upon the primary centers, or terminals, have a preponderating development of the quadrigeminal branch of the optic nerve. As soon as cortical vision becomes more developed, however, the centers standing in more intimate relation with the cortex—the pulvinar, the corpus geniculatum laterale—become more important, and the quadrigeminal portion of the opticus diminishes relatively.

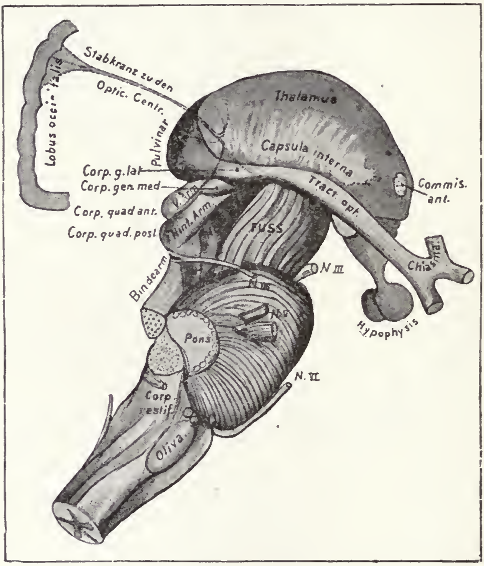

Fig. 183.—Thalamus and corpora quadrigemina seen from the side. The forebrain removed at the point where its coronal fibers pass into the capsula interna. The relations of the optic radiation to the posterior part of the capsula interna and to the point of origin of the opticus are shown diagrammatically. *Bindearm*, Peduncle. *Fuss*, Pes, or crusta. *Hint. Arm.*, Posterior brachium. *Stabkranz zu den Optic Centr.*, Coronal fibers to the optic centers. *V. Arm.*, Anterior brachium.

So much for the origin of the optic nerve as represented by a preparation of the adult human brain. According to *J. Stilling*, there is added still another root which ascends in the pes pedunculi from the medulla oblongata.

However, it is so difficult correctly to locate and trace out all these fibers and nuclei in man that we must ask ourselves the question: How far are the relations under discussion supported by investigations on other vertebrates? First of all, comparative anatomy presents us optic centers of such magnitude in the midbrain of fishes and birds that the relations may be studied there much more easily than in mammals. But in the reptiles and amphibians, as well as in fishes and birds, it is easily recognized that the principal part of the optic nerve certainly ends in the anterior corpus quadrigeminum, and that in its course past the corpus geniculatum laterale it sends numerous collaterals into this ganglion. Experimental investigations (*Gudden*, *Ganser*, *Monakow*) on mammals show that after the early extirpation of an eye the anterior corpus quadrigeminum, certain layers of the corpus geniculatum laterale, and fibers from the pulvinar degenerate. The pulvinar is, moreover, very small in most mammals, and first attains a considerable size in the Primates.

It is already evident from the foregoing that numerous methods of investigation have been made use of in order to ascertain the course and termination of the fiber-system of the optic nerve. I have purposely communicated this to you somewhat more thoroughly because the history of our knowledge here shows how much is to be gained by the application of many methods to a single object; and, moreover, because I still have something to say concerning new advances which, accruing from the purposive application of the method of degeneration and supported by the results of embryological research, give very important information concerning the combination, and the histology of the termination, of the optic-nerve fibers.

As you know, only those fibers degenerate which are separated from the cells from which they originate. According as the optic nerve is destroyed at its eye (or peripheral) end or is injured at its terminal points (or centers) very different types of degeneration are obtained. The study of such varied preparations has led *Monakow* to the conclusion that the majority of the fibers of the optic nerve do not originate from the cells of the brain at all, but from the large ganglionic cells of the retina. The neuraxons that arise there pass backward in the opticus, and in man end for the most part in the corpus geniculatum laterale and in the pulvinar—probably in a brush-like arborization around the cells situated there. The white lines which traverse the gray matter of the lateral geniculate body consist, in part, of such fibers which come directly from the retina. In fact, *P.* and *S. Ramón y Cajal* have been able to show such brush-like arborizations of the optic fibers terminating around cells in the roof of the midbrain and around cells in the corpus geniculatum laterale, for vertebrates of all classes (see Figs. 66 and 81 also).

There are fibers, however, in the opticus which originate from the brain. From the cells that lie in the superficial gray layer of the anterior corpora quadrigemina optic fibers certainly arise in the rabbit and cat, and very probably in man, which then go to the retina, and there probably terminate in an arborization around the cells of the granular layer. The optic nerve contains fibers, therefore, which arise from the retina and others that arise from the primary optic centers. Embryological studies by *Keibel* and *His* have shown that certain of the optic fibers grow toward the brain from the large cells of the retina.

While the existence of the opticus roots asserted to come from the corpus subthalamicum and from the crus cerebri has not as yet been sufficiently confirmed by the various methods of investigation, we may probably at present regard it as firmly established that optic-nerve fibers arise and terminate in the corpus geniculatum laterale, in the superficial medulla of the anterior corpus quadrigeminum, and in the outermost layers of the pulvinar. These last-named gray masses are designated as the *primary optic centers.*

A connection between these centers and the cortex of the occipital lobe has been proved in a definite and satisfactory manner. The fibers concerned in this form the *radiatio thalamo-occipitalis,* the *optic radiation,* or the *bundle* of *Gratiolet*: a not inconsiderable fiber-tract which develops from the primary centers in separate bundles and passes backward from there to become lost in the cortex of the cuneus and in about the region of the second and third occipital gyrus.

In the territory from which they originate (the cortex) and along the proximal part of their course while passing away from there, the coronal fibers to the separate optic centers (or terminals) are to be separated from one another only with difficulty. Farther anteriorly, however, it is recognized that the fibers to the pulvinar occupy the dorsal, and the fibers to the geniculatum laterale the ventral, portion of the tract. Only in the most posterior division of the internal capsule, just before the entrance into the primary centers (Fig. 165), are the separate parts of the optic radiation sharply separated from one another. The pedicle to the corpus geniculatum lies close to this as the lateral medullary field, or area. It arises from the cuneus, perhaps from the lobus lingualis also. Dorsal to it, the fibers of the optic radiation arising from the two occipital gyri enter the pulvinar.

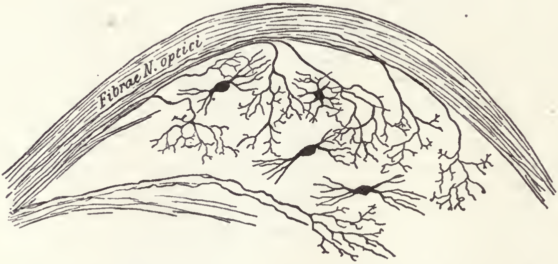

Fig. 184.—Section through the corpus geniculatum laterale of the cat. Silver method. Shows the entering optic fibers and the splitting-up of the same into terminal, brush-like arborizations. (After P. Ramón y Cajal.)

Farther dorsal to these are situated tracts that become lost in the latticed layer of the thalamus.

These relations of the central optic pathway may be plainly recognized in a frontal section, passing through the most anterior part of the corpora quadrigemina.

As I have as yet demonstrated no section from the midbrain region, Fig. 185—which is an addition to the human brain-sections demonstrated earlier—needs a few words of explanation.

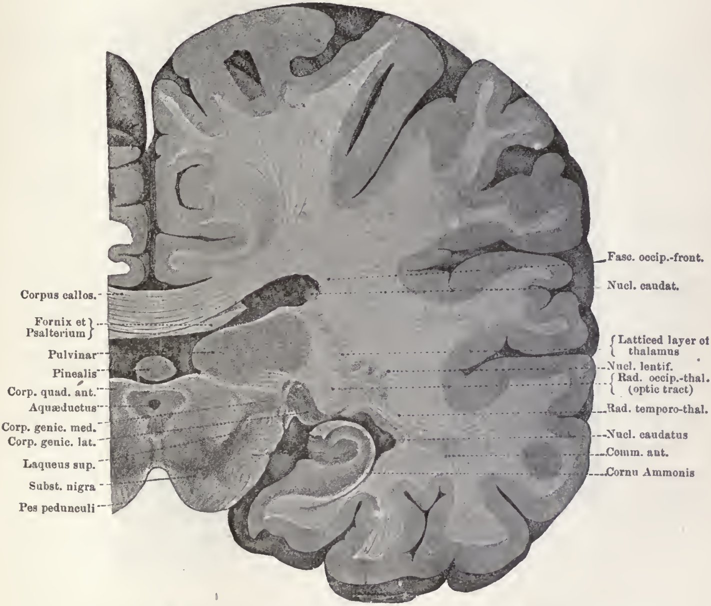

Fig. 185.—Frontal section through the forebrain and the interbrain near the place where fibers of the capsula interna become the pes, or crusta, of the crus cerebri.

The ventricle, which farther anteriorly was closed in dorsally by the epithelium of the plexus alone, has narrowed here in the territory of the mesencephalon to the aquæductus Sylvii. Over this the anterior corpora quadrigemina lie like a roof. Since these project, as Fig. 125 shows, somewhat forward between the posterior ends of the thalami, the most posterior, thalamic ganglia—those of the pulvinar—are accordingly cut on each side of the corpora quadrigemina. This division of the thalamus attains its greatest expansion exactly at the plane of this section. Under it there is met, as a glance at Fig. 183 shows, the corpus geniculatum laterale and the corpus geniculatum mediale.

The geniculatum mediale lies in a direct line with the nucleus ventralis thalami. Toward the median line it has the fiber-systems of the fillet, with which, in these planes, are now associated fibers from the roof of the midbrain.

In the ventral territory of the geniculatum laterale the tractus opticus becomes almost entirely lost, with the exception of single bundles that pass over the geniculatum mediale to the stratum zonale of the corpora quadrigemina.

The pes pedunculi and the tegmentum are now fully developed. They will be more thoroughly described in the next chapter.

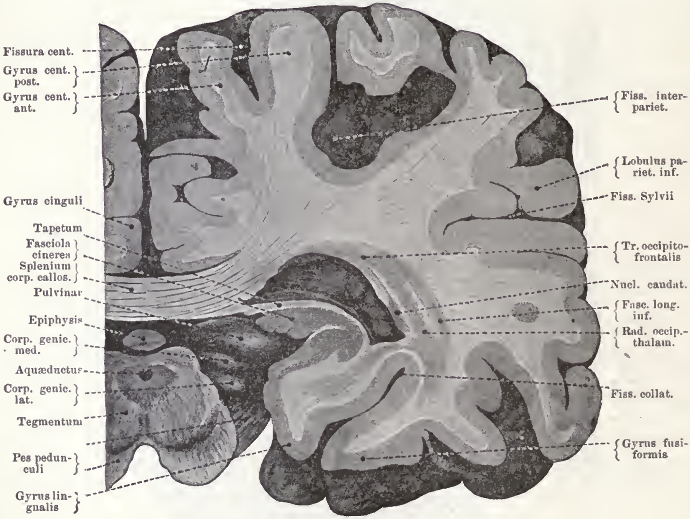

Fig. 186.

In this plane all three nuclei receive their afferent fibers from the corona radiata. The *optic radiation*, radiatio thalamo-occipitalis, and the pathway from the temporal lobe to the geniculatum mediale, which was designated as the pedicle (*Stiel*) of the same in a previous illustration, are now plainly visible.

In its dorsal region the white medullary substance principally contains fibers of the corpus callosum and short association-fibers. Of the long pathways, the fasciculus arcuatus can, perhaps, be traced here. In its ventral half the white matter consists principally of the fiber-systems that arise from the occipital lobe, which are either fibers belonging to this lobe itself or coronal fibers to the thalamus and to the lateral bundle of the pes. At about one-fourth the distance from the base of the section lies the radiatio occipito-temporalis, or fasciculus longitudinalis inferior.

The crura of the fornix are now no longer seen, but there lies under the corpus callosum the broad plate of the psalterium, on the edges of which lie the fimbriæ. Through an interchange of fibers in this territory arise the true fornix columns. Far below is to be noted the origin of the fimbria from the medullary substance of the hippocampal cortex, and its relation to the inferior horn of the ventricle.

We will now at once trace the optic radiation farther backward until within the apex of the occipital lobe, so that a clear idea may be gained of it as a whole. For this reason I here demonstrate a section in Fig. 186 that is located about three-fourths of a centimeter behind that of Fig. 179.

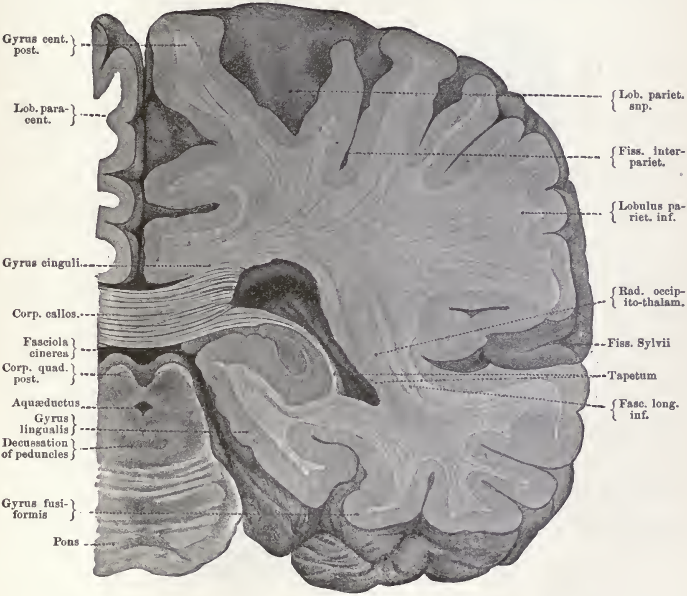

Fig. 187.

The anterior corpora quadrigemina are exactly halved. Away from the cut surface of the crus cerebri, the pulvinar and the corpora geniculata are seen in the interior of the section on the right. The development of the pes pedunculi from the capsula interna becomes especially clear upon comparison of this section with those made farther anteriorly, because the egress of the peduncles from the base of the brain is so plainly visible here.

The optic radiation has already entered its terminals in the section shown in Fig. 185; we see it only as a gray area, in transverse section, in the midst of the white medullary substance lateral to the ventricle.

The section shown in Fig. 187 passes down just in front of the posterior end of the corpus callosum. This very instructive section allows us to observe how the tapetum of the corpus callosum develops from the fibers of the splenium, and how the tapetum envelops the posterior horn of the ventricle and covers the inner side of the cornu Ammonis. A part of the hippocampal gyrus—a part that is atrophied, it is true—still lies directly under the corpus callosum in man. It is designated as the fasciola cinerea. The cornu Ammonis is here met with in its most posterior position, just in front of the occipital lobe. The ventricle opens, on the one hand, posteriorly into the posterior horn, and, on the other, ventrally into the inferior horn. It is for this reason that it appears so long and wide. Outside of the optic radiation lies the longitudinal bundle which passes from the occipital lobe into the temporal lobe. In the most dorsal territory the medulla still belongs to the radiation from the uppermost portion of the two central gyri; then follows, farther laterally and externally, the territory of the parietal lobe, and thereupon the medulla of the gyrus angularis and the temporal gyri.

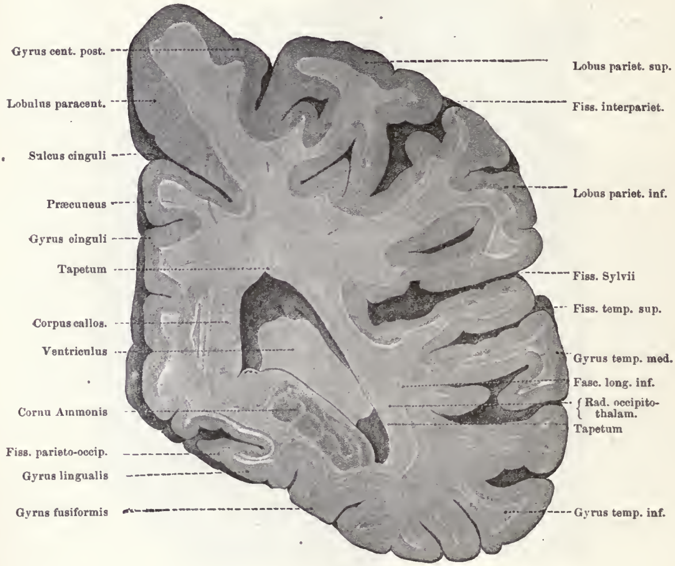

Fig. 188.

The section illustrated in Fig. 188 lies directly at the base of the cuneate occipital lobe, consequently behind the end of the corpus callosum. The ventricle, widely opened and covered by the tapetum, leads at its dorsal end into the posterior horn; at its ventral end, however,—where mesially the gyrus hippocampi is still found to be cut,—it leads into the inferior horn of the temporal lobe. Dorsal to the cornu Ammonis is found the large mass of fibers of the corpus callosum, which pass from the terminals in the occipital lobe to the forceps major (*Balkenwulst*) and are here cut just before they enter the splenium.

We now meet with the radiatio occipito-thalamica in greater width than hitherto outside of, and lateral to, the tapetum. It here lies under the convolutions of the temporal lobe, and *this position explains why lesions in the gyrus marginalis or angularis frequently lead to hemianopsia.* If the lesions are not altogether too superficial, they always of necessity involve the optic radiation.

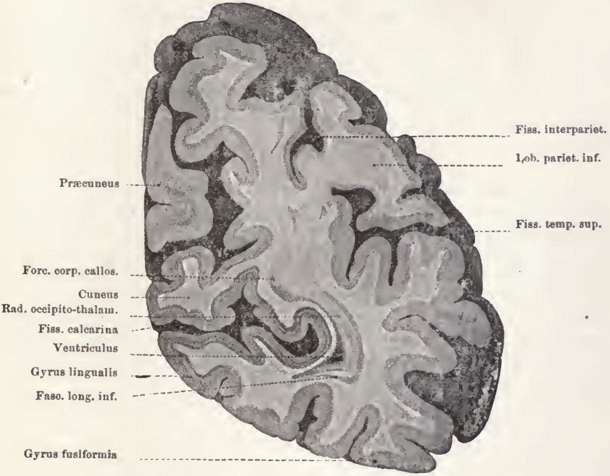

Fig. 189.

The fasciculus longitudinalis inferior also (the tract from the occipital lobe to the temporal lobe), the transverse section of which, as in the previous sections, you again find external to the optic radiation, is here wider than previously, because we now approach the territory where it originates. The peculiar oblique form of the under side of the section is explained from the fact that the hemispheres of the cerebellum, separated by the tentorium alone, here lie against the cerebrum.

You finally see a section (Fig. 189) which I have made through the occipital lobe very near to the posterior pole of the brain. The posterior horn of the ventricle, which is still just visible as a small fissure, may again serve as a point of orientation in obtaining the relation of the fibre-systems to one another and as a whole.

From the neighborhood of the fissura calcarina, which here cuts in deeply, arises the optic radiation, which we have now traced from its origin to its termination in the territory of the thalamus and in the corpora quadrigemina. The last radiations of the occipital fibers of the corpus callosum, the forceps, are separated and distinct from the gray matter of the ventricle. The fasciculus occipito-temporalis, or longitudinalis inferior, lies now no longer lateral, but ventral, to the ventricle.

The greater part of the remaining white matter visible in the section belongs to the intrinsic fibers of the occipital lobe, to the short pathways which connect its various cortical areas with one another.

It is not improbable that the fibers found in the optic radiation have two points of origin: they may originate from the cells of the primary centers and pass to the cortex, or they may originate from cortical cells and pass to these primary centers.

In cases of destructive focal lesion in the occipital lobe and in the most posterior part of the internal capsule, disturbances of sight appear that are exactly similar to those where the optic-nerve tract has been injured on the side involved. The outer half of the retina of the eye which is on the same side as the lesion and the inner half of the retina of the opposite eye degenerate.

A fiber-tract that was discovered by *Gall* and *Spurzheim* probably belongs to the system of the opticus also. It passes down laterally from the anterior corpora quadrigemina, and at the base of the brain runs for a distance transversely across the pes pedunculi before it sinks into the pes near to the median line. It then attains a ganglion of the ventral thalamic region (*Kölliker*). This tract—*the tractus peduncularis transversus*—degenerates after the destruction of one optic tract (*Gudden*). It is not always capable of demonstration, and is variable in its development. In Fig. 141 you see it (not designated) pass over the right crus cerebri. Probably this bundle is identical with that one which was described on page 132 as the tractus thalamo-tectalis.

CHAPTER XIX.

THE TEGMENTUM AND THE PEDUNCLE OF THE MIDBRAIN.

THE frontal sections through the cerebrum, with description of which the previous chapter ended, led us somewhat away from the tracing of the tracts which pass into and beyond the midbrain.

In the description these tracts had been followed to the region of the posterior end of the middle or third ventricle. One may see in Fig. 125 that just behind this the midbrain—the corpora quadrigemina—begins. At that place the thalami diverge from each other, the tegmental prominence pushes in between them, thus considerably decreasing the depth of the ventricle.

In connection with the accompanying description, study, in Fig. 190, the formation of the roof of the midbrain. In the most anterior part of this roof (see also Fig. 125) lie the fibers of the *posterior commissure*, close behind which lie the corpora quadrigemina. The narrow ventricle which passes under the roof has received, in the region of the midbrain, the name *aquæductus Sylvii*. The entrance to the aqueduct lies just under the posterior commissure. The aqueduct is everywhere surrounded by the gray matter of the central canal.

Now the posterior commissure lies in the most anterior portion just behind the epiphysis. A part of its fibers arises from ganglia which lie, one on each side, near the median line, deeply imbedded in the interbrain. This is easier to demonstrate in lower vertebrates than in mammals, but *Kölliker* has also shown that in mammals the origin is the same. Thence they pass upward to the surface and, anterior to the quadrigeminal bodies, turn to the opposite side. They pass for only a very short distance horizontally, when they plunge into the depth of the tegmentum of the midbrain, through which they pass farther back.

As very clearly seen in lower vertebrates, the majority of the fibers in question pass laterally and ventrally from the posterior longitudinal fascicle into the medulla. Through this reinforcement this fascicle becomes a thick bundle—later to be described. Spitzka and Darkschewitsch have seen a similar arrangement in mammals. In all vertebrates the posterior commissure is one of the first bundles to become medullated.

We come now to the region of the midbrain. Let us find what has become of all the fibers which were traced in the last chapter. We find only a few in the region which we have now reached. The greater part of the fibers which compose the medullary substance of the brain-mantle is not to be seen in the posterior sections of the interbrain. They have either, as association-tracts, disappeared in the cortex itself or as coronal fibers of the thalamus disappeared in the ganglia of the thalamus. A portion of the corona radiata, passing beneath the interbrain, arrives at the base of the brain as the *pes pedunculi cerebri*. Even the fiber-system of the striatum has almost completely disappeared, only a bundle to the *substantia nigra* Sömmeringi being still demonstrable (see Fig. 191).

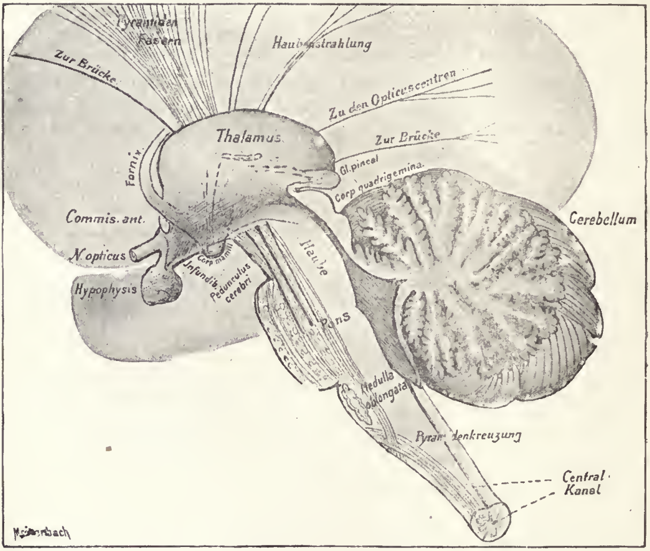

Fig. 190.—Median sagittal section through the interbrain and the structures posterior to it. The course of a number of coronal fibers is indicated by lines: *Zur Brücke,* To the pons. *Pyramiden Fasern,* Pyramidal fibers. *Haubenstrahlung,* Tegmental radiation. *Zu den Opticuscentren,* To the opticus centers. *Haube,* Tegmentum. *Pyramidenkreuzung,* Pyramidal decussation.

In the plane of the last section a part of the *laminæ medullares thalami* and especially a lateral bundle, the *superior lemniscus* from the thalamus, may be traced. Furthermore a few small bundles which arise from the corpus mamillare and the Ggl. habenulæ may be seen.

Having now made ourselves somewhat familiar with the structures in the region of the corpora quadrigemina, let us study a section through the anterior quadrigeminal bodies, the structures of the tegmentum, and the pedunculi cerebri (see Fig. 192).

Taking bearings from structures already known, note on each side externally the *pulvinar thalami*, from which the optic nerve appears to come. The *corpus geniculatum laterale* seems to be inclosed in the course of the

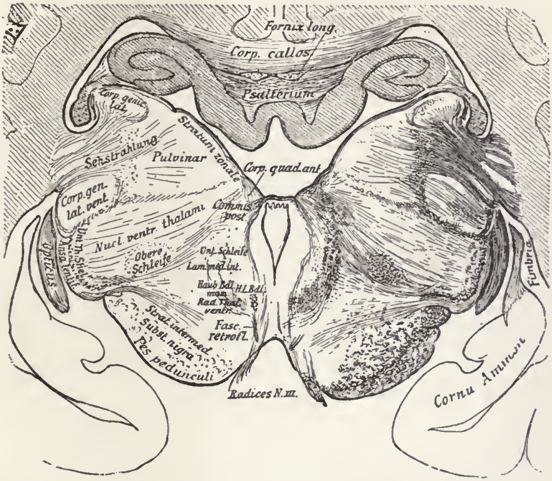

Fig. 191.—Showing the transition from the interbrain to the midbrain. The section is from the brain of a dog and is about one millimeter posterior to that shown in Fig. 177. Compare carefully the series represented in Figs. 169, 176, 177, and 191. NOTE: the *Commissura post.*, whose most anterior fibers are severed; the *stratum zonale*, fibers from the anterior quadrigeminal bodies into the opticus; the pulvinar; the *Nuc. ventralis thalami*; the *Superior lemniscus* or fillet (*Obere Schleife*), which is nearer the median line and larger than in Fig. 177; the *fasciculus retroflexus*, which has passed off from the ggl. habenulæ; the most anterior fibers of the inferior lemniscus (*Unt. Schleife*), which arises from a gray nucleus that merges into the median marrow of the corpora quadrigemina; the most anterior fibers of the *oculo-motorius* (Radices N. III); the *posterior longitudinal fascicle*, which arose in the preceding section by a few fibers from its nucleus, now grown larger; the *optic radiation* (*Sehstrahlung*), which is the pedicle of the anterior quadrigeminal body and of the corpus geniculatum laterale. The large nucleus, designated *Nucl. ventr. thalami* gradually merges below into the corpus geniculatum mediale. Note also the decussation between the cornua Ammonis and the position of the fornix longus. In the pes pedunculi the stratum intermedium composed of fibers from the lenticular ganglion in the regio subthalamica.

nerve (see especially Fig. 195). It receives a bundle from the arm of the corpus quadrigeminum anterius, well shown on the left side of the figure, above which one will recognize the *corpus geniculatum mediale.* Beneath the pulvinar the *pes pedunculi* emerges.

In the pes are contained fibers of very varied origin. Embryological studies and especially the exact tracing of secondary degenerations, which result from cerebral lesions, alone make it possible to determine where the different tracts lie. There is already a considerable number of well observed cases of partial degeneration of the pes, so that an enumeration of the parts of the pes may with due certainty be given. According to Déjèrine's investigations, which cover the largest amount of material yet studied, there lie in the outer fifth of the pes fibers which arise from the middle part of the temporal lobe. In its median fifth are fibers which pass down from the region of the operculum. In the middle three-fifths of the pes are found the fibers from the posterior portion of the frontal lobe and from the true motor region. All of these bundles arise direct from the cortical cells and degenerate when they are interrupted anywhere between the cortex and

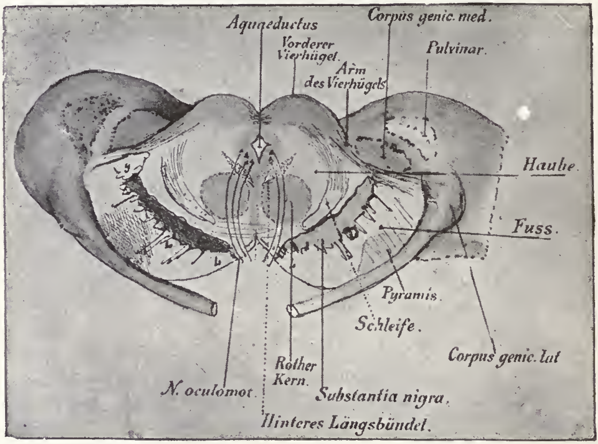

Fig. 192.—Cross-section through the corpora quadrigemina anteriora (somewhat diagrammatic). *Vordere Vierhügel*, Corp. quad. ant. *Arm des Vierh.*, Arm of the corp. quad. *Haube*, Tegmentum. *Fuss*, Crusta, or pes pedunculi cerebri. *Schleife*, Lemniscus, or fillet. *Hinteres Längsbündel*, Fasciculus longitudinalis post. *Rother Kern*, Nucleus ruber.

the pons. In about the middle third of the pes, beneath these bundles, lies also the tractus cortico-spinalis, the pyramidal tract, the only bundle of the pes which extends farther than the pons.

Dorsal from the pes pedunculi lies the *stratum intermedium* (see Fig. 191), with fibers from the corpus striatum; then comes the substantia nigra, an aggregation of fine nerve-fibrils and ganglion-cells, the significance of which is still quite unknown.

In the tegmentum one notices at once the two large, round, reddish-gray bodies; they are the red nuclei of the tegmentum: *nuclei rubri tegmenti*, or *nuclei tegmenti*. The *corpus subthalamicum* which lies near them (see Fig. 179) does not appear in the plane of this section.

The red nucleus, into which fibers pass from the thalamus and from the cerebral cortex, is at this point rich in medullated fibers. These pass ventral to the posterior quadrigeminal bodies, and, for the most part, decussate there with those of the opposite side. They belong to the anterior cerebellar peduncle and the decussation is called the decussation of the anterior (superior) cerebellar peduncles. This decussation is very prominent in a frontal section through this region. Farther posterior these tracts —Tractus tegmento-cerebellares—form thick bundles which lie external to the red nuclei, and then pass farther and farther to the side and finally reach the outer surface, whence they pass backward to the cerebellum. Since, after injury of the cerebellum, the superior peduncle degenerates as far as the tegmental nucleus, its origin must be in the cerebellum and its end in the red nucleus (Mahaim, *et al.*).

A nearly horizontal section through the thalamus, the corpora quadrigemina, and the cerebellum, following the plane of the superior peduncles, gives the relations between the thalamus, the red nucleus, the tegmental radiation, superior peduncles, and cerebellum, as shown in Fig. 193.

In the cerebellum the superior peduncle enters the *corpus dentatum.*

Exterior to the tegmental nucleus lies a thick bundle of obliquely-cut fibers (see Fig. 192), which appear to emerge from under the corpora quadrigemina. They pass downward in the region dorsal to the substantia nigra. The fibers arise mostly from the ganglia of the corpora quadrigemina and are called the *inferior lemniscus*, or lower fillet. The upper fillet from the thalamus lies, at the level now being considered (see Figs. 191 *et seq.*), somewhat external to and below the red nucleus, and appears as a separate bundle of transversely divided fibers. To the outside of it lie the fibers of the lower fillet. It thus happens that there is a broad band of transversely divided fibers just above the substantia nigra, which is called the layer of the fillet, or *stratum lemnisci* (see also Fig. 194).

The greater part of the stratum lemnisci can be traced posteriorly as far as the nuclei of the sensory nerves and of the posterior columns. Meynert first demonstrated that in it we have a segment of the sensory tract. Embryology and comparative anatomy equally substantiate this position. Later we shall trace the farther course of the fillet.

Thus the stratum lemnisci contains two elements: mesially the upper and laterally the lower lemniscus. The lower lemniscus (better called lemniscus of the midbrain) arises chiefly from a system of fibers not yet mentioned: viz , the deep marrow, or deep medullary stratum of the midbrain-roof; the remainder arises from the ganglion of the corpus quadrigeminum posterius. On an oblique frontal section through both pairs of quadrigeminal bodies this is clearly shown (see Fig. 194).

