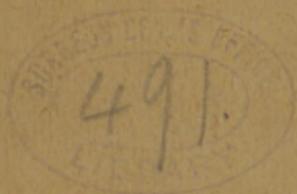


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Nervous System.

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REPRINTED FROM  
**The New York Medical Journal**  
*for June 17 and 24, 1893.*





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RECENT DISCOVERIES  
IN THE NERVOUS SYSTEM.\*

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It is a habit of the human mind, ever prone to dwell upon personal achievement rather than upon the slow course of scientific evolution, to ascribe to individuals the discoveries that seem to mark eras in the advance of knowledge. Columbus discovered America; we pause at that, rarely thinking of the preliminary work that made the discovery of Columbus possible—of the mariner's compass and of the astrolabe, then just made useful, without which the bold navigator would have been obliged to hug the coast like Vasco da Gama and his other predecessors.

Improvements in instruments and methods precede all important advances into new territory. Not until the compound microscope was invented were the tissues of the body recognized; not until achromatic lenses eliminated the errors of the instrument was the cell theory established. No accurate and certain results could be obtained from the examination of the nervous system until Stilling, in 1842, invented the cutting of serial sections; the processes of the nerve cells were first clearly made out by Deiters and Remak in 1855, after Lockhart Clarke had invented the modern method of clearing and mounting tissues; Stilling discovered the reticular character of protoplasm in 1860,

\* A lecture delivered before the Biological Society of Washington.

after hardening in chromic salts was invented by H. Müller, and Gerlach had found staining by carmine effective as a method of investigation; the boundaries of cells were not clearly understood until the accidental discovery that their metaplast would reduce nitrate of silver. Each improvement in method marked an increase in definite and exact knowledge.

The great development of microscopical technique during the last few decades, the double staining invented by Waldeyer in 1863, the osmic-acid stain discovered by Max Schultze (1865) by means of which the medullary sheath of nerve fibers is sharply defined, the gold and palladium stains of Cohnheim (1866) and F. E. Schulze (1867), and the aniline stains first introduced by Waldeyer and since greatly multiplied, have allowed us to attain extraordinary precision in delimitation of structural elements.

The discoveries to which I wish to call your attention to-night were preceded and made possible by two improvements in microscopical methods. The first is not so very recent, as counted by the great speed of these *fin de siècle* times, for it was in 1875 that Camillo Golgi\* discovered, probably by accident, that tissues that had been exposed for a long time to chromic solutions would afterward take a most delicate silver stain, which would display every filament of nervous tissue, even the finest. The great time and unusual precautions necessary for the procedure prevented its general use, and histologists for many years looked rather askance at the results published by Golgi and his pupils. The second is the discovery made by Ehrlich, in 1886, that methylene blue injected into the circulation of living animals stains in a highly satisfactory manner the endings of the nerves. It is, unfortunately, not well adapted to the higher animals.

Until a very recent date it has been held that the nervous system is composed of at least two distinct elements. The latest edition of Quain's *Anatomy* (1891) says:

“When subjected to the microscope, the nervous substance is seen to consist of two different structural elements—viz., fibers and cells.”

\* Sulla fina struttura dei bulbi olfattorii. *Rivista sperimentale di freniatria e di medicina legale*. Reggio-Emilia, 1875, i, 405-425.

Gray's *Anatomy*, last American edition (1887), is no less clear:

"All nervous tissues are composed chiefly of two different structures—the gray or vesicular, and the white or fibrous."

The prevailing conception of a fiber is tolerably clear, it being that of a fibrillary core, called an axis cylinder, invested by one or more sheaths. That of a nerve cell is more vague, it being a nucleated body, very variable in size and shape, having one or more processes which usually present a truncated appearance evidently caused by the methods used in preparing the specimen. Most of these processes branch at once into fine filaments, one remaining distinct and apparently undivided. Deiters, in 1865, distinguished the former as protoplasmic processes; the latter he believed to be connected with a nerve fiber, and therefore called it an axis-cylinder process. His view was hypothetical, no demonstration of actual continuity being made. Cells are named unipolar, bipolar, and multipolar, from the number of processes they present. Apolar cells have been described, but are regarded with suspicion.

Great interest has always centered about the protoplasmic processes, some, among whom is Golgi himself, holding that their function is the collection of nutriment for the large cell body from the blood-vessels, others holding, with Gerlach, that their terminal filaments unite in a fine plexus that forms the principal substratum of the gray matter of the nervous centers, constituting a *sensorium commune* into which the fibers of the sensory nerves pass without break, their impulses passing thus from cell to cell and finally again from cells into fibers either directly or by means of the axis-cylinder fibers. These views, too, are mainly hypothetical. Gerlach's preparations were marvels of technical skill, but he never succeeded in demonstrating the passage of either processes or fibrils into an axis cylinder.