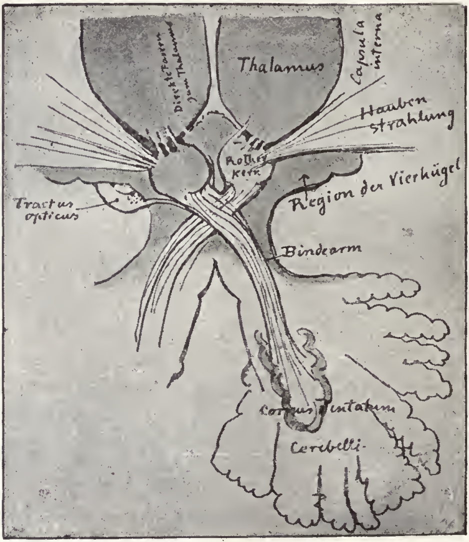

Fig. 193.—Diagrammatic horizontal section through the decussation of the superior cerebellar peduncles and vicinity. The bundle to the optic tract is questionable. *Direkte Fasern zum Thalamus,* Direct fibers to the thalamus. *Haubenstrahlung,* Tegmental radiation. *Rother Kern,* Tegmental nucleus. *Region der Virhügel,* Region of the corpora quadrigemina. *Bindearm,* Anterior or superior cerebellar peduncle.

The ganglion in question consists of a large, round nucleus filled with a net-work of fine fibers. As the ganglion of the posterior quadrigeminal body possesses only one nucleus, it does not show the stratification of gray and white substance characteristic of the anterior quadrigeminal body—the optic ganglion. It is connected with the ganglion of the opposite side through fibers which pass over the aqueduct of Sylvius.

Phylogenetically the deep medullary stratum is a very old system. It is not lacking even in the most simply constructed brains of the lower vertebrates, and in these, as in the human brain, its fibers become medullated very early. Its fibers arise in the roof of the midbrain from layers which lie ventral to those from which the optic nerve arises. From this origin they pass radially inward, but turn ventrally near the central gray matter which surrounds the aqueduct. The most lateral of these fibers, united with those which come from the opposite side, pass into the fillet, but the more mesial ones engirdle the aqueduct and mostly decussate ventral to it with those of the opposite side: *"fountain-like"* decussation (Forel). (See Figs. 195 and 199.)

Fig. 194.—An oblique frontal section in the plane indicated in the accessory figure (*Schnittrichtung*) contains the greater part of the origin of the lower lemniscus (or midbrain-fillet). Hæmatoxylin stain. For *Brach. ant.* read brachium posticum. *Tiefes Mark,* Deep medullary stratum. *Centr. Höhlengrau,* central gray matter. *Schleifenschicht d. Pons,* Stratum lemnisci pontis. *Schnittrichtung,* Direction of section.

In fishes and birds the fibers of the deep medullary layer are so strongly developed that their course is easier to recognize. But in them as in the amphibians and reptiles, one recognizes that these fibers, so far as they do not pass into the fillet, belong to the midbrain itself and end in cells partly on the same side and partly on the opposite side. At the corresponding point in the human brain there are also groups of cells, the *ganglion profundum mesencephali laterale et mediale.*

Scattered cells in the base of the midbrain probably give origin to a system of fibers, very interesting phylogenetically. It will be recalled that in bony fishes at this location there is a large ganglion, the Torus semicircularis, and that from it a large bundle may be followed into the lateral tracts. Boyce has recently succeeded in finding, in a cut through one side of the brain of a cat, a bundle which, beginning in the base of the midbrain, may, through operatively induced degenerations, be followed out of the midbrain as far downward as the anterior and lateral columns of the spinal cord.

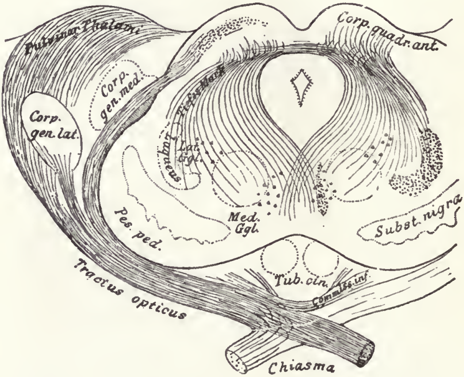

Fig. 195.—Fibers arising in the roof of the midbrain. Dorsally the Tractus opticus, ventrally the deep medullary layer (*Tiefes Mark*). Diagrammatic.

In the central gray matter, below the quadrigeminal bodies, appear the first ganglion-cells which give rise to a cranial nerve: nervus oculo-motorius. From their union, the nucleus nervi oculo-motorii, the root-fibers of the nerve pass ventrally through the tegmentum and the crusta toward the base of the brain, where they pass out united into thick bundles (see Fig. 199). The motor-oculi nerve contains fibers to several muscles within and about the eye. Since nuclear paralysis of individual muscles of the group supplied by this nerve has been observed, it is very probable that the nucleus consists of a complex of small nuclei, somewhat separated from one another.

In man a manifest division into several portions may, in fact, be observed. Quite forward, partly in the wall of the third ventricle, lies, on either side, a narrow, small-celled nucleus, the *nucleus anterior*. It sends its few fibers somewhat backward to the main trunk of the nerve. Posterior to it lies the *nucleus posterior*, composed of large, multipolar cells and extending along nearly the whole length of the aqueduct. One may recognize in this nucleus an arrangement of the cells into groups. One dorsally located collection of cells is clearly distinguishable. While all the other motor-oculi fibers emerge from the side in which they originate, the fibers from this group, as discovered by Gudden, pass toward the median line, dip ventrally, and cross to the opposite side. Besides the dorsal division, a median one may be defined. It lies exactly in the median line and sends out root-fibers both to the right and left.

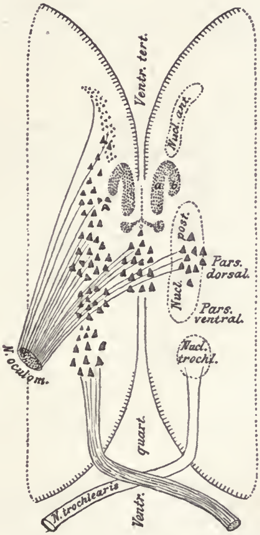

Fig. 196.—Floor of the aquæductus Sylvii, looking upward. Nuclei of the motor-oculi and trochlearis nerves. Partly diagrammatic.

Fig. 196 represents partly diagrammatically the nuclei in the floor of the aqueduct and their relations to the nerve-roots. Note in the figure two small nuclei joined together anteriorly (*a* and *b*). These two nuclei, first seen by me in fetal brains and since more carefully studied by Westphal in adult brains, lie in a dense net-work of nerve-fibers. It is not yet certain whether these fibers are in connection with the motor-oculi nerve, and if so how the connection is made. There is such an array of clinical observations and of facts derived from post-mortem dissections that one may venture to designate the portion of the nucleus from which the innervation of each individual ocular muscle comes. I give here Starr's table, the latest of these numerous attempts so happily begun by Pick. According to Starr, the nuclei of the individual muscles are arranged from before backward thus:—

Sphincter iridis.	Musculus ciliaris.	Median line.
Levator palpebræ.	Rectus internus.	
Rectus superior.	Rectus inferior.	
Obliquus inferior.		

The nerves for the intrinsic muscles of the eye arise probably from the anterior nucleus. The crossed tract, possibly also the median portion of the posterior nucleus, are to be accredited to the internal rectus. Clinical observations show that there must be a direct and a crossed connection between the motor-oculi nerve and the centers of the optic nerve, but the anatomical basis for this has not yet been established. Net-works and bundles of fibers through which the connection might take place are abundant in this region. But up to the present time there has been on this point neither a conclusive experiment nor a convincing clinical observation with a subsequent post-mortem demonstration.

The motor-oculi nucleus lies ventral to the aqueduct of Sylvius: *i.e.*, in the floor of the aqueduct. Later, as we proceed to study the tegmentum backward, we will meet in the region of this floor the nuclei of nearly all the other cranial nerves.

At the beginning of this chapter it was stated that fibers pass backward from the posterior commissure. Toward a point located mesially and ventrally from these fibers fine bundles converge, which arise in the interbrain below the anterior nucleus of the oculo-motorius. The sectional area covered by these bundles becomes progressively greater from before backward. They are reinforced by many fibers from the motor-oculi nucleus itself. We shall meet the somewhat triangular cross-section of this fascicle, which is made up of such varied constituents, in all the sections from the corpora quadrigemina down to the beginning of the spinal cord. It is called the *posterior longitudinal fascicle* (*fasciculus longitudinalis posterior*). Since along the whole course of this bundle fibers pass from it to the nuclei of the other cranial nerves (readily seen in a fetus of six or seven months, where few other fibers are medullated), and since its posterior end lies much beyond the nucleus of the abducens it is probable that the posterior longitudinal fascicle contains, besides the fibers which connect the ocular muscles among themselves, also fibers for the other cranial nerves.

The posterior longitudinal fascicle sends its most anterior fibers much farther forward than to the nucleus of the oculo-motorius. In the central gray matter just anterior to the beginning of the aqueduct is a collection of large ganglion-cells from which a number of such fibers arise,—*nucleus fasciculi longitudinalis superioris* (see Fig. 179). This nucleus is demonstrable in all vertebrates. In mammals it lies in those planes which ventrally intersect the posterior part of the corpus mamillare. Inasmuch as it is found in all vertebrates, and always from the interbrain to the region of the anterior columns of the spinal cord, it must be recognized as *one of the fundamental features of the brain.* (See also Chapter VI, Figs. 43 and 44, and text).

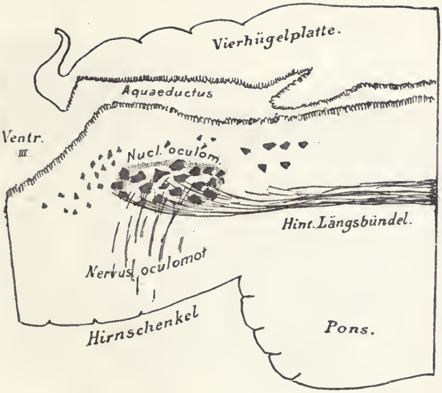

Fig. 197.—Longitudinal, nearly median, section through the midbrain of a twenty-eight weeks' human fetus, partly through the outer wall of the aqueduct, showing the end of that part of the posterior longitudinal fascicle which belongs to the nucleus of the oculo-motorius. *Vierhügelplatte,* Midbrain-plate. *Hint. Längsbündel,* Post. long. fascicle. *Hirnschenkel,* Pes pedunculi.

The boundaries of the numerous systems of fibers to be found in the region of the corpora quadrigemina can only be sharply differentiated through studying the development of their medullary sheaths. In Fig. 198 we have a section from a nine months' human fetus, through the anterior quadrigeminal bodies just at the posterior commissure. All of the fibers, which at this stage of development are medullated, are stained with hæmatoxylin.

Of the structures named in the figure the small elliptical areas (*b*), lying between the red nuclei, have not been previously mentioned. The fibers here cut arise in the ganglion habenulæ thalami and pass from it downward and backward to a small ganglion, which lies between the cerebral peduncles, the *ganglion interpedunculare*. Before entering this ganglion the fibers decussate. The bundle is called the *tractus habenulo-peduncularis*, the *Fasciculus retroflexus*, or *Meynert's bundle*. Its course is best seen in Fig. 144. In the ganglion habenulæ ends the greater part of the tænia thalami, which, as above described, passes up from the lateral portions of the olfactory area.

The ganglion interpedunculare was discovered by *Gudden* and first exactly described by *Forel*. *Gudden* showed that after destruction of one ganglion habenulæ the fasciculus retroflexus of the same side undergoes descending degeneration, and that the degenerated fibers may be followed as far as the opposite ganglion interpedunculare. *Ganser* discovered another bundle from the tegmentum to the ganglion interpedunculare.

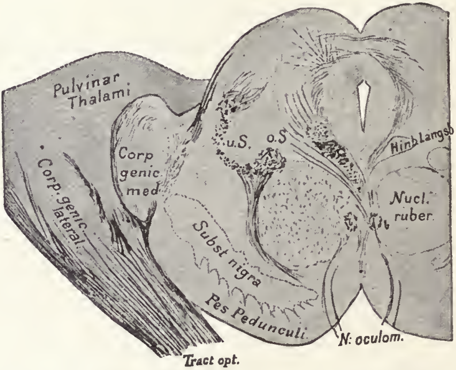

Fig. 198.—Frontal section through the anterior quadrigeminal bodies of a nine months' fetus. *o. S.*, *u. S.*, upper fillet and lower fillet. *Hint. Längsb.*, posterior longitudinal fascicle.

The author's investigations on normal dogs and on one in which the habenular ganglion had been destroyed show still further facts: The ganglion interpedunculare in dogs consists of five different ganglia, in front two pear-shaped bodies lying side by side, covered by a flat plate which lies beside the tegmentum; posteriorly this group is inclosed by a much larger, horseshoe-shaped ganglion, whose posterior portion constitutes the main body of the ganglion. The slender anterior limbs of this ganglion receive the fibers of the Fasciculus retroflexus, which lose their medullary sheaths immediately after their entrance. In the lizard the Golgi method shows that after decussation they break up into innumerable very fine terminal fibrillæ. The third ganglion mentioned (*Deckganglion*) is filled with a net-work of fine fibers. From this ganglion bundles pass ventrally between the two frontal ganglia. An afferent bundle from the tegmentum of the midbrain ends in the two pear-shaped ganglia. This bundle is of large fibers, which remain intact after destruction of the cerebrum and the thalamus.

Fig. 199 is a composite from several periods of development. In it are shown nearly all of the structures to be found in a section just posterior to the anterior quadrigeminal bodies.

Fig. 199.—Section just behind the anterior quadrigeminal bodies. A composite from sections representing different stages of development of medullary sheaths. Hæmatoxylin-copper-acetate method. (For Brach. C. quad. *ant.* read *post.*) *Tiefes Mark,* Deep medullary stratum. *Centr. Höhlengrau,* Central gray matter. *Aus Thalamus,* From the thalamus.

One may use this figure to review this chapter, finding the following structures:—

1. Midbrain-roof: (*a*) Corpus quadrigeminum anterius, from which the optic nerve arises dorsally and the deep medullary stratum ventrally; (*b*) the decussation of the latter above the aqueduct; (*c*) the central gray matter which surrounds the aqueduct; (*d*) at the outer margin of the central gray matter lies a small nucleus (not before mentioned), whose vesicular cells may be found at the same relative position in all sections of the midbrain. From it arises a slender bundle of fibers, which passes down, receiving accessions continuously to the pons, where it joins the emerging fibers of the trigeminus. It is the midbrain-roof of the nervus trigeminus. (*Rad. desc. V*, Fig. 199.)

In the roof of the midbrain one may distinguish a rather faint stratification of alternating gray and white matter. The minute structure of the layers is not sufficiently known in the human brain. In mammals one may generally differentiate in the anterior quadrigeminal body the following layers from without inward: 1. *Superficial marrow and gray matter*,—the entering fibers of the optic tract,—atrophies after extirpation of the eye, and is rudimentary in the mole (Ganser). 2. *Middle gray matter*, a direct continuation of the superficial gray matter; best studied in birds, and, according to *Cajal* and *Gehuchten*, it contains numerous cells whose neuraxons usually pass down into the fillet, but whose dendrites break up into twigs among the fine terminal ramifications which the optic nerve sends into the superficial gray matter. 3. *Middle marrow*. It lies within and below the middle gray and contains bundles from the *opticus radiation*, but also other fibers, as it degenerates only in part after removal of the corresponding cortex. 4. *The deep gray matter* and *the deep marrow*, or *deep medullary stratum*. The gray matter is the continuation of the general gray matter of the quadrigeminal bodies. The deep marrow contains the deep fibers of the stratum lemnisci, which spring from the deep and middle gray of the quadrigeminal body.

2. The Tegmentum: (*a*) In the ventral portion of the central gray matter, the *nucleus posterior medialis et lateralis* of the nervus oculo-motorius, in which pass fibers apparently from the deep marrow and some from the posterior longitudinal fascicle. (*b*) Lateral from and bordering on the posterior longitudinal fascicle, the fibers of the posterior commissure. (*c*) External to (*b*) a medullated area which comes *from the thalamus* and which left it as laminæ medullares; it probably contains a bundle from the nucleus of the trigeminus to the thalamus. (*d*) The *lower fillet* from the quadrigeminal bodies, and the *upper fillet* from the thalamus. (*e*) The *nucleus ruber tegmenti*, from which arise numerous fibers for the superior cerebellar peduncles. (*f*) The *"fountain-like" tegmental decussation*. (*g*) The *fasciculus retroflexus*.

3. On the boundary between the crusta and the tegmentum one recognizes the *substantia nigra Sömmeringi*, into which numerous fibers (the *stratum intermedium*) pass from the nucleus lentiformis.

4. The Pes Pedunculi: (*a*) The *pyramidal tract* is shown still non-medullated, as it appeared in a specimen from a child four weeks of age.

(*b*) The fibers which lie on the median side of the pyramis originate in the lobus frontalis, those which lie outside of it, in the lobus parietalis et temporalis. (*c*) A bundle leaves the pyramid at this point and, skirting the border of the pes, joins the fillet farther back, forming the *median layer* of that structure. Spitzka makes it probable, on comparative anatomical grounds, that this bundle contains the cerebral tracts of the cranial nerves. (*d*) Internal to it are visible the root-fibers of the *motor-oculi nerve.* (*e*) Just before their emergence they traverse the *pedunculus corporis mamillaris.*

The course of the fibers in the thalamic and subthalamic region is less thoroughly known than in most other regions of the brain. In this obscure field, Meynert, Forel, Gudden, Flechsig, Ganser, Wernicke, Monakow, Kölliker, the author, and others have worked.

The origin of the optic nerve has been investigated by Meynert, J. Stilling, Tartuferi, Gudden, Bellonci, and by Monakow (to whom we are indebted for most important progress), by Henschen, *et al.* The motor-oculi nucleus is better known since the labors of Gudden, Perlia, Westphal-Siemerling, Bernheimer, Kölliker, and the author.

It is of considerable importance to know what to regard as fairly accurate signs of disease of the quadrigeminal region. Disease-foci in the regio subthalamica encounter such a tangle of various fibers that the resultant symptoms show great diversity. A positive diagnosis could scarcely be possible.

Lesions in the cerebral peduncle intercept the motor fibers to the opposite half of the body and head. There may be added sensory and vasomotor disturbances. Usually, however, not only paralysis of the opposite extremities and of one or several cranial nerves results, but also weakness of the motor-oculi of the same side. When simultaneous paralysis of one oculo-motorius and of the opposite half of the body exists, one may suspect a lesion below the corpora quadrigemina. Such patients move the limbs of one side feebly or not at all, while on the opposite side there are ptosis, dilatation of the pupil, and abduction of the eyeball. A basal tumor may produce the same symptoms (*Cf.* Fig. 237); it is, therefore, diagnostically important, when paralysis of the ocular muscles and that of the extremities appear together, which could only arise (as in the last-mentioned case) through a peculiar combination of circumstances. When anæsthesia is present, it is likewise confined to the opposite side of the body. The sensory fibers probably course in the fillet.

If the disease-focus extends farther dorsally, reaching the corpora quadrigemina themselves, there ensues naturally, besides the unilateral or bilateral oculo-motor paralysis of disease of the anterior quadrigeminal bodies, also visual disturbance; occasionally nothing abnormal can be found ophthalmoscopically. With tumors here, as elsewhere in the brain, there may follow choked disk, optic atrophy, etc. Usually pupillary reaction is lost.

The symptoms of disease of the posterior quadrigeminal bodies are not known. Disturbances of equilibrium and co-ordination have accompanied it.

Disease of the quadrigeminal region may be suspected when paralysis of both motor oculi is present without peripheral (*i.e.*, basal) cause, or when only a portion of one motor oculi is injured (*e.g.*, only the fibers to the internal rectus). Lesions of the peripheral trunk could scarcely produce this, such paralysis being nearly always nuclear in its origin.

CHAPTER XX.

THE PONS AND THE CEREBELLUM.

It was learned in the foregoing chapter that the bundles of fibers from the cerebrum and the thalamencephalon[1] are, in the region of the mesencephalon, arranged in two different layers: the pes pedunculi and the tegmentum. Posterior to the corpora quadrigemina the aquæductus becomes much widened. The pes and the tegmentum pass under it farther downward into the metencephalon. Only one constituent of the tegmentum, the anterior peduncle of the cerebellum, which originates in the red nucleus, passes now from the floor of the mesencephalon dorsally to the roof of the metencephalon. This roof develops into the *cerebellum.* That portion of the central canal which lies under it is the continuation of the aqueduct and is called the fourth ventricle. The floor and lateral portions of the metencephalon contain the continuation of the pes and tegmentum.

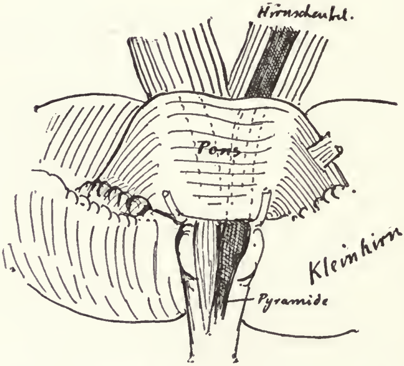

Fig. 200.—The pedunculus cerebri and the pons as seen anteriorly. The tract of pedal fibers, which does not terminate in the pons, is shaded. *Hirnshenkel,* Pedunculus cerebri. *Kleinhirn,* Cerebellum.

Note first what becomes of the fibers of the pes: Not far posterior to

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[1] See also Chapters XVI and XVII.

the corpora quadrigemina a thick white mass of fibers lies ventral to the cerebral peduncles. Descending from the cerebellum, they embrace and cover the pedal region in a thick layer. These fibers taken together are called the *pons*.

Only a part of the fibers cover the crusta externally,—*stratum superficiale pontis*,—most of them invade, from both sides, the fiber-system of the crusta, dividing it into isolated fasciculi: *stratum complexum et profundum pontis*.

It will be remembered that of the fibers which pass ventrally into the crusta from the cerebrum only a portion can be followed as far as the pons. These were the fasciculi from the frontal, parietal, and temporal lobes. The pyramidal tract, from the region of the central convolutions, passes through the pons. Almost the whole inner third and the whole outer third of the crusta terminate in the pons. Beyond the latter only the middle third of the pes—namely, the pyramidal tract—passes out (see Fig. 200).

The fibers of the pons come from above out of the cerebellar hemispheres, embrace and penetrate the fibers of the pes and in the more ventral regions,—stratum superficiale,—terminate, for the most part, in the pontal ganglia of the same side; while, in the more dorsal regions, in those of the opposite side (Minghazzini). The pontal ganglia are gray masses filled with a reticulum of fine fibers, in which one may follow both the fibers from the arms of the pons (brachia pontis) and the tracts which arise from the cerebrum.

Through the investigations of S. R. y Cajal it has become quite certain that the strong cortico-pontal fasciculi ramify around the large cells of the pontal ganglia, and that the arms to the cerebellum are formed from the neuraxons of those cells. But experiments show, also, that a part of the pontal fibers degenerates after extirpation of the cerebellum. We must, therefore, conclude that, as in many other bundles, so in the arms of the pons there are fibers which pass in both directions, namely: fibers from the cells of the cerebellum to the pontal ganglia, and fibers from the ganglia to the cerebellum.

In animals with a relatively small cerebrum the pons is also small. Compare Fig. 141 with Fig. 180. Here in the calf there is seen a transverse system of fibers, *corpus trapezoides*, lying between the pedal and tegmental portions of the pons: a system of fibers which, in man, is covered by pontal fibers. It contains the fasciculi which belong to the acusticus.

In mammals there is added to the pontal fibers that tract from the cerebellum to the tegmentum of the medulla which was demonstrated during the consideration of the brain of the lowest vertebrates. The fibers of this tract do not pass into the pontal ganglia, but diverge from their course, decussating dorsally in the raphé of the pons, and are lost in the gray matter of the tegmentum (see Fig. 201*b*).

The pes pedunculi is split up by the pontal system of fibers and in part diverted to the cerebellum; the tegmentum, however, passes through the pontal region only slightly changed.

In the last cross-section through the region of the corpora quadrigemina (Fig. 199) we had the following essential constituents of the tegmentum:—

1. The gray substance about the aqueduct, together with the nuclei of its nerves.

2. Below it the post. long. fasciculus.

3. Outside the latter are the fibers of the commissura posterior.

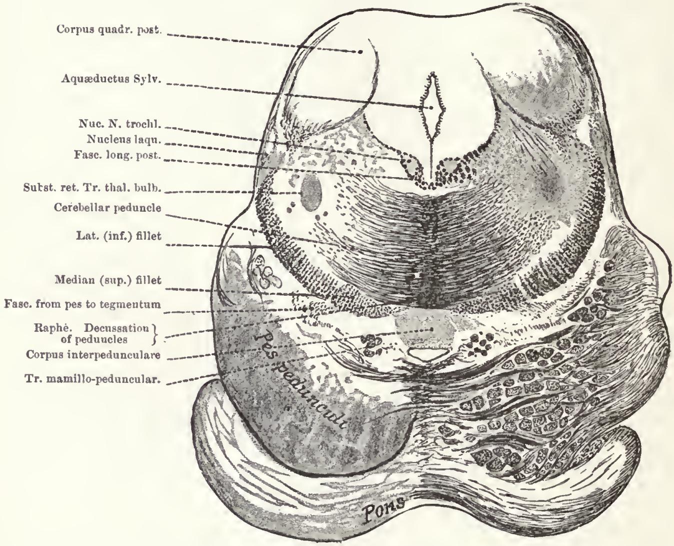

Fig. 201.—*a* and *b*, Two sections through the most anterior portion of the pons. Fig. 201 *a* shows the corp. quadr. post., ventral to which are the nucleus of the trochlearis and the decussation of the anterior cerebellar peduncles. Ventrally one sees on the left diagrammatically outlined the pes pedunculi which, on the right, is shown to be traversed by pontal fibers.

4. The fibers from the striæ medullares thalami.

5. The red nuclei in the center of the tegmentum, and the cerebellar peduncles arising from them.

6. The fillet.

7. The Pedunculus corporis mamillaris.

8. Fibers from the deep medullary stratum near the median line.

As stated above, the aqueduct widens out into the fossa rhomboidalis; and the surrounding gray substance also increases in area. A new nucleus, *nucleus n. trochlearis,* is found below the corp. quad. post. The fibers of the Trochlearis do not, however, like the fibers of the oculo-motorius, pass downward through the tegmentum, but pass backward immediately after their origin in nearly horizontal direction, then rise and decussate finally, in the velum medullare anticum, with those of the opposite side. They thus leave the brain on the dorsal side just posterior to the corp. quad. post. In Figs. 201*a* and 201*b* portions of the course of the trochlearis are visible. In Fig. 196 the whole course of the nerve is depicted.

The posterior longitudinal fasciculi and the fibers of the posterior commissure, retaining the same relation as in the midbrain, pass down into the tegmentum of the medulla. The same is true of the *stratum lemnisci.* To the latter new fibers are added from the lateral margin of the corp. quad. post. They lie outside of the horizontal layer formed by the upper and lower fillets and are usually designated as the *lateral fillet* (lemniscus laterale) to distinguish them from the former or *median fillet* (lemniscus mediale). The lateral fillet from the posterior quadrigeminal body goes almost exclusively to the termini of the auditory nerve. In them lie groups of ganglion-cells,—*nucleus laquearis,*—the neuraxons of which mostly join the ascending and descending fillets.

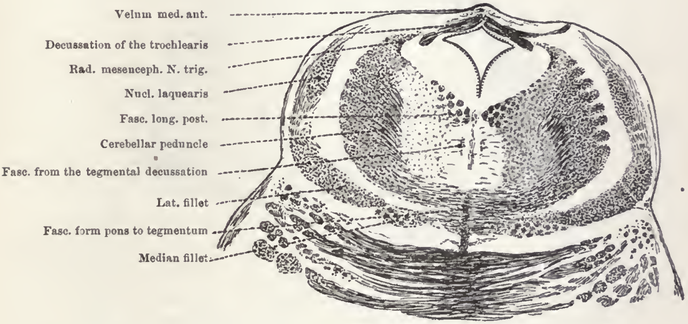

Fig. 201*b* shows clearly the changes in the tegmentum which occur just posterior to the corpora quadrigemina. Note also the decussation of the trochlearis. Compare in the two sections the corresponding fasciculi.

In Fig. 202 one sees above and externally the triangular lateral fillet passing downward to the horizontal median fillet.

The Substantia nigra, and with it the stratum intermedium, do not appear in sections in the region of the pons. Of the continuation of the striæ medullares thalami nothing is known with certainty.

Even before the pontal region begins, the red nucleus always becomes smaller, and the anterior cerebellar peduncle, which arises from it, passes farther and farther to the outside, and finally appears as two strong bundles of fibers which lie between the region of the red nucleus and the fillet. In Fig. 201*a* the fundament of the cerebellar peduncle appears; in sections which, falling slightly posterior to this, cut the velum, the peduncles lie much nearer to the periphery (Fig. 201*b*); and in Fig. 202 they form, through the velum medullare posticum, the outer boundary of the figure. Soon afterward they sink into the cerebellum (Fig. 210, *R*).

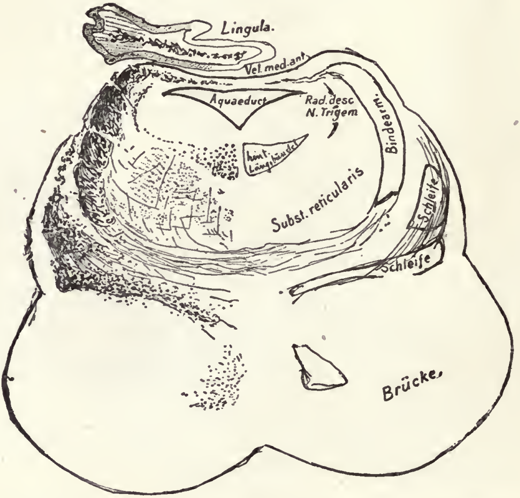

Fig. 202.—Section through the upper pontal region just posterior to the corpora quadrigemina. From a ninth-month fetus. *Bindearm*, Anterior cerebellar peduncle. *Brücke*, Pons. *Schleife*, Fillet. *Hint. Längsbündel*, Post. long. fascic.

The region which is left free through the disappearance of the red nucleus is appropriated by the now increasing fibers of the substantia reticularis, which will be studied later. These are fibers, mostly longitudinal, which may be followed from the lowest levels of the oblongata in gradually decreasing mass up to the midbrain and beyond to the most ventral region of the thalamus. They arise from cells which lie at the posterior end of the tract and from cells located along the course. In a dog lacking a thalamus they were intact. We have to do here, probably, with a system which joins together different levels of the tegmentum.

It is not difficult, if one has once thoroughly understood the significance of the separate fields of a good section through the corpora quadrigemina, to find the same in sections through the upper part of the pons and to interpret them rightly. The changes concern, in general, only the location of the cerebellar peduncle and the conformation of the gray substance under the widening aqueduct where new nerve-nuclei arise; then the accession of the lateral fillet to the stratum lemnisci and the increase of the systems of the substantia reticularis.

But when one makes cross-sections farther back the picture is essentially modified. This occurs through the formation of the *cerebellum* from the roof of the ventricle posterior to the velum medullare anticum, and through the intimate relation into which the cerebellum enters with fibers from the tegmentum and from the pes.

Cerebellar peduncles and pontal arms disappear in the cerebellum. From the medulla and spinal cord come fibers which are interwoven with those of the tegmentum and turn also to the cerebellum.

It is therefore advisable to leave for a time the tracing of the tegmental tract and pass to the study of those parts of the central nervous system into which the tracts disappear. The picture of the tegmental system will doubtless be much more easily comprehensible after the reader has become somewhat familiar with the arrangement of fibers in the cerebellum, and after he has learned to know the structure of the spinal cord and the medulla oblongata.

THE CEREBELLUM.

The cerebellum consists of a middle portion, the *vermis,* and the two *hemispheres.* It is in connection with the thalamus anteriorly through *anterior cerebellar peduncles* from the nucleus ruber, and with the cerebrum ventrally through the brachia pontis, the *middle cerebellar peduncles.* Through the first it receives principally fibers from the thalamus and from the region of the tegmental radiation; through the second bundles from the cortex of the frontal, parietal, and temporal lobes. A third connection binds the cerebellum to the medulla oblongata and the spinal cord through the *posterior cerebellar peduncles—the corpora restiformia.*

In the following figure, which shows the cerebellum from above, one may note:—

1. The position with reference to the corpora quadrigemina, from beneath which the anterior cerebellar peduncles pass to the cerebellum.

2. The general conformation, with the vermis in the middle and the hemispheres are subdivided into separate rather large lobes. Those of the vermis are arranged about the medullary portion in a position simulating the blades of a ship's propeller (see Fig. 206).

The vermis is connected on the right and left with the white substance of the cerebellar hemispheres, which are divided into lobes by deep fissures and into ridges by shallow ones.

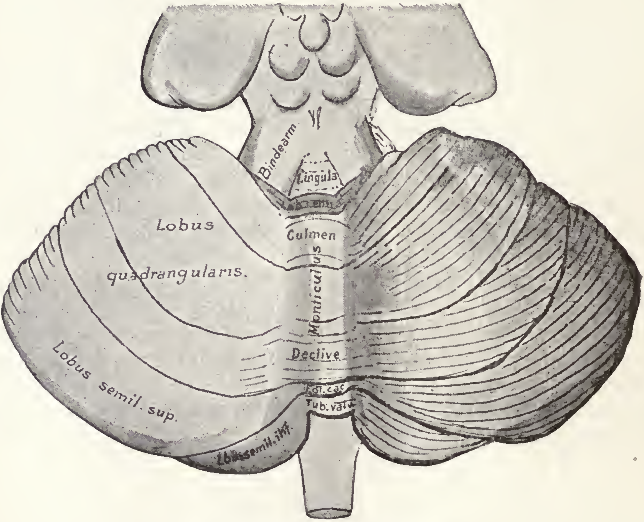

Fig. 203.—The cerebellum. (Dorsal aspect.)

The dorsal surface of the vermis is called the superior vermiform process. It is divided into:—

(*A*) *Lingula,* far forward between the peduncles.

(*B*) *Lobulus centralis,* passing into the alæ lobuli centralis on each side.

(*C*) *Monticulus,* or mount, of which the anterior part is called the *culm* and the posterior part the *declivity.*

(*D*) *Folium vermis,* or fol. cacuminis, at the posterior end of the superior vermiform process.

(*E*) *Tuber vermis,* or tuber valvulæ.

Upon the dorsal aspect of the hemispheres may be differentiated:—

1. *Lobus quadrangularis* or anterior upper lobe on either side of the monticulus.

2. *Lobus semilunaris superior* or posterior upper lobe. The two posterior upper lobes are connected by the folium cacuminis.

The lobes of the under surface of the cerebellum are shown in the next figure (204). It presents a rather complicated picture. In order to prepare specimens for this view the cerebellum must be severed from its connection with the midbrain,—*i.e.*, the anterior cerebellar peduncles must be severed,—then from its connections with the pons and with the medulla and cord. Thus on each side there are the three cross-sections of the cerebellar peduncles. Between the anterior cerebellar peduncles lies a thin membrane, the *velum medullare anticum*, which is a part of the roof of the metencephalon. The cut surface of it is to be seen in the figure.

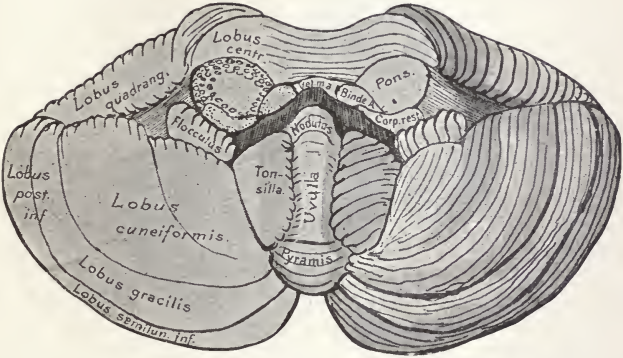

Fig. 204.—The cerebellum. (Ventral aspect.)

The lobes on the ventral surface of the vermis are called:—

1. *Nodulus.*
2. *Uvula.*
3. *Pyramis.*
4. *Tuber valvulæ,* making the boundary between the ventral and dorsal surface of the vermis (see Fig. 203).

The lobes on the ventral surface of the hemispheres are:—

1. *Flocculus,* on each side of the nodulus and moored by the slender *pedunculus flocculi.*
2. *Tonsilla,* on either side of the uvula.

3. *Lobus cuneiformis,* lying external to the tonsilla.

4. *Lobus posterior inferior,* the anterior portion of which is called the *lobus gracilis* and the posterior portion the *lobus semilunaris inferior.*

In Fig. 205 one may see on either side the three medullary processes, or commissures, which pass to the cerebellum. The fibers of these commissures pass into the central white substance of the hemispheres, thence into the medullary portion of the individual lobes, whence they extend into the lobules and ridges. These ridges are covered with gray cortex which everywhere follows the conformation of the medullary substance and thus gains an extension which is greater than the outer form and size of the cerebellum would lead one to expect.

The white substance of the hemispheres is considerable in quantity. The accompanying sagittal section of the cerebellum passes through the center of the vermis (Fig. 206). It shows how the medullary substance is continuous anteriorly with the velum medullare anticum, which extends as a thin membrane toward the corpora quadrigemina. This thin membrane, stretched between the anterior peduncles, forms a transition from the roof of the mesencephalon to the roof of the metencephalon. Upon it lies the most anterior lobule of the superior vermiform process: the *lingula.*

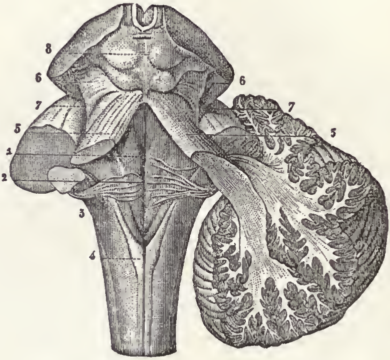

Fig. 205.—The three pairs of cerebellar peduncles. 8, Corpora quadrigemina. 5, Anterior cerebellar peduncle. 7, Middle cerebellar peduncle, or Brachium pontis. 3, Posterior cerebellar peduncle. 1, Fossa rhomboidalis. 2, Striæ acusticæ. 6, Fillet. (After Hirschfeld and Leveillé.)

The peculiar picture presented by the longitudinal section of the vermis has, from time immemorial, borne the name *arbor vitæ.* The central portion of the medullary part is called the *corpus trapezoides.* Into this there pass separately the lingula, lobulus centralis, uvula, and nodulus. A number (five) of the lobules of the monticulus are united with the *vertical branch* (*Vert. A*) before their juncture with the main truck of the arbor vitæ. The posterior portion of the monticulus, together with the folium cacuminis and the tuber valvulæ, unite to form the *horizontal branch* (*Horiz. A*) of the arbor vitæ.

Posteriorly the velum medullare posticum passes from the cerebellum as roof of the fossa rhomboidalis as far as to the termination of the posterior column of the spinal cord. This roof consists only in its lateral portions of rather dense tissue, principally neuroglia; in the median line it is simply a layer of cuboidal epithelium. From the pia numerous vascular loops pass into this membrane and press it somewhat into the ventricle (plexus chorioideus ventriculi quarti, or plex. chor. medialis). But the most laterally located portions of the membrane form, in the region of the oblongata, sack-like projections whose median wall, through vascular loops, likewise becomes a choroid plexus: *plexus chorioideus lateralis* (see Fig. 243). In the median as well as in the place of origin of the lateral plexus perforations are found (*Key* and *Retzius*). The middle one of these openings is called the foramen of Majendie. It is of great importance in the ready equalization and adjustment of variations of pressure in the cerebro-spinal fluid.

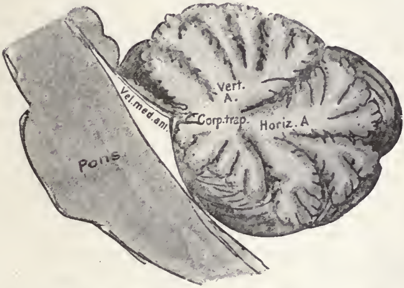

Fig. 206.—Sagittal section through the middle of the Vermis.

Into the cerebellum pass the three pairs of commissural arms. They pass into the central white substance and form connections there with gray nuclei; they also send fasciculi to the cortex of the cerebellum.

In the cortex one may even with low magnification differentiate three different layers: Externally lies the *zona molecularis*; internally the *zona granulosa*; while between them one finds a layer of very large cells—the *cells of Purkinje*.

Recall that in Chapter III it was stated that according to recent views the connection of one cell to another, in the central nervous system, is established through the protoplasmic processes of one cell being surrounded by the terminal ramifications of the neuraxons of the other. Since the term *neuron* includes the cell and its protoplasmic processes with the neuraxon and its terminal ramification, one may say: In the whole nervous system there are innumerable separate *neurons* which are associated together in the manner described above. An example of this is also found in the olfactory lobe. In the minute structure of the cerebellum we may verify the principle just formulated.

The cells of Purkinje (see 1 in Fig. 207) send neuraxons down into the zona granulosa and into the medullary layer below this. On the way they give off collaterals, some of which bend around, pass upward, and break up into branches around the body of the cell. The dendritic processes are extraordinarily profuse, especially in the sagittal plane,—less so in the transverse plane. If one wishes to get such a view as is shown in Fig. 207, the sections must be cut transverse to the fissures of the cerebellum.

The profuse dendritic branches are now interspersed with thick fibers (see 2, Fig. 207), which, coming from cells of unknown location, enter the cerebellar medulla, traverse the zona granulosa, finally breaking up into branches in the zona molecularis. Thus, every cell of Purkinje is placed in connection with a distinct locality. But there is a kind of cell in the molecular layer which is adapted to bring into connection with each other a number of the Purkinje cells. Such cells (see 3, Fig. 207) send out, nearly parallel to the surface of the cortex, a long neuraxon, which gives out fine processes at intervals along its course. A process passes to the body of one of the Purkinje cells, and breaks up into branches around it.

The granular layer consists, for the most part, of small polygonal cells with large nuclei (see 4, Fig. 207). Each one of these cells sends out a number of short dendrites and a neuraxon. The latter passes outward into the molecular layer, where it divides into two fibers which are transverse to the axis of the body. In the figure this division is indicated by a short transverse line because the section is a sagittal one,—*i.e.*, transverse to the convolutions of the cerebellum. The numerous dots scattered over the molecular layer in the lower right hand part of the figure represent the sections of these neuraxons. Besides the cells just described, there are, in the granular layer, cells whose neuraxons break up at once into very fine twigs which ramify among the elements of the granular layer and whose dendrites—not unlike those of the Purkinje cells, though less branched—are distributed to the molecular layer. Furthermore, there end in the granular layer fibers of unknown origin which enter this layer, from the medullary layer (see 6, Fig. 207).

As will be seen from this, the cortex of the cerebellum is an exceedingly complicated apparatus, an apparatus which is adapted for uniting elements of very different character and origin.

In the section presented in Fig. 208 one may note: 1. That the fibers from the central white matter of the cerebellum pass into the cortex in thick medullated fasciculi. 2. That in the region of the granular layer only curved pieces of these fibers are shown. 3. That these form a true plexus of medullated fibers lying in the sagittal plane below and between the Purkinje cells. Running in the same direction are separate, thin, medullated fibers,—not shown in the figure,—which lie just beyond the bodies of the Purkinje cells in the molecular layer.

Fig. 207.—Diagrammatic sagittal section through the cerebellar cortex. Golgi method. (After drawings by S. R. y Cajal and V. Gehuchten.)

The cortex of the cerebellum has been thus described in detail because recent investigations have shown that in progressive paralysis degeneration of fibers and other changes may take place here. The knowledge of the anatomical relations may thus become of great importance in investigations in the realm of pathology.

All parts of the cortex are connected with each other through plaited fasciculi which conform to the contour of the cortex.

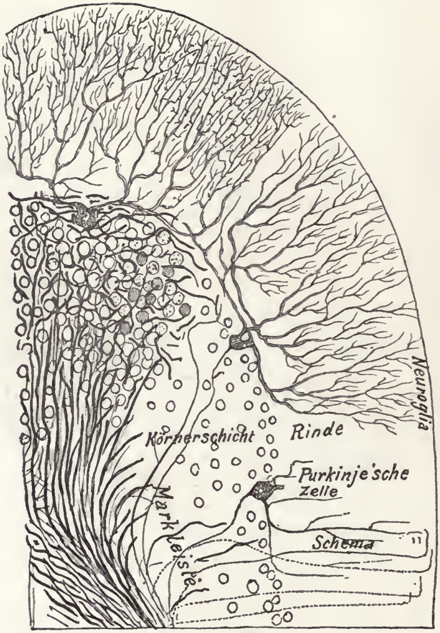

Fig. 208.—Section through the cortical layer of the cerebellum. Hæmatoxylin staining. *Körnerschicht,* Zona granulosa. *Rinde,* Cortex. *Markleiste,* Medullary fascicle.

The cerebellum presents collections of gray matter besides that which is in the cortex. On either side of the vermis lies a large, much-folded nucleus—*corpus dentatum.* On the median side of this other gray masses are met: first the *Embolus*; then the *Nucleus globosus,* an elongated structure with a tuberosity at the posterior end; and, finally, nearest the median line is the *nucleus tegmenti* (nuc. fastigii). These nuclei are best brought into view in a nearly-horizonal section through the cerebellum, as is shown in Fig. 209, taken from Stilling's Atlas.

In such a section one may note in the middle the white substance of the vermis and the nucleus tegmenti; anterior to this a decussation, the anterior commissure of the vermis. To the right and left lies the white matter of the hemispheres, in which may be seen the nuc. globosus, the embolus, and the folded medullary lamina of the nuc. dentatus. The deep clefts in the surface correspond to the fissures between the lobes. Between the peduncles (R R) upon the velum medullare anticum lies the lingula (A), cut also in the horizontal plane.

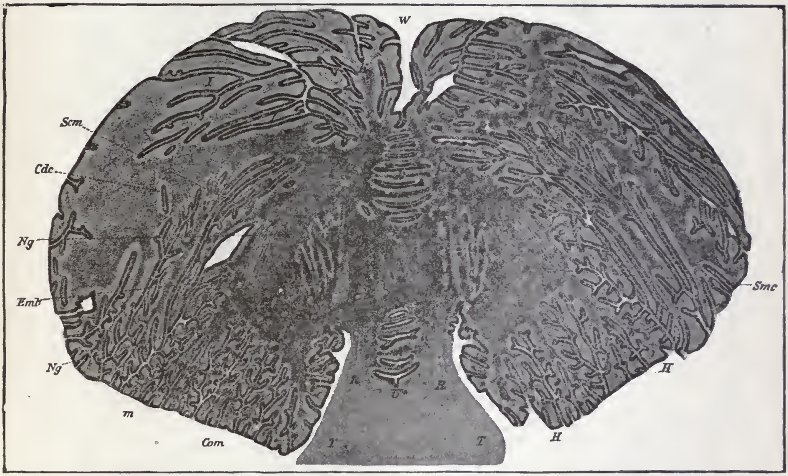

Fig. 209.—Horizontal section through the cerebellum. The section passes through the region under the corp. quad. (T) then through the ant. cerebellar peduncles (R), and between these through the lingula (A). Above this lies the nuc. tegmenti (m), to the left of the nuc. globosus (*Ng.*), the embolus (*Emb.*), and still farther to the side within the hemisphere the corpus dentatum cerebelli (*Cdc*). *Com.*, Anterior decussation-commissure. *Sem*, Fibræ semicirculares. (After B. Stilling.)

All of the nuclei here seen in the white substance are connected with each other through bands of gray matter. Their relation to the fiber-system of the white substance is almost wholly unknown.

If one make a frontal section just posterior to the point where the anterior peduncles enter the cerebellum, one will find dorsally the cerebellum, ventrally the pons and the fibers which pass from it on both sides into the hemispheres. Between the cerebellum and the tegmentum, bounded on either side by the divided peduncles, lies the fourth ventricle, which is the widened continuation of the aqueduct of Sylvius. The medullary substance of the vermis does not lie in the plane of the section. The tegmentum and the pes, the latter traversed by the pontal fibers, lie in the same relative positions as when seen in sections through the region of the corpora quadrigemina.

We have found that fibers pass through the three pairs of peduncles into the cerebellum. Their course within the cerebellum is still very imperfectly known, notwithstanding the fact that Benedict Stilling has devoted long years of work to the study.

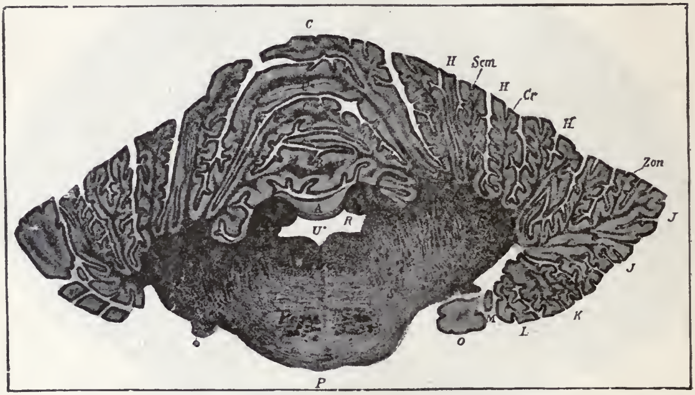

Fig. 210.—Frontal cerebellar section just anterior to the culmen. *U*, Ventriculus quartus. *R*, Anterior peduncle. *P*, Pons. *Zon*, Decussation-zone. *Cr.*, Fibers from corp. rest. passing to *Scm*, the fibræ semicirculares. (After B. Stilling.)

However, the work of the last few years, especially that directed to the tracing of degenerations which follow a total or partial extirpation of the cerebellum, has furnished a large number of important facts regarding the topography. So it is at last possible to elucidate the origin of the separate arms.

The diagram given in Fig. 211 shows upon the frontal sections, through those portions of the central nervous system which are in immediate association with the cerebellum, the most important facts at present known regarding the connections of the cerebellum.

According to B. Stilling's opinion, all of the peduncles receive fibers from nearly all parts of the cerebellum, each peduncle, however, receiving especially numerous fibers from a particular portion.

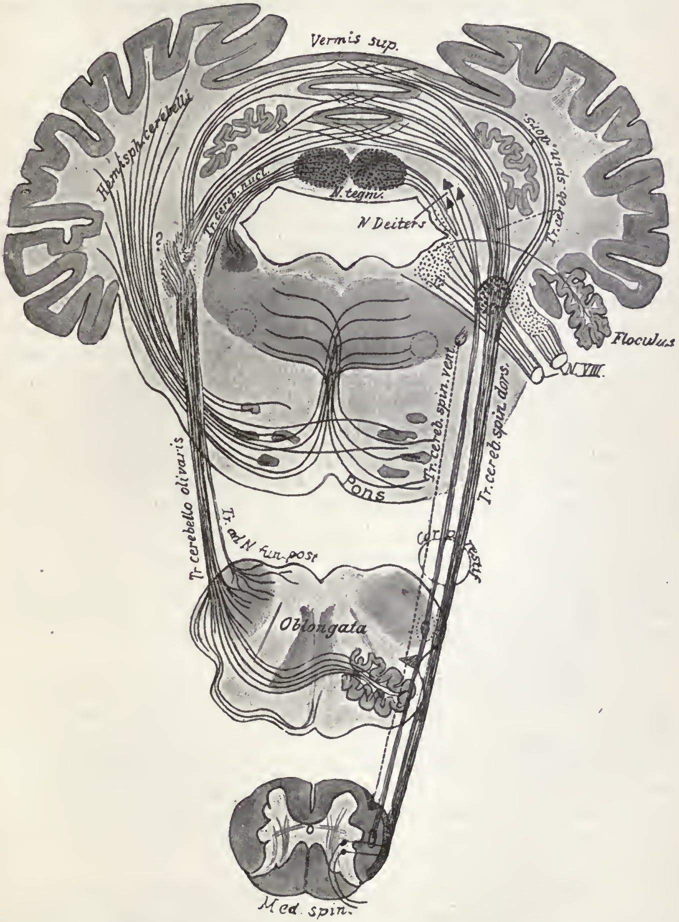

Fig. 211.—Schema showing the origin and course of the fibers of the peduncles of the cerebellum.

Comparative anatomy and experiments in degeneration uniformly show that in the cerebellar connections one must sharply differentiate between the cortex of the hemispheres and the cortex of the vermis; also between the cerebellar cortex and the ganglia. On comparative anatomical grounds the author reckons the corpus dentatum with the vermis. Not a small proportion of what is said in the literature of degeneration on atrophy after injury of the hemispheres refers to injuries of the lateral portion of the vermis.

1. In the first place it may be determined that the *cerebral connection*—first developed in mammals—is furnished by the *brachia pontis and is exclusively with the hemispheres of the cerebellum.* Whence arises the ascending fascicle which traverses the pons ending in the tegmentum? The arms of the pons contain fibers from cells of the intrapontal ganglia: the same cells with which the numerous collaterals of the cerebro-pontal tract connect. S. R. y Cajal has demonstrated this. Even degenerations of long standing involving the fibers of the pes do not cause complete degeneration of the pons. The fact that after removal of a cerebellar hemisphere a large part of the pons remains intact indicates that the fibers in question arise from the pontal ganglia and not from the cerebellum. But, nevertheless, the disappearance of a considerable number of fibers after the operation (Marchi, Minghazzini, Ferrier, and Turner) makes it presumable that at least some of the fibers of the pons arise from cells of the cortex of the cerebellum.

2. It may be demonstrated by several methods that *the anterior cerebellar peduncles arise from the nucleus dentatus*; they may possibly also receive fibers from the neighboring cortex. Much the greater part of the fibers end after decussation in the red nucleus of the tegmentum beneath the anterior quadrigeminal bodies. A smaller part of the fibers end in the nucleus ruber of the same side and send a few fibers farther forward to the ventral region of the thalamus. (This last point is, however, not yet fully established.) Since a tract from the caudal portion of the parietal lobe ends at the nucleus ruber, it is evident that there exists here an indirect cerebro-cerebellar connection.

3. The posterior cerebellar peduncles are very much more complexly constructed. In order to make their formation quite clear we must divide them into (I) *a median portion* having connections with the sensory cranial nerves, especially the acusticus, and into (II) the *corpus restiforme* proper, conducting fibers from the opposite olivary body and from the spinal cord.

The *median portion* and the *tracts* to the *spinal cord* are inherited from remote antiquity; but only in the mammals do the bundles to the olivary bodies become well marked.

The corpus restiforme ends almost exclusively in the middle portion (vermis) of the cerebellum, where its separate fascicles pass to different regions. The region of the nucleus tegmenti, and this nucleus itself, is the terminus of the nucleo-cerebellar apparatus.

In the cortex of the vermis, especially in the dorsal portion, fibers from the spinal cord end.

The terminus of the olivary tract remains yet to be determined.

The constituents of the *post. cerebellar peduncle,* or the corpus restiforme, will now be more definitely considered.

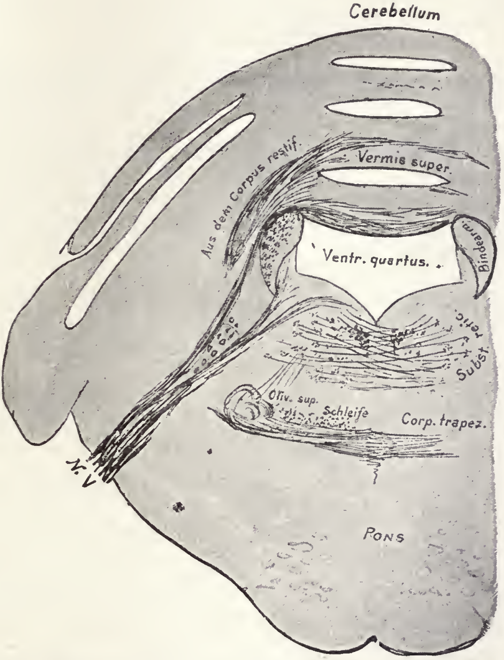

Fig. 212.—Frontal section through the cerebellum and pons of a fetus of twenty-six weeks. All medullated fibers are stained with hæmatoxylin. *N. V.,* Tr. nucleo-cerebellaris. *Aus dem Corpus restif.,* From the corp. restif. *Bindearm,* Ant. cerebel. peduncle.

I. THE MEDIAN PORTION.

The fasciculi from the cerebellum to the sensory nerves and their nuclei, with which we became acquainted in fishes, exist also in mammals. The author formerly believed that we had to do here with direct bundles to the nerve-trunks. But recently doubt has arisen regarding it, since the tract has not with perfect certainty been traced beyond the nucleus. At any rate, it is wiser at present to designate the system as *tr. cerebellaris acustici*, etc., and not as the direct sensory cerebellar tract. In Fig. 212, from a seven-month human fetus, the reader will recognize a part of the tract which passes into the N. trigeminus.

II. THE CORPUS RESTIFORME PROPER.

(a) **The Tr. cerebello-spinales.** These tracts are much better known than are the sensory fasciculi of the median portion. There are now three of the tracts known:—

1. One of these is, on good grounds, looked upon as the secondary continuation of posterior root-fibers: *the Tr. cerebello-spinalis dorsalis*, or the lateral cerebellar tract from the vesicular column of Clarke. This fascicle constitutes the major portion of the spinal connection and, curving mesially, inclosing the corpus dentatum, passes to the cortex of *the superior vermiform process.*

2. The *Tr. cerebello-spinalis ventralis,* or the bundle of Gowers, whose triangular cross-section may be seen in all the sections shown in Fig. 211, though its entrance into the cerebellum is not shown in the figure. It passes into the pontal tegmentum far forward, and, in the region of exit of the Trochlearis, turns dorsally, embracing, within the Velum anticum, the anterior peduncle which leaves the cerebellum at this point, and then turns backward into the cerebellum (Auerbach, Mott).

3. Only recently has it been demonstrated by Monakow, and also by Ferrier and Turner, that still a third spinal connection exists. There are thick fibers from a large nucleus of multipolar cells, which lies just where the posterior peduncle enters the cerebellum. The nucleus is called, from its discoverer, *Deiter's nucleus.* If it is destroyed, the descending fibers which arise from it degenerate as far down as the region of the lateral tracts (shown in Fig. 211).

(b) **The Tr. cerebello-olivares** represent another constituent of the corpus restiforme. Their fibers become, in later stages of development, medullated like the other fibers of the posterior peduncle. They degenerate completely when the hemispheres are removed. The whole bundle passes from the cerebellum to the oblongata, enters this, and passes transversely across it, dividing into numerous diverging fascicles, finally finding a terminus in the opposite *oliva inferior* (see Fig. 211).

The neuroglia of the cerebellum next to the ventricle—as usual, in the boundary of the central cavities—forms a thick net-work. In the white substance it is developed at least as strongly as in the medullary substance generally; but in the zona granulosa it is completely lacking in healthy persons. In paralytics, however, Weigert, on whose authority these statements are made, found a very marked exuberance of the glia. From the region of the cells of Purkinje to the innermost layer of the zona molecularis lie small slender plexuses, while within the molecular layer itself there are found relatively sparingly thick fibers, which extend perpendicularly to the surface: the Bergmann-Deiter fibers. The surface of the normal cerebellum lacks the superficial glia-net usually present on the surface of the central nervous system. But in all embryos—even in non-mammals—one finds, as outermost layer of the cerebellum, one or more strata of spheroidal cells which are later lost.

The outer surface of the cerebellum was described by Malacarne, Reil, and Burdach as we know it to-day. The investigation of its inner structure was accomplished by F. Arnold, Reil, Kölliker, Meynert, and especially by B. Stilling. More recent investigations on the constitution of the peduncles were made by Bechterew, Marchi, Minghazzini, Ferrier and Turner, and by Pellizzi. On the cortex of the cerebellum there is a voluminous literature to which especially Purkinje, Gerlach, Kölliker, F. E. Schultze, Obersteiner, and Bevor furnished contributions. But only through the studies of Golgi, Ramón y Cajal, Kölliker, and Gehuchten does one obtain an exact understanding of the structure. Here, as in so many other places, the improvement of the technique made possible an advance where the most diligent simple observations would have revealed little.

Diseases of the cerebellar peduncles alone are very seldom observed. Thus, little is known of the symptoms which are to be expected in the case of such a disease. Gradual destruction of one brachium pontis may apparently give rise to no symptoms. In diseases which produce an irritation—for example, hemorrhages and tumors—forced movements frequently occur, such as rolling from side to side. A forced position of the trunk or of the head alone, with or without nystagmus, has been observed in irritating diseases of one of the arms of the pons.

For the determination of the symptoms conditioned upon diseases of the cerebellum we are guided primarily by the quite frequent tumors, and secondarily by the not infrequent abscesses which accompany purulent inflammations of the ear. Hemorrhage, softening, arteriosclerosis, and other pathological processes occur in the cerebellum; but these diseases are either very infrequent and usually not confined to the cerebellum, or they lead—as is the case of hemorrhages—so quickly to death that no time is offered for the development of a special combination of cerebellar symptoms. In the case of tumors, and, in a somewhat less degree, in abscesses of the brain, there exists simply the difficulty that we are not justified in attributing all of the symptoms which appear directly to the lesion of that part of the brain involved in the tumor. Besides the so-called local phenomena, the tumor nearly always induces two other groups of symptoms:

first those which are due to the effect of the tumor upon the neighboring tissue; and, second, those which are due to general brain-pressure. We must sharply differentiate these three groups: (1) local symptoms, (2) "neighborhood-symptoms," and (3) general symptoms. Because of the narrowness of the room beneath the tentorium cerebelli, the last two groups are often especially emphasized.

As symptoms induced through affection of the cerebellum itself—*i.e.*, local symptoms—we should enumerate the following: 1. The so-called *cerebellar ataxia*, which is almost without doubt a direct focal symptom of the vermis only, and especially of its posterior half. A tumor could cause the same symptoms if it be located in a hemisphere. It is possible for the ataxia to be, in part, conditioned upon a weakness of the trunk-musculature. 2. Attacks of dizziness,—of real *vertigo*,—which are of especial importance when appearing as an early symptom. 3. Possibly a kind of *tremor* which is midway between ataxia and "intentional tremor," and a similar disturbance of speech; these symptoms may, however, be simply due to the effect of a tumor upon neighboring tissue ("neighborhood-symptoms"). The cerebellum does not appear to have direct relations to the motor functions in a higher sense. Further, its disease does not cause specific psychic disturbances.

In diseases of the cerebellum "neighborhood-symptoms" occur especially through affection of the pons, the medulla, and the corpora quadrigemina.

In the medulla oblongata and in the pons the extramedullary roots or the medullary substance itself may be affected; later both are affected together. Especially important symptoms here are alternating hemiplegia and possibly hemianesthesia, affecting the facialis and abducens on the side of the tumor, the extremities on the opposite side, or disturbance of vision on the side of the tumor. The extremities, however, may be affected upon the side of the tumor or upon the opposite side, depending upon whether the tumor exerts its influence above the decussation of the pyramid or below it. The sudden death which is common in cerebellar diseases is probably a "neighborhood-symptom" on the part of the medulla oblongata. The first symptom manifested by the extramedullary nerves is frequently neuralgia of the trigeminus.

Neighborhood-symptoms on the part of the corpora quadrigemina are bilateral ophthalmoplegias which affect mostly the outer branches of the oculo-motorius and the trochlearis, leaving the internal recti and the abducens free. These symptoms are very common with cerebellar tumors.

Prominent symptoms on the part of the cerebellar peduncles with tumors of the cerebellum proper are rare; they are described above.

The general symptoms are the same as those with other brain-tumors

They are characterized only through especial intensity. Among the symptoms are: Choked disk, which frequently leads to blindness; headache, especially in the back part of the head and frequently accompanied by stiff neck; obstinate emesis; convulsions, usually tonic and with opisthotonos.

When the symptoms are pronounced the diagnosis is usually easy. The "neighborhood-symptoms" are, through their significance, of great importance. In order to establish the diagnosis of cerebellar disease the local symptoms must naturally precede the "neighborhood-symptoms." The last alone not infrequently permit a diagnosis of the side of the cerebellum diseased.

Diseases of the corpora quadrigemina may give rise to the same phenomena as those caused by diseases of the cerebellum. Here ataxia occurs only after ophthalmoplegia—the reverse of the case with affections of the cerebellum. An ataxia due to affections of the cerebrum may be quite like the cerebellar ataxia; here the other symptoms indicate disease of a cerebral hemisphere (Bruns).

CHAPTER XXI.

THE PERIPHERAL-NERVE ROOTS, THE SPINAL GANGLIA, AND THE SPINAL CORD.

THE peripheral nerves, as is well known, contain both motor and sensory fibers. Near to the spinal cord these separate from each other. The motor division enters the cord directly as the anterior root. The sensory fibers enter the spinal ganglion.

In the spinal ganglia there are large cells, which sometimes give off two processes, but usually only one. If there is but one, it divides soon after leaving the cell-body into two; so that, in the end, it amounts to practically two cell-processes.

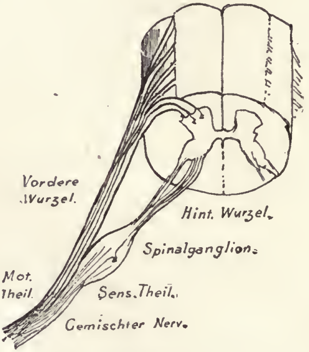

Fig. 213.—Scheme of the relationships between the spinal cord and the nerve-roots. *Vordere Wurzel,* Anterior root. *Hint. Wurzel,* Posterior root. *Mot. Theil,* Motor portion. *Sens. Theil,* Sensory portion. *Gemischter Nerv.,* Mixed nerve.

It will be remembered that, according to the observations of His, the sensory nerves grow out from these cells as peripheral processes, but that these cells also send one process into the spinal cord, a bundle of such processes constituting the posterior root.

Since, according to actual count, the posterior roots contain approximately the same number of fibers in the adult as the nerves just beyond the ganglia, it would seem that there were simply an interposition of a cell in the course of every such fiber.

It is an important question, however, whether, in reality, all sensory nerves arise from cells in the spinal ganglia. The experiment of Waller, since oftentimes successfully repeated, answers it completely.

Every nerve-fibre, separated from its source, degenerates. If one cut the fibers of a sensory nerve across, just peripheral to the spinal ganglion, all its fibers degenerate, while the ganglion itself and the fibers leaving it to form the corresponding root of the cord remain fairly normal. This shows that all the fibers have been divided from their cells. If the section be made of the root close to the ganglion, but few of the fibers in the sensory nerve die; the majority retain their vitality. These fibers must, therefore, spring from the cells of the ganglion, for they remain in connection with them. The few fibers of the nerve which have degenerated must arise in the cord itself, because separated from it alone, and not from the ganglion.

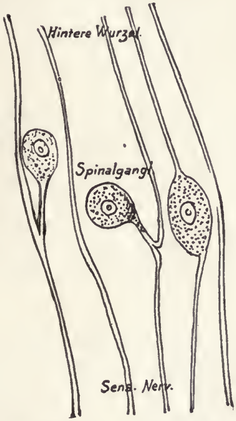

Fig. 214.—Scheme of the fibers in a spinal ganglion. *Hintere Wurzel*, Posterior root. *Sens. Nerv.*, Sensory nerve.

In fact, examination of the spinal root furnishes the proof of this. The root, being separated from its ganglion, is found to contain only a few living fibers, the majority being degenerated. The intact fibers must arise from cells in the cord, as they remain in connection with such cells only; the degenerated fibers must come from the ganglion, because they are divided only from it. (*Cf.* the text on pages 6 and 7.)

These experiments show that from the ganglion-cell processes pass in two directions, and that there are other processes from the cord which only pass through the ganglion. Probably there are still other fibers from peripheral (sympathetic) cells which end in the cord (Fig. 33). Accordingly one may consider the relations of the sensory roots to the spinal ganglia much as represented in Fig. 214.

Between the spinal ganglion and the spinal cord both the sensory and the motor roots break up into smaller fasciculi,—"root-fibers,"—which enter the cord at considerably various levels, the sensory fibers posteriorly, the motor ones anteriorly, each in a somewhat laterally placed longitudinal sulcus. The number of these fasciculi is not the same for different roots, and varies also in different individuals.

Recent investigations have shown that for the extremities not every spinal root is in relation to a particular peripheral nerve. It is established that in every nerve going to one of the extremities, are contained a large number of fibers coming from different spinal roots, and it is very probable that two muscles, functioning usually co-ordinately, are innervated from the same root, even when supplied by different nerves. The apportionment of fibers, which renders this possible, takes place partly in the plexuses (cervical, lumbar, etc.), and in part in the trunks of the larger nerves, which may themselves be regarded as a kind of plexus.

Only a few cases of disease of the spinal ganglia are reported. Besides extreme pain, an intercostal herpes zoster in the course of the respective nerve was repeatedly observed. Physiological observations (Gaule) indicate that vasomotor and trophic influences on the skin and muscles are the province of some of the cells in the spinal ganglia. Perhaps, in this connection, the sympathetic fibers, which surround the cells abundantly, come into consideration. It must not be overlooked, however, that we know of marked changes occurring in the spinal ganglia in tabes (Vulpian, Wollenberg, and others) which have been unaccompanied by herpes or anything related to it.

The roots enter the cord in longitudinal rows.

Where large roots, corresponding to the extremities, enter the cord, the latter is greater in size than elsewhere. The *intumescentia cervicalis* receives and gives off the arm-nerves; the *intumescentia lumbalis*, the leg-nerves. The smallest portion of the cord emits the intercostal nerves. The lowest, conical portion of the cord is called *conus terminalis*; from it arises, in addition to the nerves, a long, thin process, the *filum terminale*. The superior boundary is the beginning decussation of the pyramidal fibers (see below).

In examinations of patients the important question often arises, from what level of the cord emerge the particular spinal roots supplying paralyzed muscles or anæsthetic areas of the skin. It has been sought to solve this question by experiments on animals, than which anatomy itself could not serve the purpose better. With man it has been repeatedly sought to derive more knowledge on this point from cases of localized lesions of the cord (contusions, hemorrhages, etc.). Following is a list, slightly modified, taken from a compilation of all accessible reports of cases up to 1890, made by Starr. Probably experience will dictate changes here and there.

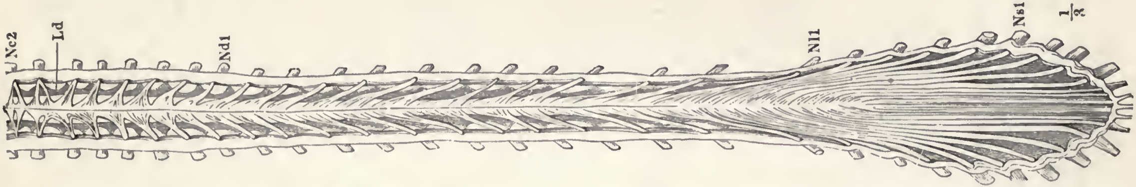

Fig. 215*a*.—Anterior view of the cord with its entering nerve-roots. The bundles penetrate the dura mater and unfold, fan-like, along the cord. Between the dura and the cord there is a dentate suspensory band, the ligamentum dentatum (*Ld*). *Nc*2, Nervus cervicalis II. *Nd*1, Nervus dorsalis I. *N l*1, Nervus lumbalis I. *Ns*1, Nervus sacralis I. (After Henle.)

Fig. 215*b*.—A spinal cord from behind, the nerve-roots having been separated. Observe the two enlargements, intumescentia cervicalis (*Ic*) and lumbalis (*Il*). The posterior columns (*Fp*) are separated by the posterior longitudinal fissure (*Fmp*). In the cervical cord a fissure (*Sip*), sulcus intermed. post., separates these columns into the funiculus gracilis (*Fg*) and funiculus cuneatus (*Fc*). *Fl*, Funiculus lateralis. *Ct*, Conus terminalis. *Ft*, Filum terminale.

LOCALIZATION OF FUNCTION IN THE DIFFERENT SEGMENTS OF THE SPINAL CORD.

SEGMENTS.	MUSCLES.	REFLEXES.	SKIN-SENSATION.
2d and 3d Cervical.	Sterno-mastoid. Trapezius. Scaleni and neck-muscles. Diaphragm.	Inspiration by sudden pressure under the edge of the ribs.	Neck and back of head.
4th Cervical.	Diaphragm. Supra- and infra- spinatus. Deltoid. Biceps and coraco-brachialis. Supinator longus. Rhomboid.	Dilatation of the pupils on irritation of the neck (4 to 7 cervical).	Neck. Upper part of shoulder. Outer side of arm.
5th Cervical.	Deltoid. Biceps and coraco-brachialis. Supinator longus and brevis. Pectoralis major (clavicular portion). Serratus magnus. Rhomboid. Brachialis anticus. Teres minor.	Scapular reflex (5 cervical to 1 dorsal). Tendon-reflexes of the corresponding muscles.	Posterior surface of shoulder and arm. Outer side of arm and forearm.
6th Cervical.	Biceps. Brachialis anticus. Pectoralis major (clavicular portion). Serratus magnus. Triceps. Extensors of hand and fingers. Pronators.	Reflexes of the extensor tendons of the arm and forearm. Wrist tendon-reflexes (6 to 8 cervical).	Outer side of forearm. Dorsum of hand. Distribution of the radial nerve.
7th Cervical.	Long head of triceps. Extensors of hand and fingers. Flexors of the hand. Pronators of the hand. Pectoralis major (costal portion). Subscapular. Latissimus dorsi. Teres major.	Blow on lower end of radius producing closure of the fingers. Palmar reflex (7 cervical to 1 dorsal).	Radial territory of the hand. Territory of the median.
8th Cervical.	Flexors of the hand and fingers. Small hand-muscles.	Pupillary reflex.	Ulnar territory.
1st Dorsal.	Extensor pollicis. Small hand-muscles. Thenar and hypothenar eminences.		

SEGMENTS.	MUSCLES.	REFLEXES.	SKIN-SENSATION.
2d to 12th Dorsal.	Muscles of the back and abdomen. Erector spinæ.	Epigastric (4 to 7 dorsal) Abdominal (7 to 11 dorsal).	Skin of the breast, back, abdomen, and upper gluteal region.
1st Lumbar.	Ilio-psoas. Sartorius. Abdominal.	Cremaster (1 to 3 lumbar).	Skin of external genitalia. Anterior part of scrotum.
2d Lumbar.	Ilio-psoas. Sartorius. Flexors of the knee (Remak?). Quadriceps femoris.	Patellar (2 to 4 lumbar).	Outer side of hip.
3d Lumbar.	Quadriceps femoris. Internal rotation of the femur. Adductors of thigh.		Anterior and internal sides of hip.
4th Lumbar.	Abductors of thigh. Adductors of thigh. Tibialis anticus. Flexors of the knee (Ferrier?).	Gluteal reflex (4 to 5 lumbar).	Inner side of hip and leg to the ankle. Inner side of foot.
5th Lumbar.	External rotators of the femur. Flexors of the knee (Ferrier?). Flexors of the foot. Extensors of the toes. Peronei.		Posterior side of hip, thigh, and outer side of foot.
1st and 2d Sacral.	Flexors of the foot and toes. Peronei. Small foot-muscles.	Plantar reflex.	Posterior side of thigh, outer side of leg and foot.
3d to 5th Sacral	Muscles of perineum.	Tendo-Achillis reflex, vesical and rectal.	Skin of sacrum, anus, perineum, and genitalia.

The course of the fibers in the spinal cord is but partially known. To understand it one must familiarize one's self with the cross-section of the cord. In such a section one finds first a peripheral white substance and a central H-shaped gray substance.

The two halves of the spinal cord are divided by the anterior and posterior longitudinal fissures, and connected by a commissure of white substance anteriorly, of gray matter posteriorly. The anterior broad portions of gray matter are called the anterior, or ventral, horns, and the posterior extension of gray matter, the posterior, or dorsal, horns.

The proportions of the white to the gray substance at different levels of the cord are not the same. Especially does the gray matter predominate from the upper lumbar region downward. Fig. 217 gives cross-sections of different levels of the cord. Beside the varying proportions of gray and white matter, one sees also that the lateral portion of the ventral horn in the lower cervical and upper dorsal cord becomes more and more prominent and finally (Fig. 217, D_1 and D_3) becomes distinct as the lateral horn, or *tractus intermedio-lateralis*. In the lower dorsal cord it is lost again. In Fig. 216 it is indicated by *o*.

In the entire cervical and upper dorsal cord, the gray matter between the tractus intermedio-lateralis and the ventral horn is not sharply defined, but presents a net-work of gray bands and fibers, which pushes out into the white substance. It is called *processus reticularis*.

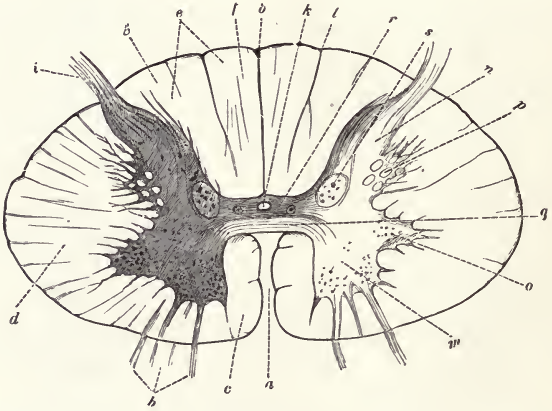

Fig. 216.—Half-schematic transverse section of the spinal cord. *a*, Anterior and *b*, posterior longitudinal fissure. *c*, Anterior column. *d*, Lateral column. *e*, Posterior column. *f*, Funiculus gracilis. *g*, Funiculus cuneatus. *h*, Anterior, and *i*, Posterior roots. *k*, Central canal. *l*, Sulcus intermedialis posterior. *m*, Anterior horn. *n*, Posterior horn. *o*, Tractus intermedio-lateralis. *p*, Processus reticularis. *q*, Anterior white commissure. *r*, Posterior gray commissure. *s*, Clarke's column, or *columna vesicularis*. (After Erb.)

In the *conus terminalis* the gray matter is inclosed in a very thin layer of white fibers (*Co* in Fig. 217).

The root-fibers of the motor nerves pass the spinal ganglia and enter the cord, penetrating its white substance to join the ventral horns. All of the axis-cylinders contained in them join, as shown in Fig. 218, each with one of the large ganglion-cells of the horns. A cell of the anterior horn with many branches is shown in Fig. 4 and in Fig. 6, *D*. Not all these cells are in direct relationship with the root-fibers.

The ventral-horn cells are largely arranged in groups. The exact relationship between these groups and the roots is but partly known. Naturally much knowledge would be gained if in every case where in life there was well-defined peripheral loss there should follow after death a careful examination, specially directed toward the localization of altered ganglion-cells. Hence it will be helpful to become acquainted with the cell-groups in the spinal gray matter, which, being confirmed by morphology, represent, for the present, all that is actually known. We are indebted to Waldeyer for a classification of these cells, represented in Fig. 219. The well-de

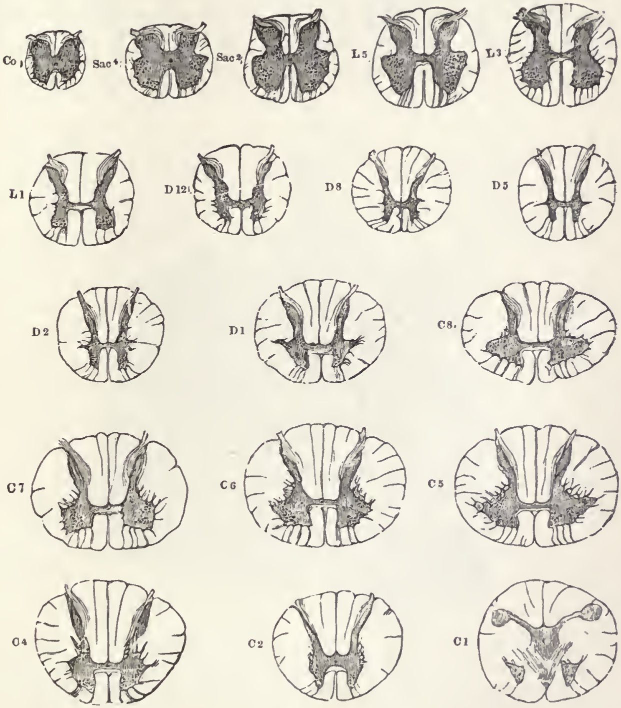

Fig. 217.—Sections of the cord at different levels. The letters and figures indicate the spinal nerves, the exits of which correspond to the respective sections. (Quain.)

fined groups of the cervical portion and those of the lumbar cord, containing especially numerous cells, are less developed in the dorsal part of the cord, corresponding to its smaller volume and perhaps also to the different functions of the nerves arising from it.

None of these groups, excepting, perhaps, the posterior median group, can be followed continuously throughout the cord. There is much to indicate that this group serves to innervate the muscles of the back. As seen in the tables on pages 336 and 337, the brachial plexus arises from the cervical cord. For its various elements a thorough investigation of all the cases in which loss of function was present as a symptom of spinal disease (Kayser, Collins) points out the nuclei. From the lateral group in the cervical cord come the flexor nerves, from the more median group those for the extensors of the arm and the hand.

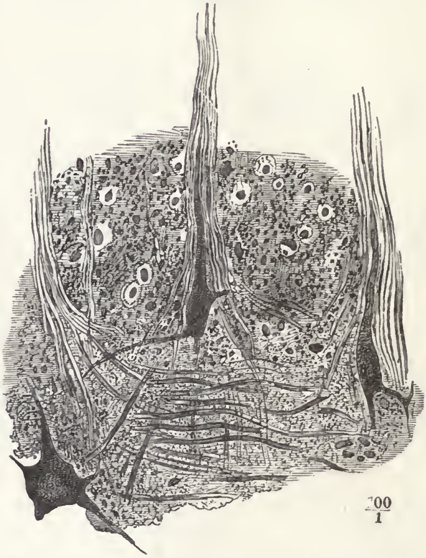

Fig. 218.—From the anterior border of a cross-section of the anterior gray horn. Transition of a cell-process into the anterior root. Carmine preparation $^{100}/_{1}$. (After Henle.)

The roots of the sensory nerves enter, after passing through the spinal ganglia, partly direct in the posterior horn, partly in the posterior white columns. The cells of the spinal ganglion form the sources of the majority of these fibers. It will be remembered that, as embryology teaches, the axis-cylinders from the cells of these ganglia extend peripherally in the sensory nerves, and centrally into the cord.

The central branches form what we call the posterior roots. With them pass other fibers, however, which do not arise from the cells in the spinal ganglion.

A case observed by Leonowa shows how independent of each other are the dorsal roots and the spinal cord in their development. The entire elementary cord was missing in a monster, but the spinal ganglia were present, and from them arose peripheral nerves, besides entire bundles of posterior roots, which, of course, ended free in the vertebral canal.

The ganglion-cells of the dorsal horns are smaller than those of the ventral horns. For the most part they have a spindle-shaped form. Their axis-cylinders divide either soon after quitting the cell-body into a fine arborization like that shown in Fig. 152, *g*, or they enter farther into the substance of the cord. They never become peripheral nerve-fibers.

Two groups are readily distinguished by the naked eye in the posterior horns, from their form and color. The group called *columna vesicularis*, first studied by Stilling, afterward more exactly by Clarke, generally known as Clarke's column, lies about where the ventral and dorsal horns come together (Fig. 216, *s*). Besides the cells, it contains a fine net-work of fibers, and bundles of especially delicate fibers running longitudinally. On cross-section its rounded form is distinct, and can be followed from about the end of the cervical enlargement to the beginning of the lumbar enlargement. Single cells, however, in appearance similar to Clarke's cells, are met with higher up even to the medulla oblongata.

Still more sharply defined than the Stilling-Clarke column appears the *substantia gelatinosa Rolandi*, in the gray matter of the posterior horn. It lies near the point of the horn, and is perforated by numerous afferent fibers from the posterior root. Until our staining-methods were sufficiently developed, the importance of this peculiar, glass-like, translucent substance remained in doubt. Only in the last few years has it been discovered that it contains cells of similar character to those lying in the posterior horns.

What became of their axis-cylinders seemed especially difficult to determine in a region so densely filled with axis-cylinders and collaterals. Recently, however, S. Ramón y Cajal and particularly v. Lenhossek were able to show that the axis-cylinders of the spindle-shaped cells (marginal cells in Fig. 219), passing around the periphery of the Rolandic substance, arrive at the dorsal portion of the lateral column, and that those of the narrower, stellate cells of the Rolandic substance itself enter the neighboring posterior column and the so-called marginal zone of the posterior horn. The latter cells possess not only one, but several processes of the histological character of an axis-cylinder.

The white matter, surrounding the gray, consists principally of longitudinally directed fibers, together with the oblique, ascending fibers of the nerve-roots and certain other fibers, which pass out at more or less of a right angle from the gray matter to the white columns. The nerve-fibers have an axis-cylinder and a medullary sheath. The thickness of this sheath varies greatly. They do not possess a sheath of Schwann.

The axis-cylinder presents a fibrillated appearance, wherever examined. Probably it is made up of numerous fibrils. Recent investigations have shown that the axis-cylinders of the nerve-fibers in the spinal cord, at their extremities, do not end as a whole, but by a kind of splitting. With all the long nerve-fibers in the white matter and also in the gray matter, one finds at certain points that a delicate fibril separates off at right angles to the axis, passes toward the gray matter, and there, as has been observed, it

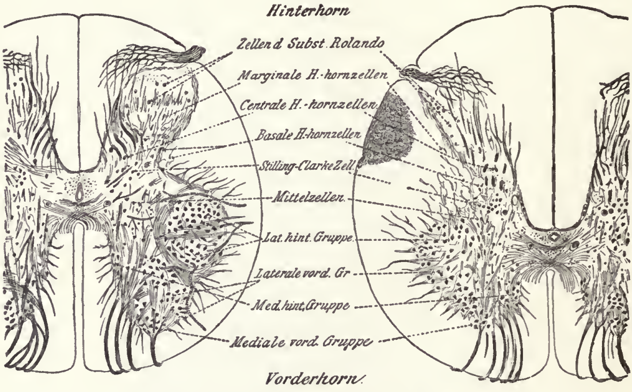

Fig. 219.—(After Waldeyer, slightly modified.)

Sections through

Inferior portion of cervical enlargement. Lumbar enlargement.

The divisions are made according to the structures brought out by staining an adult cord with carmine. Other methods show that, at least in the fetal cord, in certain regions there are a great many more individual cells than are here represented. *Hinterhorn,* Posterior horn. *Zellen d. Sub. Rol.,* Cells of the subst. Rolando. *Marginale H.-hornzellen,* Marginal cells of post. horn. *Centrale H.-hornzellen,* Central cells of post. horn. *Basale H.-hornzellen,* Basal cells of post. horn. *Stilling-Clarke Zell.,* Stilling-Clarke's cells. *Mittelzellen,* Middle cells. *Lat. hint. Gruppe,* Lateral posterior group. *Laterale vord. Gr.,* Lateral anterior group. *Mediale hint. Gruppe,* Median posterior group. *Mediale vord. Gruppe,* Median anterior group. *Vorderhorn,* Anterior horn.

ends in a minute brush. The places from which pass off these "collaterals" from the stem are usually marked by a slight enlargement.

The spinal white matter is interwoven with numerous, radiating septa, made up of neuroglia, and in them run the blood-vessels, coming from the periphery of the cord.

The nerve-fibers in the white matter are all surrounded by a loose net-work of *neuroglia-fibers*. In the gray matter it is found most densely deposited near the central canal, in the *substantia grisea*. After the Weigert stain, it appears to the naked eye as a dark-blue spot.

Fig. 220.—Longitudinal section through the lateral column of a newborn pup. On the left is shown, after an original preparation of Ramón y Cajal's, axis-cylinders sending collaterals into the gray matter, and others, coming from cells there situated, dividing into an ascending and a descending branch. The cellular connections to the right are schematic.

Less dense than this, but thicker than in the white matter, is the neuroglia-mesh of the ventral horns. It is most sparse in the substantia gelatinosa Rolandi.

The entire periphery of the cord is covered with a thin mantle of almost pure neuroglia: the peripheral gelatinous layer (Fig. 219, to the right). Also on the point of the dorsal horns there is found an especially-thick development of glia. Here the entering posterior roots suffer, mostly at the expense of their medullary sheaths, and appear very compact, as if tied together, in a section. (Obersteiner and Redlich.)

Fig. 5 explains the epithelium of the central canal in the fetus. In youth, also, the cells lie in regular rows on the layer of neuroglia. They lose their cilia probably soon after birth, although during life there remains a peculiar layer of small, evenly placed nodules on the central edge of the cells, which, during the fetal period, are found just at the bases of the cilia. With increasing age, the resistance of the epithelial cells lessens. They become separated from each other, neuroglia-fibers appear between them, they even loosen from their bases, and lie in apparent confusion or in small groups between and among the developing neuroglia-tissue. As a result, there is in the place of the original central canal a mass of cells leaving either no lumen at all or perhaps several small lumina in the center of the cord.

This much has been ascertained by the examination of sections of the adult cord. But in a knowledge of the minute structure of the cord, much more has been learned.

As one sees in the cross-section of the cord, it is divided into columns by the spinal nerve-roots and by the longitudinal fissures. Median to the roots lie the anterior and posterior columns; lateral to them, the lateral columns.

The study of embryology, as well as that of the effects of interruption of the fibers, and the examination of certain diseases of the spinal cord have taught that these anterior, posterior, and lateral columns are not homogeneous, equivalent bundles of fibers, as might appear on casual inspection of a cross-section of a healthy, adult cord, but that they are composed rather of several divisions.

It will be remembered that the *tractus cortico-spinalis,* the pyramid, passes from the cortex of the motor region down through the internal capsule and the pes cerebri to the ventral portion of the pons. Where does it pass in the medulla spinalis? It is not difficult to find. When anywhere in its long course it is destroyed by a disease-focus, its fibers gradually disappear, being displaced by connective tissue. This degeneration, called *secondary degeneration,* proceeds downward into the cord. It takes place there in two locations: one in the median portion of the anterior column of the same side as the cerebral lesion, and the other in a large portion of the lateral column of the opposite side. Higher up, at the beginning of the bulb, one sees that this crossed tract passes over to the direct tract, decussating with the sound fibers of the opposite side.

The tract, which is affected by the degeneration, is called in the cord, as in the brain, the *tractus cortico-spinalis,* or the *pyramidal tract.* In the cord it divides into the pyramid of the anterior column (median part of the column) and the pyramid of the lateral column (in its posterior half). There is ground for the assumption that these pyramidal tracts contain the majority of the fibers extending from the brain to the cord, which subtend acquired movement. They degenerate only downward; their fibers disappear regularly, if the tract be destroyed anywhere in the brain or the cord.

In the area of the lateral columns, occupied partly by the *tractus cortico-spinalis,* there are to be found other fibers, which, belonging to the association-bundles of the cord, join its different levels together. The longest fibers of this category are in this territory. So it happens, in case of lesion of the lateral column of the cord, that a larger area degenerates downward than accords with the spread of the pyramids in the medulla oblongata. From this circumstance has arisen the common error of supposing that the pyramids receive fibers from the cord itself.

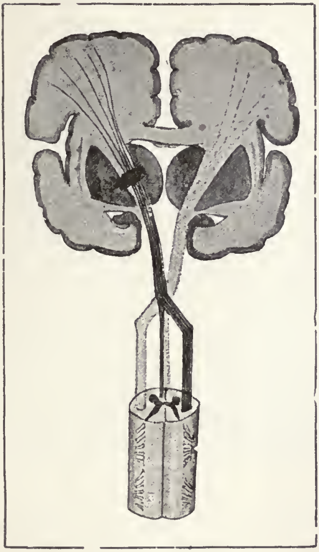

Fig. 221.—Scheme of the descending degeneration in the tractus cortico-spinalis in a case of focal lesion in the left internal capsule.

At birth all the tracts of the cord, in man, have received their medullary sheaths. Only the *tractus cortico-spinales* form exceptions. With the newborn, therefore, in a cross-section of the cord the pyramidal tracts appear gray among the white fibers surrounding.

With the lower animals, corresponding to the more meagre expansion of the cerebral cortex, the pyramidal tracts are relatively smaller than in man. Even here they contain probably only fibers for those muscles, which principally are used by the co-operation of the cortex,—hence, in such actions as are deliberate and acquired. At any rate, after the separation of those of their fibers which supply the upper extremities they are materially reduced in size, remain approximately equal throughout the dorsal cord, and after losing the fibers for the lower extremities they are so reduced in volume that they are practically wanting in the lower lumbar cord. Examinations of these tracts in animals that make greater use of the hands—apes, burrowers—and in those that use the hind-extremities the more—as some marsupials—were desirable. But they would have to be based on embryological or degenerative data, as only in such wise can the pyramidal tracts be differentiated.

Fig. 22.—Secondary descending degeneration after lesion in the left cerebral hemisphere. (After Erb.)

The examination of secondarily degenerated spinal cords enables us to know still more of the combinations of the white columns. In a cord that has been destroyed in the dorsal region by pressure or some other lesion one finds, as the foregoing leads one to expect, below the place of lesion the corresponding pyramid degenerated. But there appears also a degeneration in the other direction. It includes, near the lesion, the entire area of the posterior columns; but, a few segments higher, is confined to the median portion of these columns, that part next the median fissure. In such sections we can easily distinguish, in the posterior columns, an external and an internal tract. That which degenerates upward in these columns (as far as the medulla oblongata) is fibers coming from the dorsal roots, and cut off from their ganglion-cells in the spinal ganglia. If one experimentally divides these roots next to the cord, one produces exactly the same area of degeneration. Just above the place of division both the external and the internal posterior columns are degenerated; but farther up, where new, healthy root-fibers have entered, the latter lie external to those degenerated, and, as one ascends, these affected fibers approach ever nearer the median line.

What we have just learned by an examination of the degenerated posterior columns is reinforced by studying the development of the medullary sheaths. It teaches, too, that there are at least two fiber-systems there: one external, usually known as the prime bundle of the posterior columns; also called the *funiculus cuneatus*, or *column of Burdach*; and one internal, called the *funiculus gracilis*, or *column of Goll*. In the normal cord of the adult these two systems are separated from each other by a connective-tissue septum only in the cervical portion, while in the lower sections they can only then be distinguished when one or the other is diseased, when they differ in color. The columns of Goll increase in volume from below upward, as far as the lower dorsal cord, because they conduct portions of the continuously-

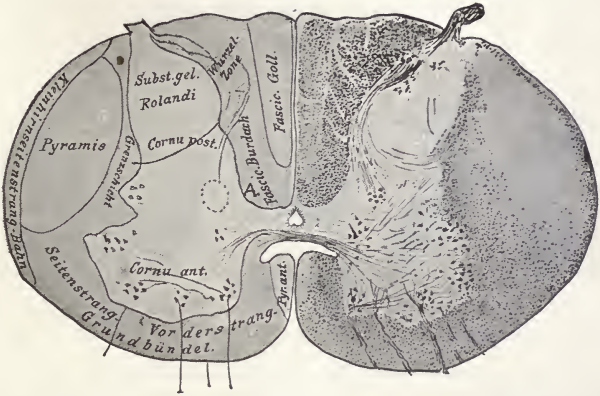

Fig. 223.—Transverse section through the cervical cord of a newborn child. The pyramidal tracts, minus medullated fibers, appear translucent and clear. The direct pyramidal tract extends far over into the antero-lateral column. *Wurzel-Zone*, Root-zone. *Kleinhirnseiténstrang-Bahn*, Lateral cerebellar tract. *Grenzschicht*, Boundary layer or zone. *Seitenstrang*, Lateral column. *Vorderstrang*, Anterior column. *Grundbündel*, Ground-bundle.

entering posterior roots from the sensory nerves of the legs to the medulla oblongata.

Later it will be seen that still other subdivisions must be made in the posterior columns.

The manner of propagation of diseases in them, particularly the results of submitting fresh lesions of the cord to the Marchi process of staining, which places the single degenerated medullary sheaths under the action of a special reagent, has largely added to our knowledge of these tracts.

That portion which closely adjoins the gray commissure (*A* in Fig. 223) must contain a separate system of fibers, because, in tabes for example, it never participates in the disease, even when the remainder of the posterior columns degenerates. It may be termed the ventral field of the posterior columns.

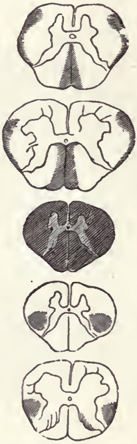

Fig. 224.—Secondary degenerations, ascending and descending, after a transverse lesion of the upper dorsal cord. (After Strümpell.)

The posterior columns consist almost exclusively of fibers entering by way of the posterior roots. These roots are so arranged that the entering fibers lie always laterally, close up to the posterior horns, but that those entering later, therefore higher in the cord, shove the more early arrived fibers toward the median line. So it happens that in the cervical part of the cord the fibers from the lower extremities occupy principally Goll's column, while the column of Burdach still contains many fibers from the upper extremities. It must not be suspected that the portions of the posterior columns named contain all the fibers of a posterior root. Many fibers, immediately after entering the cord, gain the gray matter, while others bend in their course, to pass through the posterior columns. Therefore there lie in the upper sections of the cord relatively few of those fibers in the posterior columns which entered lower down. Experimentally this has been proved by following up the cord from a divided dorsal root, when the degenerating portion of the cord grows smaller and smaller as one ascends. At the same time the degenerated field approaches more nearly the median line.

In the highest part of the cord the *funiculus cuneatus* contains fibers which do not come direct from the dorsal roots. Their origin is uncertain.

A part of the posterior-root fibers extends to the vicinity of Clarke's column of cells and there arborizes (Fig. 227). From this column of cells arises another tract of fibers. After section of the cord this tract degenerates upward. It is the peripheral portion of the lateral column (4 in Fig. 225). This tract may be followed to its entrance in the vermis of the cerebellum, and is called the *tractus cerebello-spinalis dorsalis.* We are particularly indebted to embryological research (Flechsig) for our knowledge of this, the *direct cerebellar tract*, and for our ability to distinguish it from the other lateral tracts. In the first few weeks post-partum, when the pyramidal tract

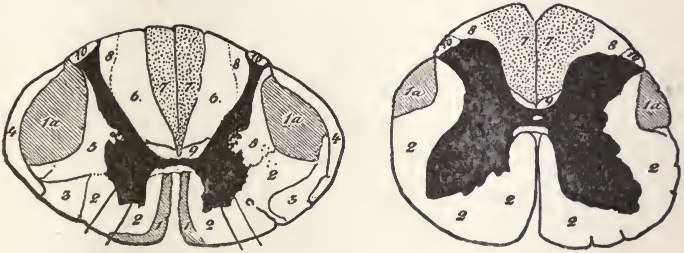

Fig. 225.

Fig. 226.

Section through the cervical and lumbar cord, with approximately-drawn boundaries of the different divisions of the white matter. Arranged from embryological principles, mainly from preparations with secondary degeneration of one or more of the tracts. 1*a*, Crossed pyramidal tract. 1, Direct pyramidal tract. 2, Antero-lateral ground-bundle. 3, Tractus cerebello-spinalis ventralis. 4, Tractus cerebello-spinalis dorsalis. 5, Lateral marginal zone. 6, Postero-lateral, or Burdach's, column. 7. Postero-median, or Goll's, column. 8, Radicular zone. 9, Ventral field of the posterior column.

still lacks its medullary sheath, the direct cerebellar tract forms a delicate-white border along the periphery of a large part of the lateral column (Fig. 223).

Later investigations (Loewenthal, Mott) have shown that the ventral portion of the lateral cerebellar tract, which Gowers, from pathological findings, had already distinguished as the antero-lateral tract, does not arise from Clarke's cells, but from other cells in the gray matter. This *tractus cerebello-spinalis ventralis* courses along with the corresponding dorsal tract up to the bulb, but is separated from it there, and, extending farther forward, enters the vermis superior of the cerebellum with the peduncles (*vide* page 328).

Up to this point then, from the study of secondary degenerations and embryology we have learned to recognize in the white matter the following divisions (systems of fibers, so-called): In the anterior columns the direct pyramidal tract; in the lateral columns, the crossed pyramidal and direct cerebellar tracts; in the posterior columns, the tracts of Burdach and Goll.

In Figs. 225 and 226 are represented all of the white tracts mentioned. The tract, marked 2, reaching from the anterior column around to the lateral column, has not been described. This area, pierced by the ventral roots, is known as the *anterior radicular zone.* That portion of it lying within the anterior column is also called the *anterior ground-bundle.* The portion lying within the lateral column is correspondingly further known as the *antero-lateral mixed zone.*

Further divisions in this region should doubtless be made; but as yet the recorded cases of secondary degeneration do not enable one to define them exactly. They would be very desirable, since it is to the anterior column that one can trace the *fasciculus longitudinalis posterior,* and it was into the antero-lateral mixed zone in the cat that Boyce followed that tract from the "deep gray" of the optic lobes (ant. corp. quad.), which corresponds to the lateral longitudinal bundle in the lower vertebrates. In this region also are to be found the prolongations of the large fibers from Deiter's nucleus in the cerebellum, shown in the diagram, Fig. 211, after Ferrier and Turner.

Most of the fibers in the antero-lateral column, which do not belong to the ventral roots, arise in the gray matter; here are found, besides, in all probability, the central continuations of the sensory paths. The region 5 (*lateral marginal zone*) contains fibers coming direct from the posterior roots, which, after crossing through the dorsal horn, ascend in this region (*Cf.* Fig. 223, right).

CHAPTER XXII.

THE COURSE OF THE FIBERS IN THE SPINAL CORD.

WHAT becomes of these fibers after their entrance through the spinal nerve-roots into the cord? How much farther have they been traced? It is not the form or shape of the particular part of the central nervous system, but rather the relationship between the different parts, and the communication between fiber and fiber, cell and cell, that must be the basis of investigations.

The anterior root-fibers may be traced backward and slightly upward, as they pass through the anterior radicular zone. Each single root seems spread out over a large extent of the cord. Arrived at the border of the gray matter, the component fibers separate. As to what occurs to them further, there are many and varied opinions. The following statement, based largely on personal investigation, includes the most important of these.

And first it is to be accepted as settled that certain fibers of the anterior root arrive at the ventral horn-cells, or rather form their axis-cylinder processes (see Fig. 218). Some of them pass over to cells in the opposite anterior horn, by way of the anterior commissure.

On pathologic grounds, it has long been recognized that, to the cell-centers of the motor-nerves, fibers pass from the cerebral cortex through the cortico-spinal tracts. It is not difficult to understand that numerous fibrils from the area of the anterior pyramidal tract (direct pyramidal tract), crossing over through the anterior commissure, enter the opposite anterior horn. Most of these fibrils are collaterals from the fibers proper of this pyramidal tract. In the anterior horn they divide up into fine tufts, which arborize around the ganglion-cells. Only in the recent past has the assumption of a connection between these cells and the lateral or crossed pyramidal tracts been proved. Here again it is mainly a matter of collaterals which are given off from these tracts and enter directly the ventral horn of the same side, and there form a fine arborization.

The pyramidal tracts, therefore, are the secondary motor tracts. Through the close contact of their axis-cylinders they enter into relationship with the cells of origin of the primary motor tract. In Fig. 7 this is schematically represented.

In the adult cord these relations are not discoverable. One must make use of embryonic cords, in which the pyramidal fibers are as yet non-medullated, then stain with silver after Golgi's rapid method, and prepare longitudinal and diagonal sections. In such sections one may often trace the collaterals, given off at right angles from the pyramidal fibers and entering the gray matter (*cf.* Fig. 227). These branches must later be medullated; for, in cases of degeneration of the pyramids, one finds invariably the corresponding ventral horn poorer in medullated fibers than normally (Fürstner). The same branches show very distinctly, when one succeeds in staining them with osmium during their degeneration (Fig. 228, sec. 5).

Many difficulties oppose themselves to the study of the relations of the posterior nerve-roots. Their fibers all, or nearly all, divide, immediately after entering the cord, into an ascending and a descending branch. From these arise numerous collaterals that pass partly to the gray matter, partly into the posterior columns (*vide* Fig. 227).

The fate of single divisions of the roots is very varied; their relations are extremely complicated, so far as is now known. In view of this, it will be well to refer frequently to Fig. 227 while considering what follows. This figure represents what is actually known. It implies that which concerns the multitude of fibers, and not any single section. Its purpose is merely to elucidate the text.

In a cross-section of the spinal cord one recognizes that the posterior roots, at their entrance, are definable into at least five parts. The most median bundles (1), mainly consisting of large fibers, nearly all enter the posterior columns immediately (*posterior root-zone*). Here, as we have learned, they turn upward toward the brain. The behavior of these roots, upon secondary degeneration following their section, teaches that those bundles which enter directly into the dorsal column are afterward pushed toward the median line by those entering at a higher level, so that the caudal root-fibers occupy above a position near the middle line, in Goll's column, and Burdach's column is largely made up of such fibers just entering and ascending diagonally (Fig. 28). We have also learned that, while running thus diagonally, there are fibrils continually being given off, which enter the gray matter.

Immediately after entering the cord, before the fiber turns cephalad, a branch is given off which turns caudad. Its course is now better known, since examinations of fresh secondary degenerations were made by the Marchi method (Schaffer, Löwenthal, and others).

In general, the traces of secondary degeneration on examination by this method appear so much more complicated than as represented in the preceding chapter that it will be well to examine the accompanying figures from cases described by Hoche (Fig. 228).

The place of compression lies in the region of the seventh dorsal vertebra. The degeneration at that point (3), as indicated by the osmium-blackened points, is irregularly spotted. Behind, toward the lumbar region, the pyramids separate into their anterior and lateral tracts. In the latter there degenerate also many bundles of greater or less length, which belong to the association-systems connecting different levels of the cord. Usually the shorter fibers lie nearer the gray matter, while the longer ones are farther away. Naturally these association-tracts are degenerated most of all at points immediately above and below the place of compression; farther away in either direction one finds only a few, and those are the longest. In the posterior columns just lateral to Goll's column there pass downward for a distance the descending fibers from those root-bundles which are affected by the compression. They form a comma-shaped tract,—Schultze's comma,—which lies in not always the same position, according to the particular, interrupted root. This tract, whose relationship to the dorsal roots is still disputed, was traced by Hoche a distance of more than eight vertebras before it disappeared in the gray matter.

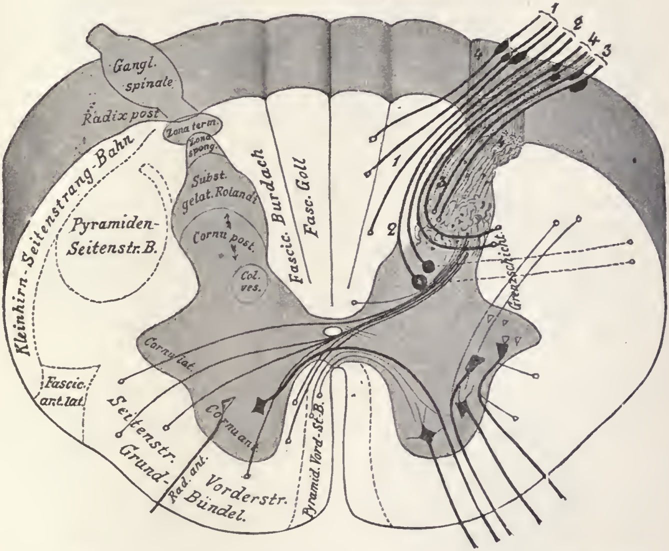

Fig. 227.—Schema of cross-section of spinal cord, in which the central course of some important bundles is indicated. Compare with it the non-schematic Fig. 223, right. The axis-cylinders from the ventral horn-cells to the posterior root are omitted. Tracts of the first order shown by dark lines, those of the second order, by dotted lines. For translation of German terms see explanation accompanying Fig. 223.

Still another small deposit of fibers, lying on the dorsal side of the posterior columns, belongs to the tracts of descending degeneration. In the lumbar cord it turns in toward the median septum, and lies close to it, as the "oval field" (Flechsig).

It can be traced into the conus terminalis. And, while its termination is well known, its beginning is not, it having been traced upward only to the cervical region. For the present it will be well to designate this long tract of very thick fibers as the *dorsal cervico-lumbar tract.*

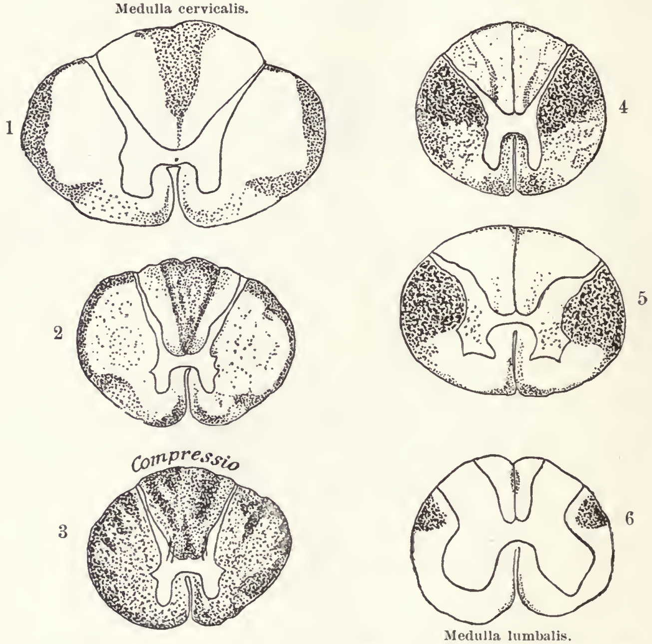

Fig. 228.—Compression of the cord at the level of the seventh dorsal nerve. Ascending degeneration to the left, descending in the sections on the right. The products of degeneration stained black with perosmic acid: Marchi's method. (After Hoche.)

A second portion (2, Fig. 227) of the posterior root-fibers does not turn into the columns, but penetrates the white matter by curves, to lose itself in Clarke's column, where its fibers arborize around the cells of that column. Some of the fibers (3) pass directly across the posterior horn, ventral to the substantia gelatinosa Rolandi, and then course farther in the marginal zone of the lateral column. They are well shown in Fig. 223.

The portions of the dorsal roots just described lie to the median side of the point of the posterior horn. Lateral to it (4) lie small bundles of coarse fibers, which may be traced through the substantia gelatinosa, and the rest of the horn anterior to it, up to the large cells of the anterior horn, around which they arborize. This tract is usually regarded as the shortest reflex path (Fig. 33).

More laterally still (5) are root-fibers which enter the gray matter after a longer or shorter course. These fibers split, just on entering the periphery of the gray matter, or soon afterward into an ascending and a descending branch. Many of them, especially large-fibered, cross through the substantia gelatinosa Rolandi before splitting. From these two divisions there pass out numerous collaterals in the gray matter, especially of the posterior horn, where they subdivide into small, thin tufts, around the cells there found. The more delicate fibers divide generally at the periphery of the posterior horn. So there arises, between the point, or extremity, of the posterior horn and the periphery of the cord, a field which is filled with these ascending and descending thin fibrils (*zona marginalis*; *z. terminalis*). From this zone pass continually fine fibrils into a net-work lying between it and the gelatinous substance,—*zona spongiosa*,—and from this net-work arise again other fine fibers, which pass through the substantia gelatinosa, and reach the fibrous tangle of the posterior horn. Probably they then enter into similar relationship to the cells there, as the coarse fibers, just described.

It must, however, not be overlooked, that much of what has just been stated regarding the fibrous tracts of the posterior spinal roots has not, with certainty, been ascertained to be true in man. As far as they have been sought, though, corresponding arrangements have been found, as in those mammals that have been thoroughly examined.

So far, therefore, can the sensory tracts be followed into the cord: As the most important of them are established, first, those entering the posterior columns and ascending in them toward the brain; second, those ending in Clarke's vesicular column; third, those—comprising the greater mass of the lateral root-fibers—which, after a greater or less course, arborize around cells of the anterior and posterior horns. Besides these there are fibers known which pass into the lateral mixed zone, some coming from the anterior horn, some going to it.

As to those fibers which arrive at the posterior horns and the gray matter just in front of these, it has been, in all probability, determined how they enter into relationship with higher centers. From the ganglion-cells around which the root-fibers arborize arises a second set of fibers. The axis-cylinders of these cells turn forward and inward to the anterior commissure, cross over in it to the anterior or lateral column of the opposite side, in which they ascend farther. What portion of the antero-lateral column is really to be regarded as sensory is doubtful. To me it seems most probable that the sensory fibers are here spread out over the entire cross-section of this column. Still, much is in favor of the view that the anterior radicular zone contains many of these secondary sensory fibers.

We have learned of two kinds, then, of extension of the posterior root-fibers: one direct in the posterior columns, and another indirect, which only by connecting with a secondary decussating tract takes a cerebral direction. We will see later that the uncrossed fibers encounter higher up in the medulla cells, there located, and then cross over; so that the whole tract finally decussates.

It were scarcely possible to draw these conclusions regarding the posterior root-fibers were it not true that in the lower vertebrates, in the spinal cord, the relations are very simple,—one might even say schematic. After it had been demonstrated with them that the majority of their posterior root-fibers ran into a central gray deposit of fibers and cells, and from there new tracts, after crossing, extended on toward the brain, it was but a step to look for corresponding conditions with man and mammals. The discovery by Ramón y Cajal that the posterior root-fibers split up around the cells of the spinal gray matter, and that from these cells there came out a tract which crossed over in the anterior commissure, gave to the supposition something of definiteness.

With this new achievement of knowledge coincide well the results of experimental and clinical pathology. If, for instance, a spinal cord were cut through its lateral half, underneath the point of section the tactile sense would be lost,—not on the corresponding side, but on the opposite one. This datum could not be reconciled with what was known of the crossed extensions of the posterior root-fibers in the posterior columns. It was, however, soon cleared up, when we learned that a considerable portion of such a root, soon after its entrance into the cord, was continued by a secondary tract over to the other side.

One must not suppose that all the impulses reaching the spinal cord by the sensory roots are identical with what is ordinarily termed "sensation." In order that an impression be perceived, it is not sufficient that it be conducted to the spinal cord, but it must be farther carried up, from the place where the peripheral path ends, to the cerebral cortex. There is, however, no doubt at all that these higher connections are few in number, and that, contrasted with the multitude of fibers in the posterior roots, the number of such central connections is quite small. This alone makes the conclusion possible that there are, indeed, many sensory impressions which arrive at the spinal cord, but that we are aware of but few of them at the time. All the viscera of the body, as the silver staining-method has distinctly shown, are traversed by an altogether unexpectedly large number of nerves, and their arrangement and course, their relations to blood-vessels and glands, and to muscle-fibers, bones, and enamel, make it more than probable that there is, in this connection, a large system which serves essentially to regulate impressions and reflex action (Exner). This is often overlooked in analyzing the results of section of certain columns. Until lately only the very coarsest qualities of sensation have been tested. And even now, when we know so much better than formerly the anatomic relations of the spinal-cord tracts, the phenomena revealed by physiologic experiments are to be very carefully interpreted; but, on the other hand, it seems to me desirable that new examinations of spinal-cord sections, whether partial or total, be made in man, because, with the lower animals, there is reaction only to the coarsest kind of impressions, which do not amount to actual pain. It is positively known, so far, that the posterior columns do not conduct those impressions which in the cortex are recognized as tactile, and it is quite probable that these are farther conducted by the portion entering into the gray matter, which there soon connects with its secondary extension. With these fibers must also be found the central paths conveying impulses of temperature and pressure sensations.

In the posterior columns run, presumably, tracts which, partly through their cerebellar connections and partly through their cerebral connections with the so-called cortical motor centers, in some manner influence the sensory regulation of movements and muscle-tone.

There remains still to be considered that part of the posterior root whose fibers arborize around the cells of Clarke's column. It has probably nothing to do with the conduction of tactile impressions, according to pathological data. The secondary tract, or prolongation upward from Clarke's column, does not join with the general sensory paths. From these cells arise fibers which leave the gray matter laterally, and on the periphery of the gray matter enter the direct cerebellar tract. With it they pass up to the cerebellum. These fibers are doubtless important for the co-ordination of movements. For not only in cerebellar disease are gait and station incoordinated, but also in tabes dorsalis, in which one meets with ataxia of the highest degree, are these fibers of the posterior column and the columna vesicularis degenerated, resulting in an interruption to the paths leading to the cerebellum.

The anatomical relations, then, which are affected by the entrance of the posterior nerve-roots into the cord, are much more complicated than are those of the anterior roots. We have already seen this to a degree. Probably there exist still other, as yet unknown, systems of fibers.

The relations of many of the cells of the ventral and dorsal horns to the root-fibers we have already learned. There are, in the gray matter, still many cells, which do not, however, stand in direct relation to the root-fibers. First, there are cells whose axis-cylinders do not pass over into a longitudinal bundle or into a root-fiber, but soon after their source form extremely fine arborizations. They are seen everywhere on the cross-section, but are especially noteworthy in the border-region of the dorsal horn. Then there have been recognized multipolar, scattered cells, which give off one axis-cylinder in the corresponding or the opposite antero-lateral tract (Figs. 210 and 227). There it splits into an ascending and a descending branch (Fig. 220). The branches from these "tract-cells" extend a short distance in the antero-lateral columns, then give off collaterals, which again enter the gray matter and there arborize around other cells. These cells unite by their processes levels of the cord, which lie cephalad or caudad from them; hence they are adapted to serve as a substratum for the long-accepted paths that connect together different levels.

To any irritation coming to the cord from the periphery there are offered a large number of conduction-paths. There is, first of all, a number of posterior root-fibers which extend directly into the anterior horn and arborize around its cells. These are well adapted to "load" such cells with impressions, or after sufficiently high irritation to call forth immediate discharge of motor reflexes. But, through cells originally in relation with each other, and through others that are so as a result of selective function, the motor cell-groups are functionally associated in such a manner that a single impression is often sufficient to bring an entire group of cells to discharge at the same time. So reflexes may consist of single muscular movements and also of very complicated actions. Besides the dendrites the "tract-cells" with their processes form the anatomic basis of these associations. It is not difficult to accept the statement that an impulse, arriving at the spinal cord, spreads in this way through these cells over different levels, and so unites in exciting motor cells of the most varied positions to simultaneous action. (Exner and others.)

All these fibers and cell-processes form an extraordinarily complicated mesh-work in the gray matter of the cord. Its unraveling has been accomplished only by the use of all the methods ever conceived. In the adult cord, colored after the Weigert method, this is impossible.

All fibers crossing from one side to the other occupy either the anterior or the posterior commissure.

Although the component elements of these commissures have already been mentioned, each in its place, still it will be well to consider them again more topographically.

In the anterior commissure, then, we find (Fig. 227):—

1. Belonging to the anterior roots: fibers from cells to the opposite root; collaterals of the direct pyramidal tract; numerous dendritic processes from neighboring ventral horn-cells.
2. Secondary sensory paths from those cells, around which arborize fibers from the posterior nerve-roots.
3. From the "tract-cells": numerous axis-cylinder processes to the opposite anterior and lateral columns.
4. Connecting fibers from the lateral column of one side to the anterior column of the other.

This tract, found by Schaffer in vertebrates of different classes, is, according to him, made up of posterior root-fibers, which first enter the lateral column, and higher up cross over into the opposite anterior column. It has been demonstrated, also, in animals that have no medullary pyramidal fibers (reptiles); therefore it cannot be an accessory pyramidal tract: a supposition which otherwise might seem true.

Of the posterior commissure we know much less. Of a certainty it contains medullated fibers, and these surely arise from the posterior roots and from tracts into which the posterior root-fibers have entered.

In the fetus of different mammals different dispositions of fibers have been found in this commissure, according to the class of animal examined. In the dog, for example, three divisions of these commissural fibers can be distinguished; in the cow only two, and so forth.

As far as the anatomic relations of the component tracts of the spinal cord could be determined macroscopically, Burdach, Sömmering, and J. Arnold rendered important service. Bellingeri was the first to recognize the connection between the gray matter of the ventral horns and the anterior nerve-roots; Grainger, that between the dorsal horns and the posterior nerve-roots. The minute structure of the cord was first revealed by B. Stilling, later Kölliker, Goll, Deiters, Gerlach, Clarke, and others have added to our knowledge of it. To the labors of Türck, Flechsig, Charcot, and Gowers we are indebted for the major part of our ideas of the disposition of the fibers of the white matter. Within more recent times, however, through the advances made by His, Golgi, and S. Ramón y Cajal (collaterals, arborization of axis-cylinders, etc.), through the researches of Kölliker, Van Gehuchten, and Lenhossek, of whom mention has already been made in the introductory chapter, a very important gain has been made in our knowledge of the spinal cord. Besides them, Singer and Münzer, Löwenthal, Mott, and others have cleared up much that was not understood, and we are indebted to Waldeyer for a critical revision of accumulated data, together with many new subjects.

One might carry the study of the most important fiber-systems in the cord much farther, going into many interesting details. But we have already found so many places where uncertainty prevails that, adhering strictly to the limits, beyond which one finds only a complex of details and contradictory opinions of authors, we need hardly pursue it farther.

In the introduction to his great work on the structure of the spinal cord, Stilling says: "We must not forget, following in the train of the noble Burdach, that in the examination of the spinal cord we are exploring a wonderland, which we know very little about; and we may only gaze at the rivers and mountains, to get a clear general understanding of the whole, leaving to our successors to explore every brook and to seek out every height."

Thirty-six years have passed since, with these prefatory words, one of the most valuable books appeared with which the anatomic department of science has been enriched, and to-day we are still far from the goal; it will be long still before that field-map will be completed, of which Burdach and Stilling dreamed.

In the cord there lie in close proximity to each other, physiologically widely differentiated fibers; the cells, which may be regarded as central cells, are thickly surrounded by peripheral conducting paths. It is clear from this that it is very difficult to learn the results and to establish the symptoms which appear upon disease or lesion of any of these component parts of the cord.

Still, close observations at the sick-bed and at autopsies have taught much in this connection. A number of spinal-cord diseases affect invariably certain portions of the cord, always certain tracts or particular groups of ganglion-cells, and leave the other tracts of the cross-section intact, forever or for a long time. The observation of such forms will be of prime importance for the question confronting us. We also discover much as the result of wounds, sections and compressions of the cord, as often arise from caries of the vertebræ, and tumors.

Much less effective than pathology is the examination of animals. Compared with pathologic processes occurring in the fine mechanism they affect, the necessary experimental attempts are exceedingly coarse and bungling.

We cannot, of course, in this work give even a short *résumé* of the valuable finds for which we are indebted to numerous researches made in the pathology of the spinal cord. There are many excellent works in this line.

Only a few especially important and well-established points should be here mentioned.

Disease of the posterior columns causes different symptoms according to its location in them. Destruction of the entering posterior roots must interrupt the entire sensory apparatus they contain, entailing the loss not only of every quality of sensation, but also of the reflexes, which, indeed, are possible through the sensory paths. Then, also, the tendon-reflexes disappear. Those degenerations of the posterior columns which do not affect the entering nerve-roots, or do so but partially, run their courses without special disturbance of cutaneous sensibility, although the muscular sense seems invariably to suffer. The motor power is in nowise affected by disease of these columns.

If the gray matter of the ventral horns be destroyed by a disease-process there ensues, as in the case of destruction of peripheral nerves, paralysis of the muscles which derive their nerve-supply from the respective level of the cord. To this paralysis is quickly added atrophy of the paralyzed muscles. In this respect does it also resemble peripheral paralysis: viz., that the particular muscles react to the electric current exactly as if the supplying nerve were severed. Since the nerve and its end-organ in the muscle are but processes of the cell, it is not difficult to understand this relation.

From the last-described symptom-complex one will always be able to diagnose an affection of the lower segment of the motor path.

Entirely different signs appear if there be an interruption in the upper segment of the motor path, the tractus cortico-spinalis.

If the pyramidal tracts are diseased, voluntary movements are disturbed or lost. In addition, the paralyzed muscles, or those which may be only slightly weakened, show a permanent increase in tension, tend toward contractures, and are much more irritable to mechanical stimuli than normally. Always, in the presence of these symptoms alone, or when met with in conjunction with other symptom-complexes, one can, with entire certainty, accept the fact of a participation of the pyramidal tracts in the disease. Not seldom has unilateral interruption to the pyramidal fibers been followed by bilateral paresis and increase of muscular tension.

There occur diseases of the primary (lower) and secondary (upper) motor tracts in combination. Of these the best observed is the amyotrophic lateral sclerosis. Here the clinical signs—paresis, spasms, muscular atrophy—correspond to the anatomic condition: disease of the pyramidal tracts and of the ventral horn-cells.

These relations are readily understood by a glance at the preceding schematic representation (Fig. 229). A lesion, located in the line *x a c* (*i.e.*, in the fibers it represents), produces paralysis. If it interrupt this line above the ganglion-cell, as at *x* or *a*, it assumes the character of a central paralysis, without atrophy, and eventuates often in improvement or cure, probably through the substitution of other paths for those represented by *x a*. If, however, the line *x a c* be broken at the ganglion-cell or anywhere in *c*, then there follows not only paralysis, but also wasting of the paralyzed nerves, and atrophy of their corresponding muscles. As a consequence, the outlook toward recovery in the paralyzed members is very slight. At times after a

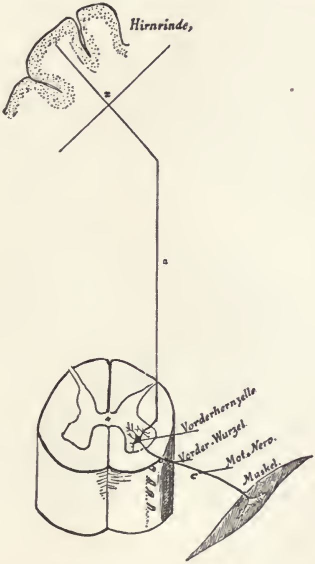

Fig. 229.—Schema of innervation of a muscle. *Hirnrinde*, Brain-cortex. *Vorderhornzelle*, Cell of ant. horn. *Vorderwurzel*, Anterior root.

long-continuing lesion of x a, there ensues gradual participation of the part c. But this occurs seldom. Interruption of the path a leads to descending degeneration from the point of lesion to the level of the respective ventral horn.

As an example of paralysis and muscular atrophy, occurring with disease of the ventral horns, may be mentioned "infantile spinal paralysis." In this affection complete paralysis of single muscle-groups occurs suddenly, and there follows very quickly wasting of the muscular tissue. Examination of the spinal cord reveals then disease-foci in the gray matter of the ventral horns. The nerves also, as well as the anterior nerve-roots, atrophy gradually.

We do not yet possess sufficiently exact evidence to be able to say what symptoms arise from disease of the gray matter of the dorsal horns. But from the analysis of cases of tabes dorsalis, in which they were spared, and of those in which they were affected, we may conclude that lesions involving them lead probably to disturbances of cutaneous sensibility, and particularly to trophic changes in the skin. In syringomyelia and with tumors located within the gray matter among other disturbances appear those of temperature and pain-sense.

CHAPTER XXIII.

THE MEDULLA OBLONGATA.

At the upper end of the spinal cord the white fibers of which it is made up are disposed in various ways, the extent and form of the gray matter changes considerably, new deposits of neuroglia and of ganglion-cells appear, and the well-known picture of the cross-section of the spinal cord rapidly disappears; especially is it indistinct when, at the upper segment of the cord, right and left, there where the lateral tracts were, the inferior olive arises,—a gray, much folded, richly cellular layer,—and when the central canal, approaching more and more nearly to the dorsal surface, expands into the fourth ventricle.

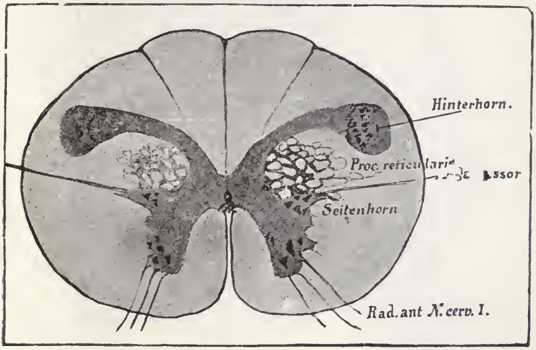

Fig. 230.—Section through the upper cervical cord. *Hinterhorn,* Posterior horn. *Proc. reticularis,* Association-field. *Seitenhorn,* Lateral horn. *Rad. ant. N. cerv. I,* Ant. root of I cervical nerve.

The series of transverse sections here presented is intended to explain the evolution of the medulla oblongata out of the spinal cord.

Fig. 230 represents a section of the cervical cord, corresponding to that part from which passes the first cervical nerve. It but recalls the relations as already described in the preceding chapter. Three points, however, distinguish it. The first is the peculiar form of the posterior horn, which is connected only by a thin "neck" with its dorsal extremity, here greatly thickened by substantia gelatinosa, forming the "head of the dorsal horn."

Through the substantia gelatinosa pass numerous fine fibrils, which are partly posterior root-fibers. Another portion of them comes from a greater distance, namely from the Gasserian ganglion. The cells of this ganglion emit peripherally the *nervus trigeminus*, and centrally the trigeminal root. A part of these latter fibers turn downward, and from them pass continuously fine fibrils to the end-nucleus of the trigeminus: a column of gelatinous substance, which is demonstrable from the pons down to the substantia gelatinosa of the upper cervical cord. The crescentic transverse section of the tractus spinalis of the fifth nerve lies in the cervical cord in close proximity to the substantia gelatinosa, as in the oblongata and the pons. It can be seen in all the sections hereafter represented (Figs. 232 and 238, for example). It has, until now, been called the ascending root of the fifth nerve (see also Fig. 251).

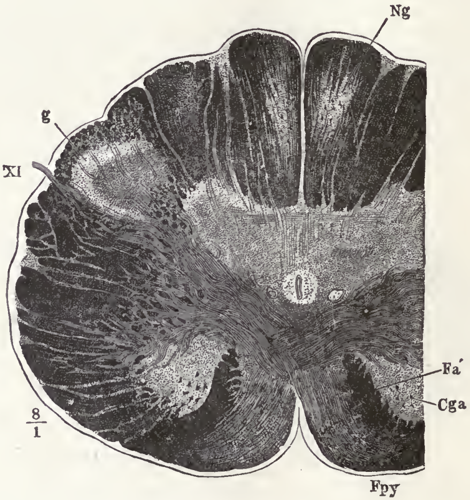

Fig. 231.—Cross-section of the oblongata through the pyramidal decussation. *Fpy*, Pyramidal tract. *Cga*, Anterior horn. *Fa'*, Remnant of anterior column. *Ng*, Nucleus funiculi gracilis. *g*, Substantia gelatinosa. *XI*, Nervus accessorius. (After Henle.)

Further one finds the lateral horns here well developed. From cells lying at their bases and higher up, appearing on the lateral edge of the anterior horn, comes the *nervus accessorius Willisii*. Its root-fibers, which arise below as far as the sixth cervical nerve, and above as far as the beginning of the oblongata, do not arise in exact order, as might appear from Fig. 230, but extend first toward the brain, and later they bend outward forming a knee (Darkschewitsch). Only the horizontal limb of this knee has been caught in this section, represented in Fig. 230.

The most anterior fibers of the *accessorius* in animals, and in one case observed in man, contain the inhibitory fibers to the heart. I have seen pronounced slowing of the pulse on defecation arise from the existence of a varix in the frontal accessorius region, and I saw this patient die with symptoms of increasing slowing of the heart's action, when the varix became larger and finally burst. (*Berliner klinische Wochenschrift*, 1898.)

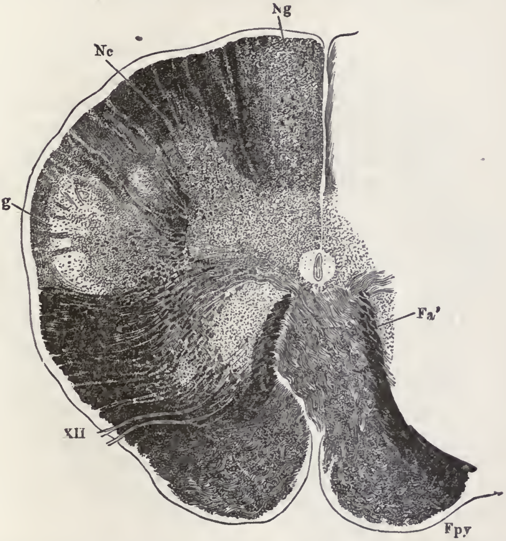

Fig. 232.—Cross-section of the oblongata in the region of the lowest hypoglossal roots. The pyramidal decussation nearly complete. *Nc,* Nucleus funiculi cuneati. *XII,* Nervus hypoglossus. Other marks same as in Fig. 231. (After Henle.)

Notice also, that in the space between the anterior and posterior horns the gray matter passes through the lateral column in the form of a complicated net-work; this is the formation of the *processus reticulares.*

Their gray matter consists almost exclusively of commissural cells, which join the different levels together. Earlier in this work, in the consideration of the brains of lower animals, attention was called to the fact that regularly at the border between the spinal cord and the bulb this great commissural system appears, or strengthens that already existing. It was there designated as the *association-field of the medulla.*

Above the level just described begins the rearrangement of fibers, etc., which brings about the changes observed in the cross-section of the bulb.

We have learned in the cord of two fasciculi cortico-spinales, one of which, lying in the anterior column, conducts toward the brain fibers which are derived on the opposite side from all the different root-regions, and a second, the crossed pyramidal tract, which contains fibers from the corresponding ventral horn.

At the upper end of the cord this latter tract enters the anterior column of the opposite side, by large bundles, which break through the ventral horn of the same side. There it meets the anterior or direct pyramidal tract, and beyond this the uncrossed tractus cortico-spinalis passes with the crossed as pyramidal tract to the brain. The dorsal horns move farther forward, just as the place in the lateral column occupied by the crossed pyramidal tract becomes free.

A few millimeters higher still the pyramidal decussation is complete. There lie, then, now the crossed pyramidal fibers with the direct pyramidal fibers in one large bundle, ventral in the medulla. This is distinctly shown in Fig. 232. It will be seen, too, that the anterior ground-bundle (*Fa′*) is placed dorsal to the pyramids. External to the separated remnants of the ventral horn a small gray focus is seen. It belongs to the lowest point of the olivary body. The olive enlarges materially as one ascends, and fills a large part of the room in the lateral tracts. These latter, from the appearance of the processus reticulares, have become richer in fibers. The association-field develops more and more. However, the paths are only traceable a short distance. Many end in scattered, small groups of ganglion-cells (nucleus of the lateral tract, nucleus reticularis tegmenti, etc.).

The rearrangement of fibers, the crossing of the lateral pyramidal tract over to the opposite anterior column, is well shown in the accompanying drawings by Henle (Figs. 231 and 232). The separated ventral horns can be traced farther upward, but disappear at about the level of the pons.

The pyramidal tracts are seen on all the following sections, lying between the olivary bodies anteriorly (see illustrations in following chapter). Later they are covered over and divided into bundles by the transverse fibers of the pons. How they emerge farther on beyond the pons and pass through the pes cerebri into the internal capsule has been repeatedly described in preceding chapters. It has also been explained that the secondary degeneration, which takes place downward after interruption to the cortico-spinal tract in the brain, affects in the bulb the posterior part of the opposite lateral column and the anterior column of the same side.

Opportunity to follow the course of the pyramidal tract is offered not so seldom, if in autopsies on cases of long standing cerebral unilateral paralysis one make transverse sections of the pes cerebri, the pons, the bulb, and the cord. The gray pyramid of the diseased side appears usually in marked contrast to the white fibers of the other side; in the cord a grayish spot is noticeable in the posterior part of the opposite lateral column.

At the level of the pyramidal decussation appear also changes in the dorsal columns. In their centers, first in the postero-median, later in the postero-lateral tracts, arise groups of gray deposits, containing ganglion-cells: the nucleus gracilis and the nucleus cuneatus. These nuclei blend with the gray matter, whose form is correspondingly altered. (In Fig. 231 the first of these may be seen; in Fig. 232 both of them.)

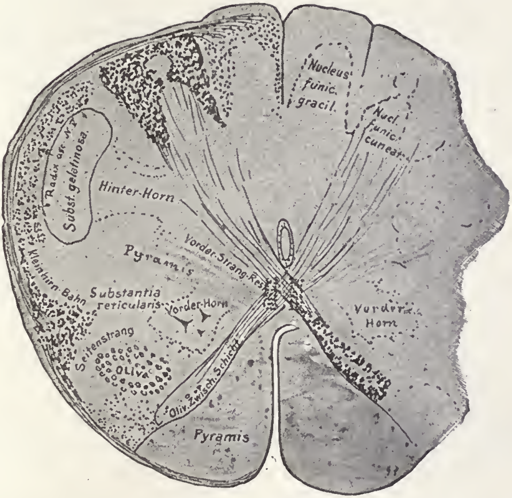

Fig. 233.—Section through the beginning of the oblongata of a human embryo at the twenty-sixth week of gestation. One sees the fibers going from Burdach's column to the decussation of the fillet, and the fibræ arciformes externæ dorsales from Goll's column, later described. Notice the position of the cerebellar tract. *Hinter*, *Vorder Horn*, Post., Ant. horn. *Oliv. Zwisch. Schicht*, Interolivary layer. *Vorder-Strang-Rest,* Remains of ant. column.

Probably all the fibers of the posterior columns ultimately end in these nuclei. From them, in turn, spring masses of fibers through the gray matter forward, and cross over to the other side anterior to the pyramidal crossing. These fibers later make up the fillet, hence this crossing is called the *decussation of the fillet.*

It is not very easy to be convinced of the existence of a fillet-crossing in a fully-developed brain. But there remains no doubt at all, when one examines sections of the bulb in a fetus of seven months. There the medullary fibers of the pyramidal decussation do not yet disturb the picture, the fibers of the posterior tracts being more distinct through being earlier provided with medullary sheaths. At first one sees principally only fibers coming from the nucleus cuneatus; toward the ninth month, however, a little higher up, one may recognize the decussating fibers from the nucleus gracilis.

Comparing Fig. 233 with the two figures preceding it, one notices behind the central canal the gray matter, much wider than before.. In the column of Goll is seen its nucleus; also in the column of Burdach its nucleus; both are continuous with the gray matter. External to them, surrounded by a thin layer of medullated fibers (spinal root of the trigeminal nerve), lies the substantia gelatinosa of the dorsal horn. In front of it, in the space which in Fig. 232 is occupied by the dark pyramidal fibers, is a clear place, because these fibers have not yet received their medullary sheaths. The anterior ground-bundle and the cerebellar tracts lying at the periphery of the lateral column are already medullated.

From the nuclei of the posterior columns may be seen issuing fibers which pass in curves (*fibræ arciformes internæ*) through the gray matter, decussate in front of the central canal, and dispose themselves in a thick layer dorsal to the previously decussated pyramids. The territory occupied by them corresponds to the anterior ground-bundle of the cord. The major portion of the fibers ascending in these already decussated sensory tracts are hereby pushed backward and outward by these newly arrived fibers. Therefore, the united, crossed, sensory paths of the second order (secondary neurons) gradually fill up all the space lying between the two new gray masses, which arise in this level of the medulla oblongata, the olives (*olivæ inferiores*). The higher one goes in the oblongata, the poorer in fibers become the posterior columns. Gradually they all pass by the arcuate fibers into the fillet-crossing, and so to the opposite side, near the median line, where they form the interolivary bundle, or, as we from now on may know it, the fillet, for its fibers pass upward to the fillet of the midbrain (lemniscus).

In Fig. 235 is presented a scheme of the course of the sensory fibers. One may trace the direction of each bundle by it, beginning at the entrance of the root-fibers, and finally demonstrate where each one ends in the medulla oblongata. Especially noteworthy is it that the fibers which have decussated in the cord lower down are joined by those which here cross over, forming one bundle.

There are then, in this region of the bulb, two important decussations:

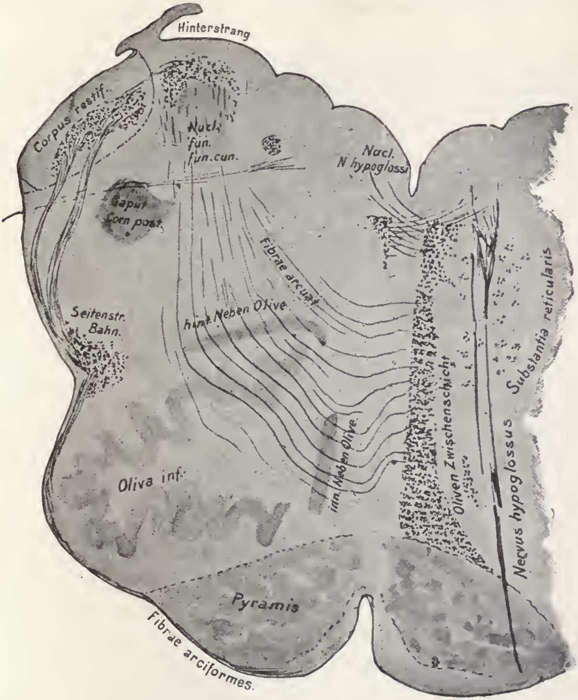

Fig. 234.—Cross-section through the medulla oblongata of an embryo of twenty-six weeks. The medullated fibers stained with hæmatoxylin. The left interolivary tract and the tractus spinalis nervi trigemini are not shown. In the restiform body only the spinal portion is medullated. *Fibræ arciformes*, Fibr. arc. ext. ant. The fibr. arc. ext. post. are above, to the left and externally, between the restiform body and the posterior column. The bundle marked "*Seitenstrang*" is the tractus cerebello-spinalis ventralis lateralis, which remains in this location as high up as the anterior part of the pons; the tract. cerebello-spin. dorsalis, as here seen, leads direct to the corpus restiforme. *Oliven Zwischenschicht*, Interolivary layer. *Inn. Neben Olive*, Internal accessory olivary nucleus. *Hint. Neben Olive*, Posterior accessory olivary nucleus. *Hinterstrang*, Posterior column. *Seitenstr. Bahn.*, Lateral cerebellar tract.

that of the pyramids and that of the fillets. In the former are motor fibers, in the latter, fibers serving to conduct sensory impressions.

Two new fiber-areas have arisen: ventrally the pyramidal bundle and dorsally from it the fillet. We will be able to follow them both higher up to the region of the corpora quadrigemina.

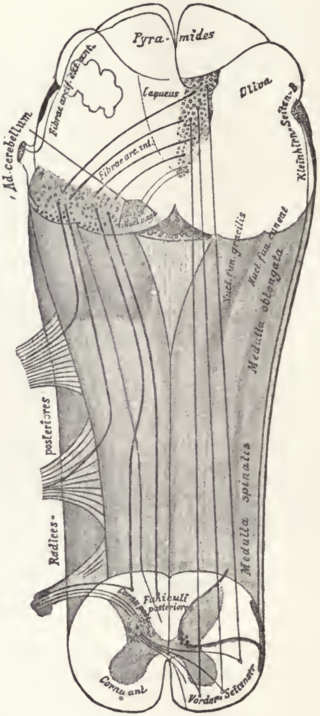

Fig. 235.—Schema of the course of the sensory fibers from the posterior roots up to the medulla oblongata. *Kleinhirn-Seiten B.*, Lateral cerebellar tract. *Vorder Seitenstr.*, Antero-lateral column.

The fillet contains many more fibers in adult man than appear in the specimen from the fetus, just demonstrated. With the latter all the fibers from the antero-lateral ground-bundle belonging to the sensory tract are, as yet, non-medullated, and only those appear distinctly which arise from the nuclei of the posterior columns.

By reason of the two decussations the appearance of the cross-section changes materially. In addition, the gray matter, as presently to be described, also changes its form, and new masses of it appear in the medulla; three of these—the two posterior nuclei and the olive—we have already

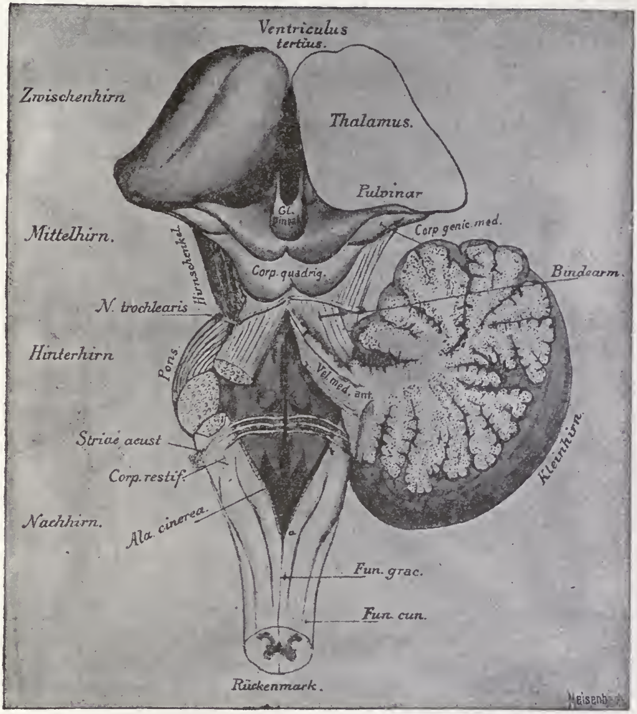

Fig. 236.—The hind- and after- brain exposed by removal of their roof. Velum medullare anticum and cerebellum still visible. Velum medullare posticum has been removed along the dotted line, *ba*. *Zwischenhirn*, Thalamencephalon. *Mittelhirn*, Mesencephalon. *Hinterhirn* and *Kleinhirn*, Pons and cerebellum. *Nachhirn*, Medulla oblongata. *Rückenmark*, Spinal cord. *Hirnschenkel*, Cerebral peduncle. *Bindearm*, Peduncle of cerebellum.

studied. Above all, however, the external form of the medulla is greatly changed. As the fibers of the posterior columns gradually run into their respective nuclei and end in them, the gray matter of these nuclei become more and more exposed and finally lie on the dorsal surface of the bulb. But the posterior columns at this level separate gradually from each other. This brings the posterior or gray commissure of the cord distinctly into view, where these columns separate. Here, also, the central canal broadens and forms the *fourth ventricle.* What covers it becomes thinner and more expanded, and can be followed as far as the cerebellum, being called the *velum medullare posticum.* With the commissure this forms the roof of the fourth ventricle.

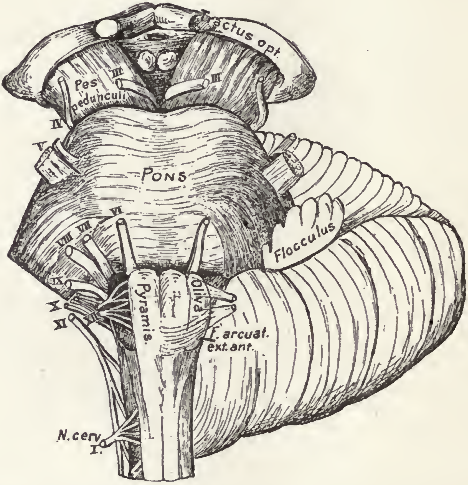

Fig. 237.—Medulla oblongata, pons, cerebellum, and pes pedunculi (anterior view); to demonstrate exits of cranial nerves.

In the longitudinal section represented in Fig. 206 can be seen the combined coverings of the fourth ventricle, namely: the velum medullare posticum, the cerebellum, and the velum medullare anticum. Close to the beginning of the fourth ventricle, in the velum medullare posticum, is an opening, or foramen, leading into the ventricle from without. This is the *foramen of Majendie,* already mentioned, through which the fluid in the ventricle communicates with that which flows about the entire central nervous system in the subarachnoid spaces.

In Fig. 236 this entire roof is represented as having been removed, allowing free view into the fourth ventricle. Its floor is bounded below by the diverging posterior columns, above by the superior cerebellar peduncles, which converge toward the corpora quadrigemina. This gives it its peculiar diamond shape.

In this figure the view of the medulla posteriorly indicates the gradual disappearance of the posterior columns as they ascend, and that in place of them the inferior cerebellar peduncles, the restiform bodies (see below), appear. The protuberance in the upper part of the posterior median column is called the *clava*; it arises from the deposit of the nucleus funiculi gracilis.

An anterior view of the medulla (Fig. 237) shows, first, the thick swelling of the pyramids, arising out of the cord. External to them appear the olivary bodies, at the head of the lateral columns, as two large tumefactions. A little higher up the large transverse fibers of the pons apply themselves across in front of the pyramids. In the extension of the anterior radicular groove upward, between the olive and the pyramid, arises the *nervus hypoglossus* (*XII*) from the medulla. The *nervus accessorius Willisii* (*XI*) arises from the cervical cord, and higher, from the medulla, external to the olive, by numerous small bundles. Above, in the same groove ex-

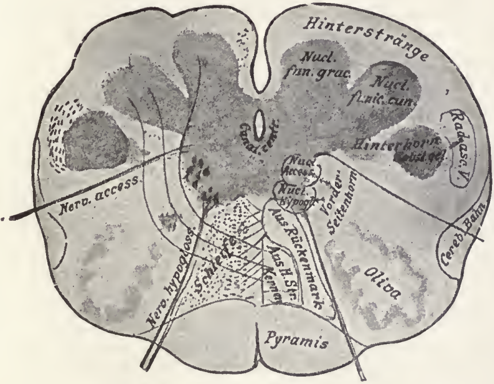

Fig. 238.—Section through the oblongata at the level of the posterior hypoglossal roots (schematic). *Hinterstränge*, Posterior columns. *Hinterhorn*, Posterior horn. *Vorder-Seitenhorn*, Antero-lateral horn. *Cereb. Bahn*, Lateral cerebellar tract. *Aus Rückenmark*, From the spinal cord. *Aus H. Str. Kernen*, From the nuclei of the posterior columns. *Schleife*, Fillet.

tended, the *nervus vagus* (*X*) and the *nervus glosso-pharyngeus* (*IX*) have their exit from the medulla. Just behind the pons, and laterally, are the origins of the *nervus acusticus* (*VIII*) and the *nervus facialis* (*VII*). The sixth cranial nerve, the *abducens*, arises internally from the two last named. From deep in the pontile fibers springs the *trigeminus* (*V*). The origins of the *trochlearis* (*IV*) and the *oculo-motorius* (*III*) we have already learned. The trochlear comes from the velum medullare anticum behind the corpora quadrigemina; the motor oculi ventrally from the pes cerebri.

The last section of the medulla considered was at that level where the central canal expands into the fourth ventricle. Even before this the first nuclei of the cranial nerves have appeared in the gray matter surrounding it. The fibers of the accessorius arise from cells in the most lateral portion of the ventral horn, and from a place anterior to it, which corresponds to the base of the former anterior horn, the *nucleus hypoglossi*, the fibers of the hypoglossal nerve develop.

In the two accompanying figures this is represented. If it be noticed how the central canal, following the separation of the posterior columns, spreads out and becomes the fourth ventricle, it will then be easily understood that from this point on all the nerve-nuclei must lie in the floor of this ventricle. This is clearly shown in Fig. 239. Laterally from these centers lie the posterior columns, now sparsely provided with fibers. The posterior horn, discernible by the substantia gelatinosa of its head, is entirely separated; and the basal part of the lateral horn, too, from which come the fibers of the motor accessorius, loses its connection with the compact gray matter a little higher than the plane of the figure. It continues as a column rich in ganglion-cells ventral to the gray matter as far as the pons, and, after the accessory has made its exit, gives out fibers to the vagus (and glosso-pharyngeus?), which first ascend in a dorsal direction, and then bend around to the respective nerve-trunk (motor vagus, etc., nucleus). Higher still it is met as the facial center. It must, therefore, be remarked, that, with the exceptions of the hypoglossus and the motor nerves to the eye, all the motor fibers of the cranial nerves arise from a cellular column, which lies in a prolongation upward of the lateral cells of the ventral horn.

Next one sees, in Fig. 238, what has become of the remainder of this horn, and how greatly the olivary bodies have enlarged. When the lateral horn has become separated, there appears where the posterior horn was inserted—in a place, therefore, which held nuclei of sensory nerves lower in the cord—a new, large nerve-center, with spindle-shaped cells, very similar to those of the dorsal horn, the *sensory center of the vagus nerve*. It lies in the floor of the fourth ventricle, median to the *ala cinerea* (Fig. 236), and extends forward to about the middle of the white striæ acusticæ.

Into this anterior part of the center pass fibers of the *glosso-pharyngeal nerve*, The greater part of this nerve, however, comes from its descending root (see below). We have learned, then, two nuclei for the vagus: a ventral one, which from its position (in the prolongation of the ventral horn) and from the appearance of its cells (multipolar with axis-cylinders passing directly into the nerve) is motor; and a dorsal one, which, lying in the prolongation of the gray matter of the base of the posterior horn, is also, by its structure, characterized as sensory. The first of these nuclei is designated *nucleus ambiguus*. The fibers to which it gives origin pass, all of them, dorsally, and, bending to form a knee, join the much coarser fibers of the sensory root, which pass out straight (Fig. 239). Besides these two nuclei, the vagus receives fibers from at least two other places. From the upper cervical cord downward one may see a fine column, which may be traced upward to the oblongata, to the place where the last glosso-pharyngeal root emerges. On its median side lies a column of gelatinous matter, in which cells are

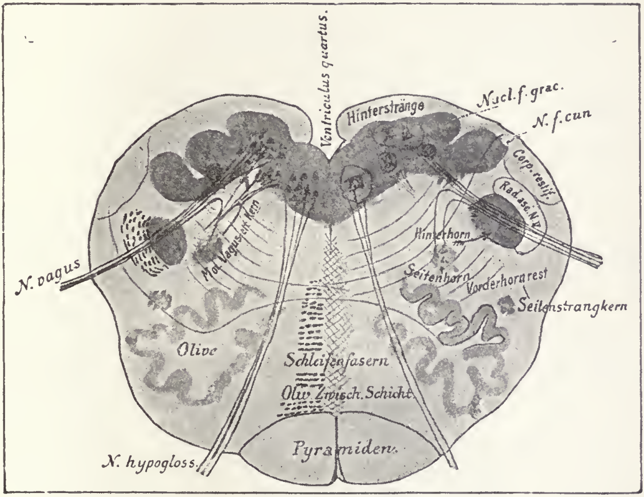

Fig. 239.—Section through the bulb at the level of the exit of the vagus (schematic). *Mot. Vagus, etc., Kern*, Nucleus of motor vagus, etc. *Seitenhorn*, Lateral horn. *Vorderhornrest*, Remnant of anterior horn. *Seitenstrangkern*, Nucleus of lateral column. *Schleifenfasern*, Fibers of fillet. *Oliven Zwisch. Schicht*, Interolivary layer. For other terms see Fig. 238.

sparingly imbedded. It is called the *tractus solitarius*, or *combined descending vagus glosso-pharyngeal root.* It can be seen in Figs. 234 and 239, lying dorsal to the vagus roots. Only a small part of the entering vagus roots turns caudally into the funiculus solitarius, and enters, after gradually splitting into end-ramifications, into the neighboring gray column.

This column is, therefore, the *nucleus of the glosso-pharyngeus* and a portion of the *vagus.* S. Ramón y Cajal has recently shown that just at the place where the central canal widens to form the fourth ventricle the two terminal nuclei of the vagus and glosso-pharyngeus nerves approach each other, and, eventually, at the point where it opens, coalesce to one common mass, the *nucleus commissuralis.* A considerable number of the fibers of the funiculus solitarius cross over to the other side at this point.

The *glosso-pharyngeal nerve* sends the larger mass of its fibers to end in the gray matter of the funiculus solitarius, while only a relatively small portion of them branch in that of the floor of the fourth ventricle. Again we have the plan of the sensory nerves: nerve, nucleus of origin in the spinal ganglion; for the nerve-root, ultimate center (sensory vagus center); and the decussated ascending central tract.

In the floor of the fourth ventricle, between the vagus center and the median line, lies another small swelling, Clarke's *eminentia teres,* in which may be found, from the frontal end of the hypoglossal center on up to near the origin of the trifacial, a slender group of spindle-shaped cells: the *nucleus funiculi teretis,* Meynert's *nucleus medialis.* Its importance is as yet unknown.

The hypoglossus center consists of several groups of ganglion-cells, all bound together by a fine net-work. From its large multipolar cells develop delicate twigs, which, converging like a brush, form a number of small nerve-trunks. From this center there develop fibers, fibræ afferentes, just as from the spinal anterior horns, which cross over the median line; they do not go far over in the other side, however, but extend, after passing the raphé, cerebrally, and within the pons are joined by other fibers (from the facialis center). The combined bundle then passes to the pes cerebri. If this course be, perhaps, a little different from that of the secondary (central) motor tracts in the spinal cord, still it is materially the same: nerve-root, nucleus, decussating tract to pes.

A net-work which binds the parts of the hypoglossal center together is of especial interest; it occurs only in one other center, the motor oculi. There are, however, no other nerves whose fibers are called into action so simultaneously and harmoniously as those of the hypoglossus in deglutition and those of the oculo-motorius in movements of the eyes.

However, there is demonstrable in the prolongation of the hypoglossal net-work, immediately under the epithelium of the ventricle, on both sides, a meshed bundle of medullated nerve-fibers from which fibrils are given off ventrally (to the nerve-centers). This bundle—*fasciculus longitudinalis dorsalis* of Schütz—lies in the bulb between the vagus center and the eminentia teres. It may be traced as far upward as the corpora quadrigemina, where it passes under the fibers of the gray matter surrounding the aqueduct of Sylvius.

In Fig. 240, a representation of the hypoglossal center, Koch, to whom we are indebted for our knowledge of its net-work, has well-shown its wealth of fibers and cells. Ventral from the center are a few cell-groups (Roller's hypoglossal center), from which, however, no hypoglossal fibers arise.

Fig. 240.—Frontal section through the nucleus of the hypoglossal nerve. (After Koch.)

The pyramidal crossing was discovered as early as 1710 by François Petit. The olives were first described by Vieussens. Macroscopic differences in the development of the oblongata from the cord, especially the surface-changes, have been known since Santorini, Reil, Burdach, and Rolando. The nuclei arciformes and their covering, fibræ arciformes anteriores, were first well described by Arnold, who regarded them as "antepons." The striæ acusticæ were discovered by Picolhomini. As to their relationship to the auditory nerve, there arose even before the time of microscopes a lively discussion. Real light on the construction of the medulla oblongata was due to researches of Stilling, Kölliker, Meynert, Schroeder, Van der Kolk, and Deiter. In recent times attention has been given to the nerve-centers there found (Gudden, Roller, Freud, Duval, Koch, Darkschewitch, v. Kölliker, S. Ramón y Cajal, and others).

The existence of this "glosso-pharyngeal center" immediately in front of the vagus center is disputed. It is, in fact, difficult to find by the usual methods the small portion of the nerve dipping into it. The employment of the Golgi method, however, teaches (Held) that the relations met are as just described. When the glosso-pharyngeal nerve is found and has started on its course, one sees that the small column of gray matter, in which it terminated, extends still farther anteriorly. Wallenberg demonstrated in a case of degeneration of the *trigeminus*, in which principally the sense of taste suffered, that fibers coming from this anterior nucleus enter the *trigeminus*. It must therefore be conceded that this long, thin column of gray matter near the *fasciculus solitarius* is the taste-center, and that fibers enter it which run partly in the *trigeminus* and partly in the *glosso-pharyngeus*. The supply of the *dorsum linguæ* with taste-fibers from the glosso-pharyngeal and *chorda tympani* seems, accordingly, to depend upon a single nucleus. The pneumogastric and glosso-pharyngeal very probably have an additional descending root. It comes from the cerebellum, where we have already recognized it as the *direct cerebellar sensory tract*. Exactly which of its fibers reach the vagus is, in man, very difficult to demonstrate. Naturally the sensory fibers of the nerve just mentioned arise from the cells of the root-ganglion, from which they (His) develop, the same here, near the cerebrum, as do the sensory spinal nerves. The sensory cells just mentioned are their end-stations. There the fibrils divide up around cells. On the ventral side of the center one sees many fibers entering in by curves. By the aid of the comparative-development method it has been demonstrated that they arise from the lemniscus-layer of the opposite side. Therefore we have for the sensory part of the vagus (and the same is true of the glosso-pharyngeus) a decussation of its fibers soon after their entrance into the cerebro-spinal axis.

CHAPTER XXIV.

THE MEDULLA OBLONGATA AND THE TEGMENTUM OF THE PONS.

HAVING seen how, through the rearrangement of fibers, and the appearance of new ganglion-groups and the disappearance of the posterior columns, the oblongata is formed, there remain still a number of fibrous tracts to be followed upward from the cord. The posterior columns are continued upward indirectly by the lemniscus, and in it also are to be found those sensory fibers of the second order which ascend in the antero-lateral columns of the cord. The pyramidal tracts from both the anterior and lateral columns lie now united, ventral, forming the thick pyramid of the bulb. The lateral cerebellar tract retains its position at the periphery as high as the olivary body. There its dorsal fibrils begin to turn toward the cerebellum, ascending dorsally. They soon afterward form the nucleus of a large bundle, which first appears here: the *inferior cerebellar peduncle, corpus restiforme.* Its ventral portion occupies its original position as far as the pons, and then turns backward toward the vermis superior.

The corpus restiforme arises laterally from the upper end of the posterior columns, at first because, as just stated, the lateral cerebellar tract there passes upward toward the cerebellum. To it pass also fibers from the posterior columns of the cord, which, as shown in Fig. 233 and Fig. 234 (above, to the left), curve around the postero-lateral periphery of the bulb to join it, *fibræ arcuatæ externæ posteriores.* Other fibers come to them from in front. These, the *fibræ arcuatæ externæ anteriores,* come apparently from the lemniscus between the olives,—hence from the opposite posterior columns,—pass near the median line anteriorly along the periphery, and extend partly ventrally to the pyramids, partly behind them, partly also through them, around laterally to the corpus restiforme. The latter fibers have also been called the fibræ arciformes of the pyramids (Fig. 237). Among them lies a nucleus of varying size, the *nucleus arcuatus* (Fig. 241). Accordingly, to the corpus restiforme there pass from the spinal cord (1) the lateral cerebellar tract, (2) fibers from the corresponding posterior column, and (3) fibers probably from the opposite posterior column.[1]

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[1] The fibers under No. 3 receive their medullary sheaths months before those of the pyramids and olives, probably at the same time as the posterior columns.

In the period of development represented in Fig. 234 only the medullated fibers of the cord are shown. It accordingly shows well the position and extent of this part of the inferior cerebellar peduncle. Fig. 241 also shows the different kinds of arciform fibers.

In the corpus restiforme, however, besides the fibers from the cord, is a second and much larger tract, which, since it is medullated much later than the former, must be differentiated from it. There are fibers to the opposite olivary body. Since they come from the cerebellum, and cannot be traced farther than the olive, they may be known as the *tractus cerebello-olivares* of the restiform body. By their addition the inferior cerebellar peduncle has now become of considerable size.

The *olive, nucleus olivaris inferior,* is a hollow formation of the form of a rather pointed egg whose surface is greatly corrugated. Toward the median line it has a long, broad opening—*hilum nuclei olivaris.* With the much folded cross-section one is already familiar. When fresh, the olive has a gray, transparent color, because it consists principally of a thick mass of neuroglia, in which are imbedded much-branched ganglion-cells. These cells send out a long axial process (Vincenci), and around them arborize the terminations of another fiber-system, from the cells of Purkinje (Kölliker).

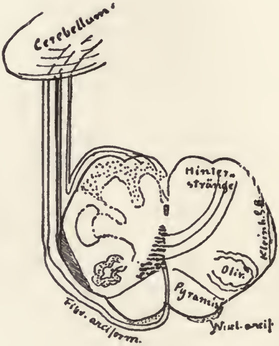

Fig. 241.—Origin of the spinal portion of the corpus restiforme. The fibers end mainly or entirely in the vermis. *Hinterstränge,* Posterior columns. *Klein. S. B.,* Lateral cerebellar tract.

Where the axis-cylinders of the olivary cells go is not yet known. Kölliker thinks they have relations to the lateral columns of the cord.

The tractus cerebello-olivares are large bundles of fibers, which leave the ventral edge of the restiform body, extend in graceful curves downward to the olive, and, then piercing the nucleus olivaris from the outer side, enter the olivary body. Thence the fibers, again collected in a more compact bundle, leave by way of the hilum, cross over the median line, and terminate in the opposite olive. In general, they pursue the same course as the fibræ arcuatæ from the fillet, from which they can be distinguished only after degeneration (Fig. 242). If a cerebellar hemisphere be destroyed, they dwindle away together with the opposite olive. Dorsal to the olive in the region of the substantia reticularis are a few strands of fibers, which are connected with fibers from the net-work surrounding the ganglion, and extend upward in the tegmentum (*Bechterew's central tract of the tegmentum*: Stilling's remnant of the lateral column).

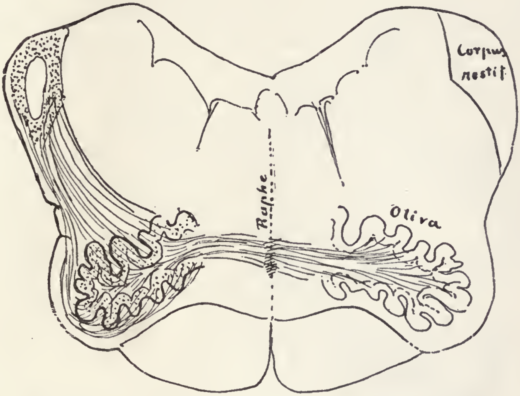

Fig. 242.—The cerebello-olivary division of the corpus restiforme. The blank field in the left restiform body shows the position of the spinal division.

The cerebello-olivary tract of the corpus restiforme comes principally from the outer side of Stilling's "fleece." The latter is, in turn, connected with the superior peduncle of the cerebellum (Brachium conjunctivum) by means of the cerebellar nucleus dentatus, which it surrounds. Consequently it will be seen that the olive, the opposite restiform body, the "fleece," the superior cerebellar peduncle, and the red nucleus of the tegmentum (also of the opposite side) form one conducting path. There is much evidence, such as experiments on animals, which indicates that this path is important for the maintenance of equilibrium and of muscle-tonus. Only mammals have large, distinct olives (*vide* page 98).

At the level of the pneumogastric nucleus in the medulla most of the fibers from the cord have entered the restiform body. Likewise it receives there a portion of the olivary tract. The inferior cerebellar peduncle lies to the side of the last remnant of the posterior columns, forming a thick bundle.

We have here a cross-section typical of the medulla. After knowing the single component parts of this section it will be well to consider them all together. Much additional will appear thereby (Fig. 243).

Ventrally lie the pyramids. The long triangular bundle of fibers, cut across just behind the pyramids, is the *lemniscus* (*fillet*), the decussated prolongations of the posterior nerve-roots. The nuclei of the posterior columns lie posteriorly and laterally, covered only by a few nerve-fibers. Numerous fibræ arcuatæ internæ arise there and crowd through the space between the posterior horns and the fillet to the raphé, and so to the other side.

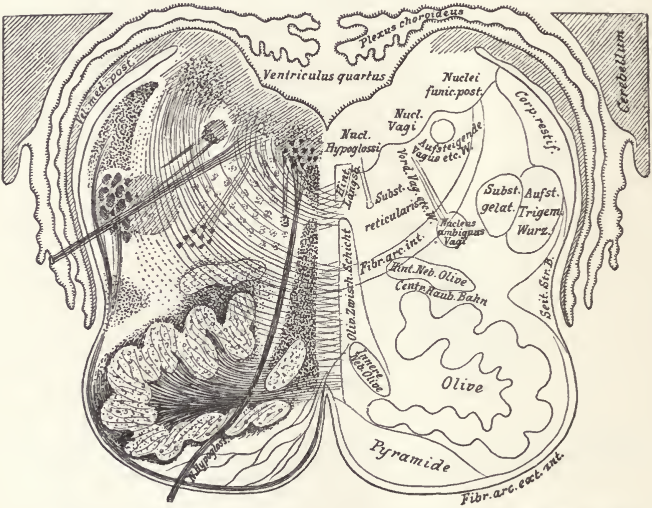

Fig. 243.—Section through the medulla oblongata. *Aufsteigende Vagus, etc.*, W., Ascending root of vagus, etc. *Vord. Vag., etc.*, W., Anterior root of vagus, etc. *Hint. Längsb.*, Posterior longitudinal fasciculus. *Aufst. Trigem. Wurz.*, Ascending root of trigeminus. *Seit. Str. B.*, Lateral cerebellar tract. *Central Haub. B.*, Central tegmental tract. *Oliv. Zwisch. Schicht*, Interolivary layer. *Hint. Neb. Olive*, Posterior accessory olivary body. *Innere Neb. Olive*, Inner accessory olivary body.

A similar course is taken by the cerebello-olivary fibers. In the figure they are represented by dots, but in the adult the two kinds of fibræ arciformes internæ are not to be differentiated. The examination of their periods of medullation first rendered them distinct from each other.

In the median line all these tracts must naturally cross with those from the other side. This line, with its many crossing fibers, is called the *raphé.*

The lemniscus, or fillet, contains in this level, besides the ascending paths of the antero-lateral tract, also the largest part of those coming from the nuclei of the posterior columns. The latter extend further forward into the upper lemniscus.

Notice also in the figure the fibrils passing from the fillet to the opposite vagus nucleus; they are analogous to the decussating fibers from the antero-lateral column to the posterior horn, the secondary vagus path.

Dorsal to the lemniscus we find for the first time again the posterior longitudinal fasciculus, mentioned in Chapter VII. As low as the first cervical nerves its fibers are found deep in the anterior column.

On either side, external to the pyramids, lie the lower olives. They are penetrated by the fibræ arcuatæ, which, as we have learned, end in it in so far as they come from the cerebellum, but pass through it in so far as they come from the nuclei of the posterior columns.

Lateral and dorsal to the olive lie the *inner and posterior accessory olives,* nuclei similarly constructed to the olives themselves, and, like them, are penetrated by the arcuate fibers. Through the first, the internal one, pass the fibers from one olive to the other, while the posterior one is principally pierced by the fibers from the posterior columns, as shown in the figure.

Dorsal to the olive, in the region of the posterior accessory olive, a field of white matter that from now on remains visible in the middle of the tegmentum, may be distinctly followed above, beyond the center of the trigeminus. The whole of its fibers (*central tegmental path*) connects probably the olive with the midbrain (Bechterew).

The dorsal periphery of the section is occupied by the nerve-centers. Innermost lies the nucleus of the hypoglossus, whose fibers, passing through the olivary region, press forward (*cf.* Fig. 240). From the raphé many fibers pass to join it. External to it lies the pneumogastric nucleus. A remnant of the lateral cells of the ventral horn lies as ventral or motor vagus nucleus just anterior to the posterior horn. The fibers arising from it form an angle before their exit, around which roots from the sensory nucleus arborize.

The thin bundle of cross-cut nerve-fibers, lying external to the last-mentioned sensory nuclei, is the combined *vago-glosso-pharyngeal root,* with its nucleus attached.

External to this common nucleus of the two nerves lie the nuclei of the posterior columns, in front of which is the substantia gelatinosa from the extremity of the dorsal horn of the cord. It is bounded externally by a thick, much separated bundle of medullated fibers, which are found in its vicinity from the upper cervical cord, growing larger as they ascend. This bundle can be traced as high as the pons. There it joins with the trigeminal fibers just issuing. Regarding this *spinal root of the trigeminus, cf*. page 364.

The territory between the olive and the nuclei of the posterior columns, bounded externally by the lateral cerebellar tract and the ascending trigeminal root and internally by the fillet, contains, besides the numerous fibræ arciformes internæ a number of short fibers, and, lying between these, scattered multipolar nerve-cells.

The reticular appearance of the bundles of fibers in a cross-section of the medulla justifies the appellation *substantia reticularis*. The group of cells have been named *nucleus reticularis tegmenti* by Bechterew, and it can be traced upward to near the corpora quadrigemina. The cells and the fibers are, as far as we now know, of the same character as the column-cells in the cord; by their much divided axis-cylinders they join different levels of the bulb together. And so the entire system found in the lateral columns of the cord corresponds closely with this in the medulla. It is well, then, to call this characteristic field of the elongated cord the *association-field of the medulla oblongata*. It has already been mentioned (page 80) that upon this wealth of association-fibers probably is dependent the property of the oblongata to co-ordinate various functions, as it does.

If one make other sections of the medulla higher up, the cross-section does not change materially for about two millimeters. One sees that the sensory nucleus of the pneumogastric, extending farther upward, continually receives from the periphery root-fibers in its ventral aspect. From the fasciculus solitarius the fibers of the glosso-pharyngeus pass in small bundles near the frontal end of the vagus nucleus. The restiform body alone here increases greatly in circumference. To it pass in this level the olivary fibers from the cerebellum.

The last sections before reaching the pons (Fig. 244) show that the posterior columnar nuclei have disappeared, and in their place lies the thick mass of fibers of the restiform body. To the inner side of it is a new set of fibers cut transversely, the *direct cerebellar sensory tract*. Where it began is hard to say; perhaps it already existed in the nuclei of the posterior columns. Besides this, in this section we have a *descending acusticus root*. From the corpus restiforme pass fibers to the inferior olive, which in this level is much smaller than below. The lemniscus and the tegmentum occupy the same positions as in the last-described sections. Three new nuclei have come to view. One, occupying the place where lower down the motor fibers of the vagus arose (Fig. 243), sends its fibers dorsally and inward, where they soon collect in a bundle near the median line: the *nucleus facialis*. The second of the three new nuclei lies external to the restiform body. At times we may observe fibers entering it, which come from the dorsally-placed *nucleus acustici dorsalis,* which here begins to be visible, while in the following section may be recognized a very large center, the *ventral*—formerly anterior—*nucleus of the acusticus.* One can see already in this section how it is placed between the cerebellum and the restiform body. A protuberance lateral to it, on the surface of the medulla oblongata, is called the tuberculum acusticum.

Passing upward again, we come to the place where the first fibers of the pons Varolii are ventrally superimposed on the pyramids, coming, as they do, from the cerebellum.

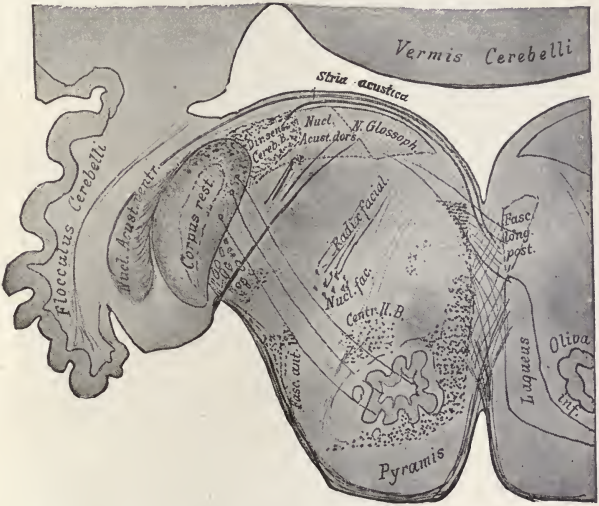

Fig. 244.—The relations of the oblongata to the inferior edge of the pons. *Dir. sens. Cereb. B.*, Direct sensory cerebellar tract. *Centr. H. B.*, Central tegmental tract.

All the following sections, therefore, will show in the ventral portion the greatly intertwined crus portion of the pons. It changes relatively little up as far as the levels described in Chapter XX.

Much more complicated than the crus portion is the tegmental part of the pons. Here begins a locality of the brain in which in a relatively very narrow space are crowded together important structures, the region into which passes the *acusticus,* and from which arise the *facialis* and *abducens.*

The eighth cranial nerve consists of two nerves, which have, as is well-known, different functions. It has been proposed, in view of this fact, to separate the two bundles—nervus cochleæ and nervus vestibuli—and to consider only the first as the auditory nerve, regarding the other as the tonus nerve.

The *cochlear nerve* originates in cells of the spiral ganglion of the cochlea. These cells send out peripherally a delicate branch, which rapidly splits up between the auditory cells (Fig. 16, *b*), while centrally, analogous to the posterior root from the spinal ganglion-cells to the cord, the auditory nerve-root passes: the *nervus cochleæ.*

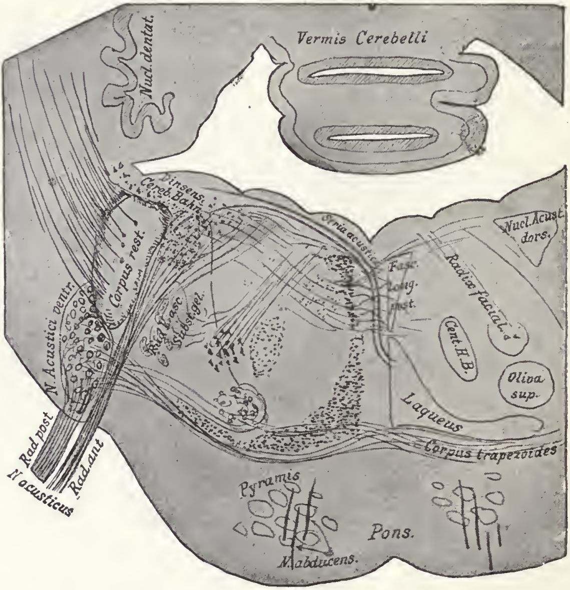

Fig. 245.—The most important features in the region of the origin of the acoustic nerve.

In the section (Fig. 245) one sees how this bundle, earlier known as the *"radix posterior,"* enters with delicate fibers into the above-mentioned *nucleus acustici ventralis.* It divides into a delicate arborization around the large cells of this nucleus. To a less extent it passes into a relatively small ganglion in man, in animals often very large, situated between the cerebellum and pons, dorso-lateral from the cochlear nucleus. This is the *tuberculum acusticum.* This portion also arborizes around cells. And so the primary neuron of the cochlearis terminates in these two places.

From the two primary termini arises a new fiber-tract, which in its secondary and tertiary prolongation reaches eventually the lateral lemniscus, or, rather, forms this lemniscus.

1. The cells of the nucleus ventralis send out their axis-cylinders toward the median line, where they are seen to leave the center as a strong bundle. This tract is called the *corpus trapezoideum.* It lies directly dorsal to the pontile fibers, and in animals, because their pons is shorter than in man, is visible free on the base of the brain (*vide* Fig. 246).

Within the trapezoid body are scattered large cells, *nucleus trapezoideus* (Kölliker), whose axis-cylinders take the same direction as the thick trapezoid fibers of the cochlear nucleus.

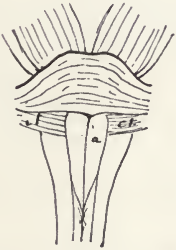

Fig. 246.—Medulla oblongata and pons of a monkey, demonstrating the corpus trapezoideum or trapezium, *ct.* *a,* Pyramids.

The entire, rather important mass of fibers extends to a small group of ganglion-cells, the *superior olivary nucleus,* and as much to the same side as by decussation to the opposite side (Fig. 245). And here, seemingly, the secondary auditory neuron ends. To the upper olive come the fibers of the lateral fillet, a dense arborization. In this way connection between the acusticus and the posterior, perhaps also the anterior, corpora quadrigemina is established.

Degeneration changes (Bumm, Baginski) make it appear that not only the fillet-fibers descending here give off a great many collaterals around the upper olivary nucleus, but also that from this nucleus itself, from the nucleus trapezoideus, and from the striæ acusticæ, presently to be described, pass numerous tracts of fibers into the fillet, and extend upward with it to the posterior corpora quadrigemina. To these would be associated, also, fibers arising in the nuclei situated in the lateral fillet just back of the corpora quadrigemina (*vide* Fig. 206, *b*, outer side). *The lateral fillet, therefore, contains principally numerous neurons from the tertiary acusticus end-stations.*

2. Regarding the fossa rhomboidalis from above, one's attention is drawn to several thick strands which, emerging out of the raphé, extend laterally and lose themselves in the tissues close up to the cerebellum. They do not all arise near together; it occurs rather often that one or another of these bundles arises much farther forward in the floor of the sinus, and extends backward in relatively long reaches, before it joins the other bundles at the level of the *acusticus.* This striation is called the *striæ acusticæ;* to the long, occasionally aberrant bundle in front Bergman has applied the name *conductor sonorus.*

While the first division of the cochlearis is connected with the fillet through the medium of the corpus trapezoideum and the upper olive, it is different with the part ending in the tubercle. This sends its strands direct into the secondary acusticus tract, in the opposite fillet, and these fibers are, in fact, the striæ acusticæ.

Following their course more topographically, the striæ arise out of the *tuberculum acusticum,* situated between the pons and the cerebellum, and to a smaller extent from the large cochlear nucleus (nucleus ventralis in the figure), and then pass laterally around the corpus restiforme, just under the ependyma of the ventricle toward the median line. Near the raphé they dip down deeper, and, while in the raphé itself, they turn anteriorly and cross over to the opposite side, where they join the lateral fillet, considerably augmenting its volume.

Monakow saw atrophy of the striæ after destruction of the opposite lateral fillet high up near the corpora quadrigemina. Bumm and Baginsky observed them degenerate toward the corpora quadrigemina after destruction of the cochlea. The lateral fillet must, therefore, contain fibers running in opposite directions.

It will be seen that the point of greatest importance in this complicated arrangement is that the nervus cochlearis, after once terminating in the nucleus cochlearis and the tuberculum acusticum, has a higher tract going to the posterior corpora quadrigemina. It runs by way of the lateral lemniscus. Still, only a portion of its fibers enters the lemniscus directly through the striæ; a second very considerable portion passes first to the oliva superior, traversing the trapezoid body, and thence arises the tract, which enters the fillet and there joins the fibers from the striæ acusticæ.

The upper olives, interposed as they are in the central auditory nerve-fibers, must be centers of importance. Their constant occurrence through the entire list of mammals, their frequently large development, and, above all, the wealth of fibers entering into relation with them are evidence of this. Among these are fibers from the cerebellum, still but little understood, and a large strand from the center of the nervus abducens, well represented in Fig. 248. Since in this center of the sixth nerve, however, fibers end which pass through the fasciculus longitudinalis posterior to the centers of the

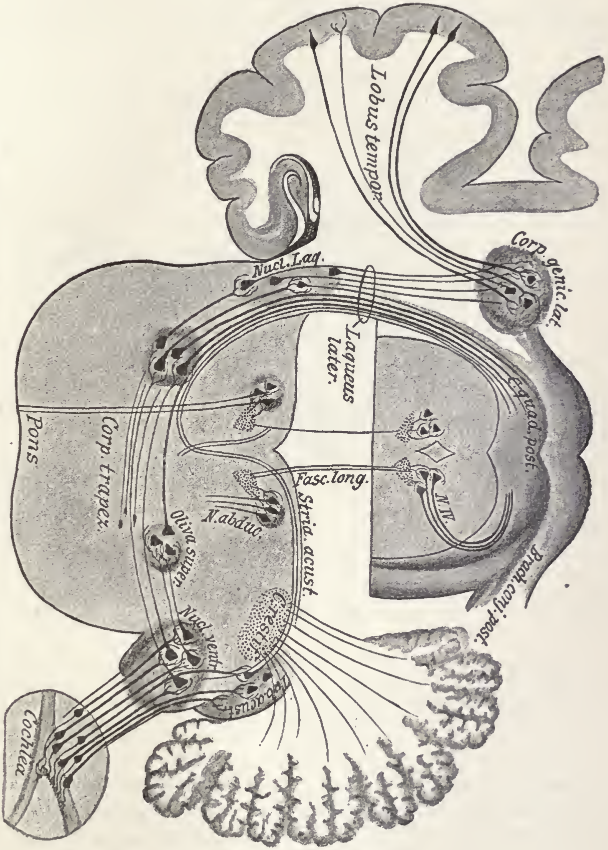

Fig. 247.—Schema of the course of the cochlear nerve. Simplified as far as possible, retaining only the necessary features. For example, with tracts having a double course there is indicated only one fiber.

other motor nerves of the eye and to the thalamus, there is here apparently a well organized, synergetic apparatus, well deserving further experimental research.

Much less is known of the other branch of the eighth nerve, the *nervus vestibularis*. It arises from ganglion-cells lying in the labyrinth and also in the nerve-trunk itself. These cells send a small branch into the sensory epithelium in the ampullæ, where it arborizes in extremely delicate filaments around the base of the epithelium, and a second branch into the nerve.

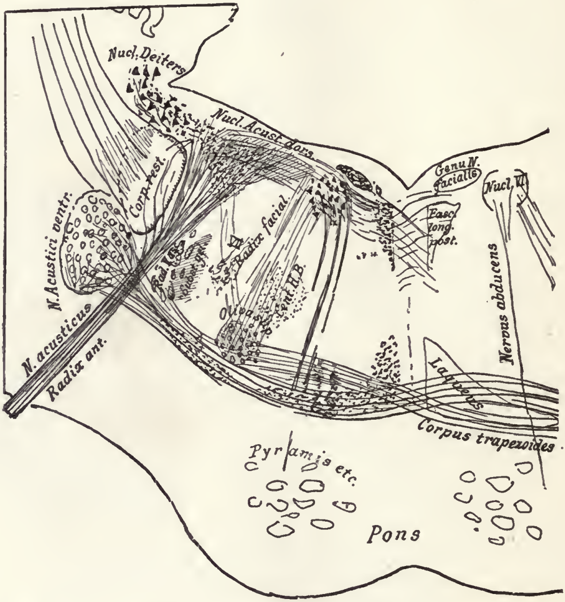

Fig. 248.—Section through the region of the origin of the abducens. Origin of the nervus vestibularis.

Of the two fasciculi converging to the acusticus, the anterior one is the vestibular. It extends, median to the restiform body and the ascending trigeminal root, dorsally through the medulla to the gray matter in the floor of the fourth ventricle. A portion of its fibers ends there with terminal branches in the dorsal nucleus. These fibers, just like the sensory spinal roots entering the posterior columns, before splitting up in the gray matter, emit fibers posteriorly, the *descending root of the acusticus* (Roller). A part of the fibers of the nervus vestibularis does not end in the dorsal nucleus, but is distributed to nuclei, as yet insufficiently known, lying between the vermis cerebelli and the medulla oblongata.

The nucleus dorsalis, *nucleus nervi vestibularis,* is an elongated body, prismatic on cross-section, which appears in sections lower down, where the anterior vagus root is given off (*vide* Fig. 244).

Of the other end-stations, at present the most certain is Bechterew's nucleus, which lies in the lateral wall of the ventricle median to the fibers of the corpus restiforme rising to the cerebellum, and which extends in scattered gray clumps upward to near the cerebellum.

The vestibular nerve has, too, a large number of anatomical relations with other regions of the brain. The nucleus dorsalis is connected with the superior olive by one tract, and with the cerebellum by another issuing laterally. About the cerebellar relations of the vestibular fibers, which extend farther upward above this nucleus, we know, as yet, nothing certain.

The origins of the acusticus, which remained long obscure, have been studied in late years by different investigators, who did not all arrive at the same conclusions as those given here, the results of personal examinations. Freud and the author, working on human embryos, came to practically the same conclusions; Bechterew and Flechsig contend that the anterior root does not come from the dorsal nucleus, but rather from cells in the neighborhood of Deiter's nucleus. The origin of the posterior root in the ventral nucleus is admitted by all. This nucleus becomes atrophic after pulling away the auditory nerve (Forel, Onufrowics, Baginsky). We are indebted to Kölliker for a very exact examination of the entire apparatus.

Retzius and Gehuchten have studied the end-branches in the ear, so important to our understanding of the acusticus, and the relations of the ganglion-cells there found. For the finer details as to the arborization in the single nuclei, the directions of Held have been followed; his examination, made prinicpally by the use of Golgi's method, based on earlier studies, has recently been corroborated by Bumm in experimental work.

Lateral from the nucleus acustici dorsalis lies the field of the direct cerebellar sensory tract. From it probably pass fibers to the acusticus. It passes to the cerebellum, occupying at this level the *inner division of the restiform body.* In its substance at this point lies a nucleus, of as yet unknown significance, formerly termed the *external auditory nucleus.* It atrophies when the corresponding half of the cervical cord is cut through (Monakow). Its connection with the auditory nerve is not yet established. For the present it is, perhaps, better to call it *Deiter's nucleus,* after its discoverer, who has rendered such distinguished service in bulbar anatomy.

In those sections which contain the ventral acusticus center the *nucleus of the facial nerve* is visible (Fig. 248). It consists of a long row of cells arranged in groups. From these arise continually fibers, extending dorsally. They are gradually gathered to form a good-sized bundle, which, arrived within the floor of the ventricle, suddenly turns forward, and then as sharply bends around to the external side of the bulb. The root of the facialis accordingly makes a double knee (*vide* Figs. 245, 248, 249, and 250). In this knee is deposited the *nucleus of the abducens nerve.*

To the trunk of the root of the facial nerve pass fibers from the ascending root of the trigeminal. This is, perhaps, important, because we know that from this portion of the trigeminus are derived the sensory fibers for the face.

At precisely the place where the facialis makes its exit from the brain there enters in a thin, delicate nerve-trunk, that has accompanied the peripheral course of the facial. It is the *portio intermedia Wrisbergi.*

Duval first discovered that it arises from the superior end of the glosso-pharyngeal nucleus (Kölliker says from the nucleus of the fasciculus solitarius), and P. Martin and His corroborate this. The latter were able to demonstrate in the embryo that fibers grow into the brain from the ganglion geniculi nervi facialis.

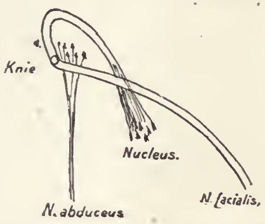

Fig. 249.—Schema of the central path of the nervus facialis and nervus abducens.

The ganglion geniculi—besides being principally a sympathetic ganglion (Lenhossek)—is then the nucleus of origin of the portio intermedia, while the anterior portion of the fasciculus solitarius is its central nucleus.

The *roots of the abducens* arrive by several extended bundles, which pass through the tegmentum and the pons, at the base of the pons externally. On the median side the nucleus is connected with the posterior longitudinal bundle. It is claimed, though not well proved, that these fibers higher up enter the opposite motor-oculi nerve. Without doubt, however, there is a remarkable connection between the abducens nucleus and the superior olive. This connecting tract, which is shown in Fig 248 parallel to the root of the facial, must place the acusticus in connection with the motor nerves to the eyes, and is, perhaps, of importance for the maintenance of position in space.

Before ascending farther it will be well again to consider the above-mentioned, but not particularly described, tegmental region, and to learn its position and relations in this level. One feature, the nucleus reticularis tegmenti, which lies with the fibers of the substantia reticularis scattered over the region between the raphé and the facialis root, is not included in the illustrations, in order to preserve their clearness. It is to be found, however, in all the sections thus far considered.

The accompanying Fig. 250 follows the sections just described, and is to demonstrate how the facialis turns about after coursing a short distance ventrally, and how the direct sensory cerebellar tract now passes upward into the cerebellum.

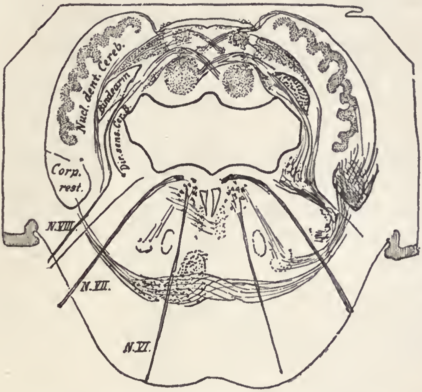

Fig. 250.—Section at the place where the inner division of the corpus restiforme merges into the cerebellum.

In the cerebellum are to be seen in this level the peduncles coming from in front.

When the acusticus, the facialis, and the abducens leave the tegmentum, the cross-section appears naturally much more simple.

We come to the place of entrance of the *nervus trigeminus,* and first the motor nucleus of the trigeminal appears in the continuation of the nucleus facialis, though somewhat more dorsal. From it arises, also by a slight "knee," the *motor root,* the portio minor, supplying the muscles of mastication. Probably there pass with it fibers coming from the opposite motor nucleus, which cross over the raphé.

With the motor trigeminus, course, also, fibers from the pons, which arise, not in the motor nucleus, but high up in the quadrigeminal region, where laterally from the aquæductus Sylvii (in Fig. 199 above to the left) scattered ganglion-cells give rise to the *radix mesencephalica nervi trigemini.* These cells continue downward always in the lateral wall of the canal, and one can detect a more considerable collection of them through the thin ventricular ependyma, forming a dark bunch on either side at the beginning of the fourth ventricle. It is there called the *locus cœruleus.*

The nucleus of the motor nerves of mastication is made up much the same as the other motor centers in the spinal cord. Lately, however, S. Ramón y Cajal has discovered in it a peculiar arrangement. The root from the midbrain, coming from the large, swelled cells around the aqueduct, gives off to the large motor main nucleus a great number of extremely fine collaterals. Each cell there is surrounded by a very thick net of such fibrils. The discoverer of this remarkable arrangement is of the opinion that it is possible by these collaterals for a relatively weak impulse, originating in the higher nucleus, to be transformed in the main, or lower, nucleus to a powerful stimulus. The large motor cells might be, as it were, laden, and at times simultaneously discharged, bringing about the strength and the co-ordination of the act of mastication.

The *main portion of the nervus trigeminus,* the sensory, arises, without doubt, from the cells of the Gasserian ganglion, whose peripherally directed branch forms the nerve, just as in the spinal ganglion-cells, while a thick "root" running centrally enters the pons. It penetrates this and disappears, to a small extent, in the nucleus there situated (*sensory trigeminal nucleus*).

As the fibers enter the nucleus the majority of them split into a delicate ascending branch and a descending one. The former terminates soon in the part of the nucleus above where the fiber enters, forming a delicate arborization; the latter terminates more gradually, giving off large numbers of collaterals, and the nucleus in which this occurs, the caudal continuation of the nucleus just mentioned, is unusually long and extends, as the *nucleus terminalis nervi trigemini,* as far downward as the cervical cord. Throughout its extent it is accompanied by the mass of trigeminal fibers, naturally growing continually thinner. Their cross-section is seen in all the series from the cervical cord up, as a slender, crescentic bundle. This *tractus bulbo-spinalis nervi trigemini* is in close proximity to the long, vitreous column of the nucleus, as far as the posterior horn of the cervical cord, and there finally vanishes.

In Fig. 251 is shown a schematic representation of the tracts of the separate trigeminal roots. Many of the details included are after preparations by Ramón y Cajal.

From the long bulbar nucleus of the sensory portion of the trigeminus arises the *secondary trigeminal tract.* Several years ago, based on investigations in comparative anatomy, it was demonstrated that there is a decus-

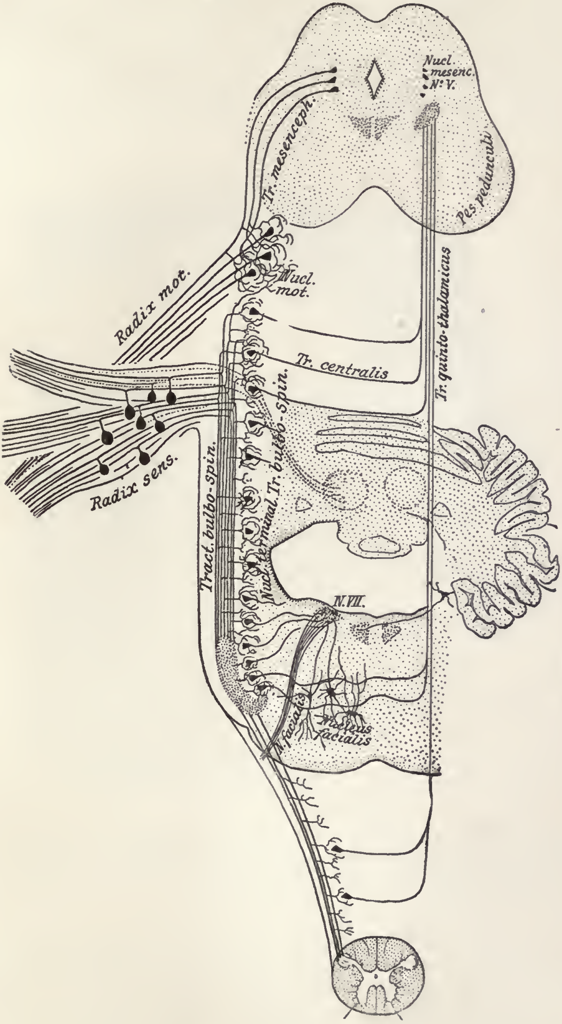

Fig. 251.—The origin of the nervus trigeminus.

sating path reaching upward from the bulbar trigeminal nucleus. The fibers, which throughout its extent leave this nucleus and cross over the median line, have since then been frequently seen; but only lately Wallenberg succeeded in making a section of them and demonstrating where the central path of the trigeminus lies in the brain and where it ends. His examinations were made on rabbits. It was seen that the degenerated path, appearing after separation of the bulbar nucleus, was within the great association-field in the lower bulbar sections, close under the hypoglossal nucleus, on the opposite side to the lesion, and was connected with it by long, curved fibers. Higher up one finds it gradually taking a more lateral

Fig. 252.—Section at the place where the ascending trigeminal root turns around externally. Trigeminal roots. *Dir. sens. Cerebellarbahn,* Direct sensory cerebellar tract. *Centr. V. Bahn,* Central tract of fifth nerve. *Centr. H. B.,* Central tegmental tract.

position and somewhat ventral to the posterior longitudinal bundle. In man one finds in the same place as in rabbits a large number of transversely-divided fibers (Fig. 201, *a*). But the demonstration by the degeneration-method is wanting to show their connection with the trigeminus. Compare, also, the area in Fig. 199, marked "*aus Thalamus.*" In the midbrain one finds the central trigeminal path lateral to the descending fibers of the posterior commissure, and they may be finally traced, according to Wallenberg, into the ventral nucleus of the thalamus, where it approaches the upper fillet, or its end-station.

S. Ramón y Cajal discovered the same path independently of Wallenberg, at least in its place of origin, and has given us an exhaustive description of the structure of its bulbar nucleus. This contains a multitude of conspicuous multipolar cells. Around these peripherally arborize the fibers of the trigeminal root, and from these cells arise the axis-cylinders of the central tract. Of these the majority pass over to the other side, as stated above, and there extend upward as the most dorsal bundle of the substantia reticularis, a smaller number, however, according to R. y Cajal, remaining on the same side. There is here a contradiction to the results furnished by the degeneration-method of experiment.

From the central trigeminal path issue numerous collaterals to the facial nucleus, furnishing the sensory-motor reflex-arc for the face. Section of the trigeminus is, therefore, accompanied by not inconsiderable motor disturbances in the face, due to the loss of the sensory control.

The main branch of the fifth, where it enters the pons near the motor nucleus, is called the *portio major*. In this portio major trigemini are included also the fibers of the direct sensory tract descending from the cerebellum.

From the exit of the fifth up to the exit of the trochlearis the pontile tegmentum presents a relatively more simple structure than that we have learned lower down. In the last section demonstrated the corpus restiforme began to separate from the great mass of the cerebellum. It leaves it entirely now and approaches on either side laterally to the tegmentum, thus forming its outermost boundary in the dorsal area.

The lateral boundary further ventral, just over the pontile fibers, is formed by the *lemniscus*, and more especially by that part of it coming from the cell-bodies of the sensory nerves, is distinguished as the *lateral* or *inferior lemniscus*, as differentiated from the median portion, which comes mostly from the nuclei of the posterior columns of the cord. The frontal portion of the tegmentum is imbedded in the lemniscus fibers, as in a trough (Fig. 253). The horizontal part of this trough belongs mainly to the median lemniscus. It separates in wide extent the tegmental fibers from the already numerous fibers of the crura in the region of the pons. And so arises again the picture of the quadrigeminal region, already considered, and it remains so on upward.

The median fillet extends at first in the lemniscal layer upward, and finally arrives, as has been described, frontal to the corpora quadrigemina in the area ventral to the thalamus, where it ends in the ventral nucleus of the thalamus.

The lateral fillet—which contains besides the acusticus-fibers, all the fibers from the deep bulbar nuclei of the sensory nerves to the roof of the mesencephalon—in the levels above the exit of the trigeminal turns out of the lemniscus layer dorsally, and extends on the external side of the pontile tegmentum, diagonally upward to the corpora quadrigemina, under which it disappears. Its well-marked band is easily recognizable laterally in the uninjured cerebral axis. Where the fillet turns dorsally are found its ganglion-cells imbedded (*lateral lemniscal nucleus,* Obersteiner). This group may be traced anteriorly as far as the *superior nucleus of the lemniscus,* situated on the outer edge of the substantia nigra.

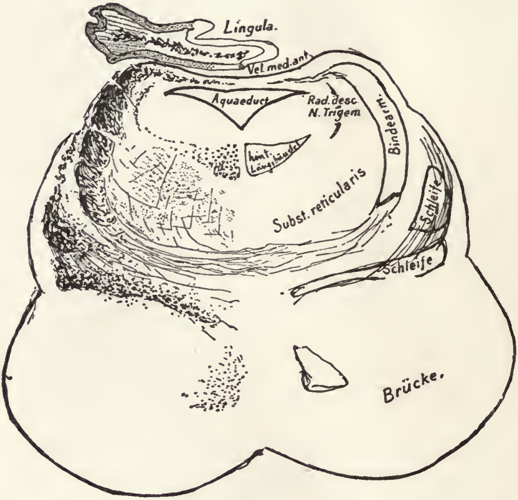

Fig. 253.—Section through the upper region of the pons, in a nine-months' fetus. *Bindearm,* Anterior peduncle of cerebellum. *Hint. Längsbündel,* Post. longitudinal fasciculus. *Schleife,* Fillet. *Brücke,* Pons.

Flechsig and Hösel have proved that the median fillet ends in the nuclei of the posterior columns of the cord. They consider the whole bundle direct from the cerebrum as the *cortical fillet*. It has already been stated that the cerebral tract, here concerned, ends in the ventral thalamic nucleus, and that there the median, or superior, fillet arises.

So we have lemniscal fibers to all the sensory bulbar nuclei. *The lemniscus contains, therefore, the secondary sensory fibers, and conducts them upward to the mesencephalon and the thalamus.* Monakow succeeded in demonstrating the experimental proof of this at the same time that the author called attention to it from comparative anatomy. In experimental production of degeneration the fillet may, indeed, be separated into its various bundles for the different nerves, trigeminus, acusticus, etc.

In the same horizontal level as the fillet, dorsal to the pons, one finds, near the median line, another bundle of thick fibers. It comes from the pyramidal region of the crura. It has already been shown how it separates there, and, passing around the entire crus internally, reaches the median side of the fillet. Spitzka, from comparative anatomy, has made it seem probable that this bundle contains the central paths of the motor cranial nerves. As a matter of fact, one can convince himself that from it fibers ascend continually toward the raphé, and can see on the dorsal end of the raphé fibers crossing over the median line to the nuclei, at least to that of the hypoglossus.

We arrive now gradually in the region of the pons, where the roof of the metencephalon is no longer formed by the cerebellum, but rather by the velum medullare anticum. Here the fourth ventricle begins to narrow down into the aquæductus Sylvii.

The single component parts of the tegmentum in this level appear distinctly in the accompanying, not schematic, transverse section through the uppermost portion of the pons in a fetus of nine months. In the crus at this time there is but a small bundle of medullated fibers. In the tegmentum, however, the lemniscus, the brachium (superior cerebellar peduncle), the posterior longitudinal fasciculus, and many fibers of the substantia reticularis are completely developed. The brachium passes directly into the velum medullare anticum, on which rests the anterior part of the lingula. Below, above the lemniscus, can be seen the hindmost fibers of the brachia crossing.

The descending trigeminal root lies on either side of the aqueduct as a thin bundle of fibers. Median to it, underneath the floor of the fourth ventricle or the anterior portion of the sinus rhomboidalis, must be imagined the cells of the locus cœruleus, which were not distinct in the preparation copied. The substantia reticularis here consists principally of longitudinal fibers, which can be followed upward only as high as the anterior quadrigeminal bodies. Near the middle line on either side lies the fasciculus longitudinalis posterior. From this point on to the quadrigeminal region there are no important changes in the appearance of the cross-section of the tegmentum. The fillet extends dorsally on the outer side. The brachia retreat toward each other, and finally decussate higher up.

The fibers of the crus, and those of the pons passing through it, have been considered. It remains still to be said that in the superior levels of the pons there is a system of fibers which becomes medullated shortly before birth, rising out of the pontile fibers through the raphé, and then emitting its fibers right and left in the substantia reticularis of the tegmentum. According to Bechterew, these fibers end in the foremost part of the nucleus reticularis.

Ganglia, similar to those of the pons, are scattered on both sides of the raphé, and in it as far upward as the tegmentum.

CHAPTER XXV.

FINAL REVIEW.

THE preceding chapter treats of the tegmentum, in continuation of the subject of the eighth chapter.

A few millimeters anterior to the last-described sections the fibers of the crus cerebri appear out of the pons, and extend to the cerebrum as the pes pedunculi. In the medulla oblongata the pyramids formed the single factor in the formation of the crus; but from the pontile ganglia are developed the thick tracts, which extend in the median and lateral divisions of the crus upward to the temporal lobe and to the frontal and parietal cortex.

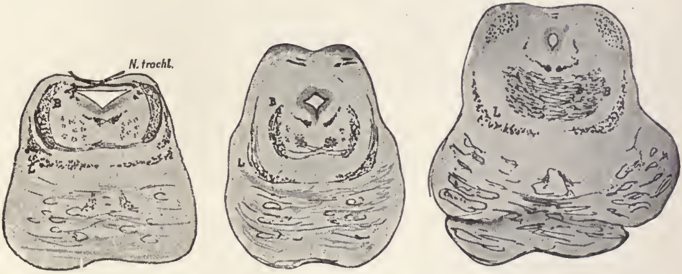

Fig. 254. Fig. 255. Fig. 256.

Three sections through the pons and corpora quadrigemina of a newborn child, demonstrating the course of the cerebellar peduncles and the lemniscus. The latter lies closely above the pontile fibers; the peduncles (*B*, Fig. 254) appear farther internal in Fig. 255, and their decussation begins, and in Fig. 256 is at its greatest. Hæmatoxylin stain.

There appears at this level in the crura, between the tegmentum and the crusta, and separating them, the substantia nigra.

The peduncles of the tegmentum are lost in the red nucleus. In the place of the velum medullare anticum the corpora quadrigemina form the roof.

A few schematic representations may elucidate the manner of transition from the pons to the midbrain.

The symptoms appearing in affections of the pons and oblongata form, in their various groupings, the proofs of the anatomical relations, herein described.

In a small compass are collected here the most important paths for the movements of the body-muscles, for sensation, for the movements in speech, for those concerned in deglutition, etc. A lesion needs not to be very large here to produce the most varied symptoms.

The central motor and sensory tracts, arising in the cerebral cortex, in the thalamencephalon and mesencephalon, extend through the pons and oblongata, giving off there only such fibers as pass to the nuclei of the cranial nerves.

Since interruption to these long tracts produces the same symptoms, no matter if it occur in the forebrain, midbrain, or after-brain,—namely, anæsthesia or paralysis on the opposite side,—it is important to remark that one may only suspect a lesion of the sensory or motor paths in the *pons oblongata* when simultaneously there are present symptoms which indicate that one or more cranial nerve-nuclei are involved.

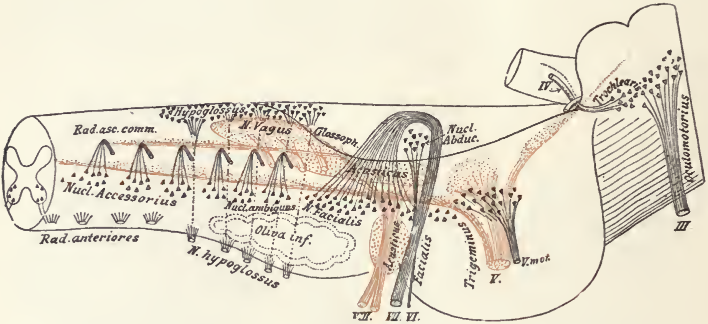

Fig. 257.—Position of the nuclei of the cranial nerves. The oblongata and pons to be imagined as transparent. The nuclei of origin (motor), black; the end-nuclei (sensory), red.

Muscular atrophy, which appears only in affections of the nuclei, must be carefully sought, if it requires to locate the place and extent of such an affection. Fig. 257, representing the position of the nuclei in a longitudinal section of the oblongata, facilitates in such localization rather more than the preceding cross-section.

Speech, respiration, and deglutition will be probably disturbed by an affection of the oblongata; paralysis of mastication (motor part of the trigeminal), of the facial, or of the abducens, by one of the pons.

But since the central fibers going to the centers of the oblongata pass through the pons, affections of the latter may occasionally provoke troubles of deglutition, etc.

The motor paths to the extremities lie ventral in the pyramids, and do not pass over to the other side until much later, just above the spinal cord. The motor fibers for the cranial nerves, however, lie near the median line, ascend in the raphé of the tegmentum, and cross over in proximity to their respective nuclei.

A disease-focus in the pons will affect, accordingly, in the majority of cases, the opposite extremities, but the facial, abducens, or trigeminal of the same side as itself.

Fig. 258 may show better than words this most important symptom of many lesions of the pons and medulla, viz.: crossed paralysis. It represents the motor supply to the nerves of the face and extremities. It will be seen that a lesion at *A* in the cerebrum, or in the right pes cerebri, would paralyze the left facial and the left extremities; but that one at *B*, in the territory of the pons on the right side, would paralyze the left extremities as before, but may affect the right facial; again, that such a lesion extending slightly over the middle line might render both facials and the extremities of one side helpless. It will also be seen that a lesion in the pons at *C* may affect the fibers going to the opposite side of the face as well as those to the opposite extremities, not producing an alternating hemiplegia, but a direct one, just as if situated higher in the cerebrum. Crossed hemiplegia can only be produced, except when there are several lesions present, by affections of the pons or by tumors, etc., located ventrally to the pons, destroying the cranial nerves in their periphery and the pyramidal tracts. Since, besides the facial, the nuclei of the sixth and fifth nerves lie in the pons, it follows that they also may partake in the varied forms of paralysis induced by pontile lesions. The behavior of the acusticus in this connection is not clearly understood.

Through the pons also there pass fibers to the nuclei of the oblongata, which preside over the muscles concerned in speech. In this way, with affections of the pons and bulb, there arise at times disturbances of speech, while the power of speech remains intact. This symptom is called, according to its severity, dysarthria, or anarthria.

Lesions in the tegmentum of the pons and the bulb may also lead to disturbances of sensation. We have reason to believe that the central sensory paths lie in the lemniscus, and that the median fillet especially contains those fibers which serve the very important static sensation. Accordingly, after interruption of the interolivary tract in the oblongata light disturbances of the muscular sense are observed. But later clinical investigations make it appear probable that, at least in the bulb, the tracts for cutaneous tactile sensation do not lie in the median portion, but belong to the long tracts, lying external to the interolivary tract. In the pons, also laterally located lesions may produce crossed sensory disturbances. If the lesion be somewhere in the tegmentum of the bulb or pons, it affects not only those central tracts, which pass to nuclei of the opposed side, but also the peripheral parts of many sensory nerves. For instance, a lesion located laterally in the oblongata may encounter on the right side the ascending trigeminal root, and the crossed sensory tracts, resulting in right-sided facial and left-sided body anæsthesia.

Generally a single focus does not destroy all the central and peripheral sensory tracts; hence occasions no such complete hemianesthesia as occurs with disease of the centrum ovale. One or another nerve remains usually free. This is especially true of the taste-tracts and of the auditory tracts, in which complete intrapontile interruption to the conducting paths has been seldom known.

If a lesion, relatively large, is located anywhere near the median line, there may result naturally double hemianesthesia: at all events, a rare occurrence.

Difficulties of mastication and of deglutition are observed since the motor trigeminal, the glosso-pharyngeal, and hypoglossal nuclei are easily involved.

It is often difficult to decide whether a disease-focus be located in the oblongata or in the pons. By reason of the position of the motor vagus, spinal accessory and

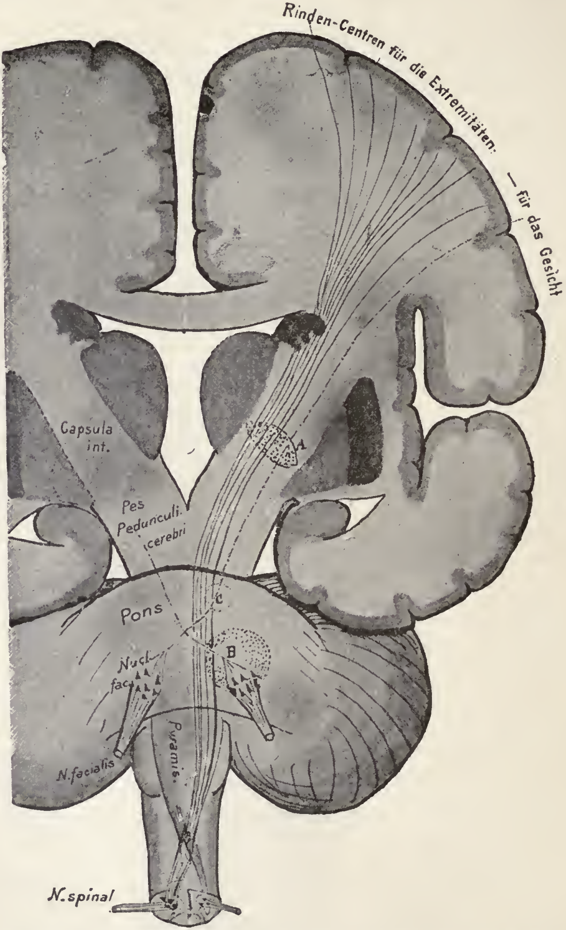

Fig. 258.—Schema of the motor path for the facialis and the nerves to the extremities. Frontal section through the cerebrum, pes pedunculi, pons, oblongata, and spinal cord. *Rinden-Centren für die Extremitäten,—für das Gesicht,* Cortical centres for the extremities,—for the face.

glosso-pharyngeal nuclei, hoarseness, aphonia, and respiratory troubles are observed principally only in lesions of the oblongata. Speech-difficulties—dysarthria, anarthria (nucleus nervi hypoglossi)—and circulatory disturbances occur also more often in affections of the oblongata.

Nearly all those symptoms can, in rare cases, be caused by troubles of the cerebrum, since lesion of the central course of the cranial nerve-fibers leads to paralysis the same as that of the nuclei or the peripheral nerves themselves. Paralysis of the various muscles supplied by nerves from the bulb can only with certainty be referred to a lesion in the oblongata, when accompanied by muscular atrophy and when destruction of the respective nerve-trunk after its exit from the central axis can be excluded.

In the presence of cases which, through a combination of symptoms,—participation of widely-spread tracts and only certain cranial nerves, alternating sensory or motor symptoms,—suggest that the lesion must be in the oblongata or the pons, it will be serviceable to study the illustrations given above, to determine whether there is any place whose destruction might cause all the symptoms. In this way it will be possible in many cases to determine fairly exactly the location and size of the lesion. It should not be forgotten, however, to consider the basal aspect of the brain, as there disease-processes may produce pressure on the longer tracts as well as destruction of the nerve-trunks.

With this we have practically finished our task. A large number of important fiber-systems have been studied in their relations to the central gray masses, and in their course from the cerebrum to near the end of the midbrain, or from the spinal cord upward to about that point. But it may be of assistance to consider certain ones again briefly in their interrelationships, because they are of particular interest physiologically and pathologically, or because the general view of their relations to each other was impeded by the interruption, after Chapter XX, of the series of investigation, due to didactic interests.

The following is, then, in the nature of a repetition: a short representation to be used with the illustrations:—

1. **The motor nerves** are the continuations of the axis-cylinders of the great ganglion-cells in the motor nuclei of the spinal cord and brain. Around these ganglion-cells arborize the terminals of the central motor paths. These run, at least to a large extent, in the pyramidal tracts.

2. **The pyramidal tracts,** the most important of the motor paths, arise from the upper two-thirds of the central convolutions and the paracentral lobule and extend downward to a place just behind the knee of the internal capsule. From there they enter the pes cerebri, occupying its middle third. Below this, in the pons, their fibers are but little separated by transverse fibers. When they emerge from the pons their fibers form two large bundles in the ventral portion of the medulla oblongata. So they descend to the spinal cord, where the larger portion of their fibers crosses over to the lateral column, while a smaller portion (anterior pyramid) remains on the same side. Both tracts enter into relationship with the cells of the anterior horn of the

side opposite to the origin of the pyramids in the cortex, by means of collaterals. From the cells in the anterior horns arise the motor roots.

3. The central path for the motor cranial nerves is better known for the facial and hypoglossal.

The *facial tract* arises in the region of the lower third of the central convolutions, probably only for its lower branches, the source of the frontal part of it being unknown (gyrus angularis?); extends from there inward transversely over the nucleus lentiformis, and arrives very close to the pyramidal tract in the internal capsule. At any rate, in the pes cerebri it is clinically not distinguishable from the pyramid. Its fibers then leave the general motor tracts probably with the familiarly called "bundle from the crusta to the tegmentum." Certain it is, that in the pons it is separated from the other motor paths (see Fig. 258). How it reaches the nucleus is as yet unknown. But it finally arrives at the crossed facial nucleus in the inferior portion of the pons. From this arises the nerve.

In the most ventral part of the anterior central convolution probably lies the cortical area for the *hypoglossus*. From this region, at least, there passes downward a bundle, ventrally to the facial fasciculus, whose interruption has caused at times bilateral hypoglossal disturbances. As it extends from the cortex to the capsula interna it passes over the upper edge of the nucleus lentiformis, and must lie in close proximity to the speech-fibers just external to the beginning of the tail of the caudate nucleus. In a case observed by the writer, a focal lesion of about the size and thickness of a dime interrupted both tracts at this place. In the capsule the hypoglossal fibers probably run between those of the facial and those for the extremities. Within the pons its fibers must be separated from the pyramid, and probably pass in the above-named bundle median to the fillet, posteriorly and upward in the raphé. It joins the opposite nucleus (and that of the same side?) after reaching the oblongata, and from the nucleus arises the nerve.

4. The motor speech-tract. Of this we know certainly but few facts: the starting-point in the lower frontal convolution, the termination in the nuclei of the facial and hypoglossal, and an intermediate point, lying external to the tail of the caudate nucleus. Probably (Wernicke) this tract extends from Broca's convolution—the inferior frontal—somewhat internally and in a nearly horizontal direction dorsal to the capsula externa, under cover of the insula. Its fibers then arrive in the portion of the internal capsule posterior to the general motor paths and then in the pes cerebri. In the pons they must rise gradually out of the crusta and into the tegmentum. In all of these places mentioned disease produces disorders of speech.

Every motor nerve then arises in a nucleus in the central organ. The nerve and its nucleus form the first division of the path; to the nucleus there extends

from the cortex of the cerebrum the converging pyramidal fibers, as the second division of the chain: nerve, nucleus—pyramidal tract, cortex.

As long as the first division remains intact, the corresponding muscles may be made to contract by electric, mechanical, and reflex irritation in animals, even also to a certain degree by voluntary impulse; if nerve or nucleus be destroyed, however, positive paralysis results.

To a complete voluntary ability it is necessary that both divisions be sound; indeed, with the highly developed brain of man when the second division is interrupted there is no movement possible as a result of the will. When one suffers a stroke of apoplexy with tearing of the internal capsule, the muscles of the opposite side of the body are not really paralyzed; they can no longer be brought into contraction by the will, but may by other means. It is different when in infantile spinal paralysis, for example, a nucleus itself is destroyed; then follows a real paralysis, which, generally irreparable, leads to atrophy, and reacts but little to reflex or other stimulation. It makes a great difference as to the prospect of the recovery of function whether the cerebral tract be interrupted or some place lower down.

5. **The coronal fibers to the pons** arise from the cortex cerebri, especially the temporo-occipital lobe; perhaps also from the frontal lobe. They extend through the internal capsule to the crusta of the pes and then to the pons. Experiments made by the degeneration method show that they extend no farther than to groups of ganglion-cells there found. But to these same groups one can trace fibers coming from the opposite half of the cerebellum (cerebellar peduncles).

6. **The sensory nerves** arise from cells in the spinal ganglia. At least in vertebrates no other origin has been demonstrated for them. Since we know, however, that the optic and olfactory nerves contain fibers which, arising from sense-epithelium, pass centrally; since, further, it has been shown in invertebrates that there are fibers arising out of epidermal sense-epithelium, it were not impossible that there should be fibers in sensory nerves which originated in the periphery. The process of secondary degeneration after section of the nerve speaks against this supposition.

From the cells of the spinal ganglia arises a second tract: the spinal root, which enters into the cord. A part of the root splits up in the posterior horns, or, it may be, in the nuclei of the cranial sensory nerves, arborizing around cells (distal nuclei of the sensory nerves).

Another portion first courses a distance in the central organ, either upward, as the spinal nerve-fibers of the posterior columns, or downward, as many roots of the cranial sensory nerves, before it ends in distal nuclei.

From the cells of these nuclei arises the *central sensory tract*, or the tract of second order. It arrives either at the level of the entrance of the root into the central axis, or higher up, always in the territory of the decussated lemniscus. But it extends toward the cerebrum with the lemniscus.

7. We do not yet know the cells of origin nor the terminations of

the sensory paths of second and higher order. Those of higher order lie in the **median fillet from the thalamus,** and in the **lateral fillet** or the **fillet of the corpora quadrigemina.**

The fibers, arising in the nuclei of the posterior columns, perhaps also those arising in the nuclei of the spinal cord, extend in the median line within the lemniscus tract upward, and terminate in the ventral portion of the thalamus opticus. The fibers from the nucleus of the trigeminus have the same terminus, but they extend to the thalamus, not through the lemniscus tract, but more dorsally and median. Besides the ending of the median fillet, the tegmental radiation from the parietal lobe also ends in the region of the thalamus. By it is established a connection between the sensory nerve and the parietal lobe of the brain. It presents a tertiary sensory path.

The tegmental fibers arise in the parietal lobe, possibly in the same convolutions as the pyramidal fibers, and from there extend to the posterior third of the internal capsule. In this region are joined to them the *visual radiation* of the occipital lobe and the *central auditory path.* A part of the tegmental tract extends inward (to the right). A second portion extends to and through the lentiform nucleus; another arrives at the thalamus.

The central fibers from the nuclei of the cranial nerves, perhaps also some from nuclei of the spinal nerves, ascend in the inferior or lateral fillet. These end, in large part, in the ganglia of the corpora quadrigemina, and in another part in the median corpus geniculatum, here principally the acusticus paths of higher order.

To these nuclei passes, principally from the white substance of the temporal lobe, but also from more anteriorly situated cortical areas, a fibrous tract, the cortical path of the acusticus, etc.

In this manner all the various fibers of the lemniscal tract are connected with their centers, lying on that side which is crossed to the lemniscus. The decussation takes place in the oblongata for one portion, for another in the cord itself. In the nuclei terminate always the fibers of the posterior roots, or the cranial sensory nerves.

8. A portion of the sensory nerves ends in the neighborhood of Clarke's column of cells. From them arises the **direct cerebellar tract,** which extends in the periphery of the lateral tract of the cord up to the cerebellum.

9. Some cranial sensory nerves receive additional fibers, coming from the cerebellum **(direct sensory cerebellar tract).**

10. The cortical area and the central path of the sensory portion of the **nervus trigeminus** from the cortex to the capsula are yet unknown. Following pathological experiences, its fibers must lie in the posterior third of the capsule. The cortical tract of the trigeminal ends, in rabbits at least, in the ventral portion of the thalamus. Leading up to it is a large bundle from the opposite nucleus of the bulb. And in this nucleus itself terminate the processes from the cells of the Gasserian ganglion.

The trigeminus also arises in part from nuclei lying in the central organ itself. So far we know two of these: one in the lateral wall of the aqueduct beneath the corpora quadrigemina; the other, the so-called motor nucleus, lying in the pons.

The ascending root contains the tactile nerves of the face, as is shown by pathology.

11. The nervus acusticus is conveniently regarded as two nerves: the nervus cochlearis and the nervus vestibularis.

The cortical origin of the nerve of hearing, the *cochlear*, must be sought in the region of the temporal convolutions. Clinical observations allow the conclusion that from there a tract leads to the inferior portion of the internal capsule, and probably through the arm of the posterior corpus quadrigeminum to its gray matter. Thence the lateral lemniscus extends downward toward the superior olive in the oblongata, and in this end also the fibers from the nucleus acustici ventralis, the trapezoid body. In this nucleus, however, arborize the end-branches from the ganglion-cells of the ganglion spirale cochleæ: the auditory nerve-roots.

About the central course of the *nervus vestibuli* but little is known. Its fibers, coming from the cells of the macula and the crista acustica, end partly in the dorsal nucleus and extend partly to the cerebellum. Besides, this nerve contains fibers from lower levels of the oblongata, and additions from the lemniscus as striæ acusticæ (compare description given previously).

The *upper olive*, with which not only the cochlear, but also the vestibular, stands in relation, is intimately connected with the nuclei of the motor nerves of the eye and with the cerebellum; probably also with the corpora quadrigemina. It is likely that it belongs to the equilibration-apparatus of the body.

The trigeminus, as well as the acusticus, receives fibers from the cerebellum.

12. Nothing is known about the central tract of the **vagus.** If the much-mentioned place in the posterior part of the capsule be destroyed, vagus symptoms do not appear; instead, there come disturbances of taste (glosso-pharyngeus). The course of the fillet-fibers to the opposite pneumogastric and glosso-pharyngeal nuclei has been mentioned. Both these nerves also probably receive additional fibers from the cerebellum.

13. The central course of the **opticus** has already been considered in its relations.

It may be repeated that this nerve arises from the pulvinar thalami, the corpus geniculatum laterale, the tuber cinereum, and the corpora quadrigemina; that it receives fibers, arising in the retina, which end in the parts of the brain mentioned. To all these "primary optic centers" come fibers from the optic radiations, beginning in the occipital lobe. These extend along the lateral side of the posterior horn, and under the inferior parietal lobule, on their way from the cortical origin to the primary optic centers. From this fact arise visual disturbances, having the character of cortical lesions, which have been noticed in disease of this lobule or by experimental lesion of the corresponding locus in animals.

The fibers of the optic tract pass to the chiasm. There the larger portion passes to the opposite side, while a smaller portion, up to this point not separated from the bundle, remains on the same side. The long-cherished dispute about the chiasm has recently been decided, as stated above, finally and convincingly by Singer and Münzer. The bundle which does not cross over is very unimportant in some animals, and is entirely wanting in certain orders. In the latter case there is, accordingly, a total decussation.

The optic tract must, in addition, contain the pupillary fibers from the oculo-motorius. It has not yet been definitely demonstrated how they join it.

The central course of the **olfactorius** was described in its relations, in Chapter XIII. Compare especially Fig. 144, relating to this subject.

INDEX OF AUTHORS.

The figures immediately preceded by an asterisk (*) refer to illustrations.

INDEX OF COMPARATIVE NEUROLOGY.

Only nouns are indexed. The figures immediately preceded by an asterisk (*) refer to illustrations.

GENERAL INDEX.

Only nouns are indexed. The figures immediately preceded by an asterisk (*) refer to illustrations.