The first clear and certain light on this subject came from the investigations of His, published in a series of articles from 1879 to 1891. As in so many other cases, embryological development furnished the necessary clew.

Permit me to recall to your minds the well-known early stages in the history of the central nervous system. After

the ovum has become shaped into a hollow sphere or blastula there forms on its surface the medullary groove, a shallow furrow that gradually deepens and, by closing at its edges, forms the medullary canal, which is therefore an infolded portion of the exterior surface. (See Fig. 1.) From the epithelial lining of this canal the brain and spinal cord develop.

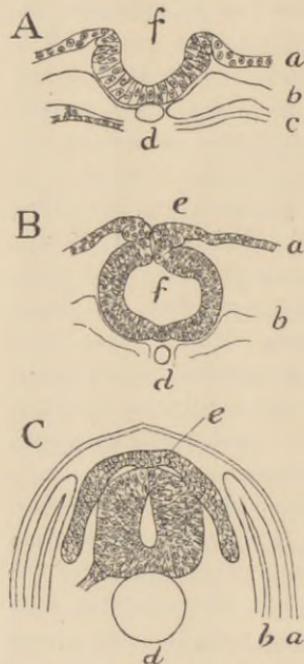


FIG. 1.—Formation of the medullary canal. A. Section across the medullary groove. B. The groove closed to form the medullary canal. C. The formation of the neural crest. *a*, ectoderm; *b*, mesoderm; *c*, entoderm; *d*, notochord; *e*, neural crest forming rudiments of the spinal ganglia; *f*, medullary groove or canal.

This lining, at an early stage, is composed of a single layer of cells, which, however, already show some differentiation. Between regular columnar cells forming a pavement epithelium there occur large round cells with well marked nuclei showing signs of active proliferation—the *germ cells* of His. (See Fig. 2.) These two classes of cells have a totally different history. The columnar cells form the principal sustentacular tissue of the nerve centers, while the germ cells develop into the proper neural elements.

*Spongioblasts and Neuroglia.*—On examining the gray matter of the adult cord it is seen that, besides the ordinary form abounding in large cells (substantia spongiosa), there occurs in some situations a semi-transparent variety (substantia gelatinosa) abounding

in small cells, with great numbers of thread-like processes. (Fig. 3). Two areas exist in which this is the predominant tissue—one about the central canal (substantia gelatinosa centralis), another near the tip of the posterior horn (substantia gelatinosa Rolandi). Its characteristic cells are also scattered throughout the cord, even

in the white substance. The same general features occur in the brain.

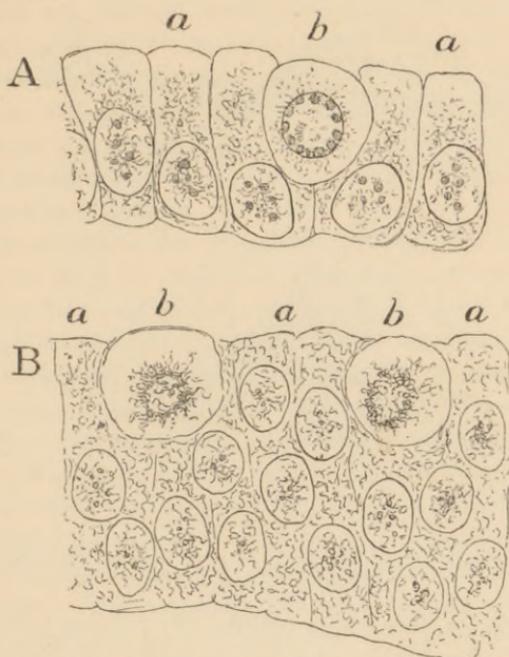


FIG. 2.—The epithelium of the medullary groove of the rabbit (His). A. Before its closure. B. At the time of closure. *a, a, a*, columnar cells; *b, b, b*, germ cells.

The exact nature of this small-celled tissue, which early received the name of neuroglia, has long been a subject of controversy. Noting its sustentacular character and the similarity of its cells to those of connective tissue, it has usually been assigned to that group, although there has been given no satisfactory explanation of the occurrence of a tissue supposed to be characteristic of the mesoderm among cells of unquestionable ectodermal origin.

His shows that it has developed from the columnar cells of the medullary plate in the following manner (see Fig. 4): The cells increase greatly in length, their nuclei lie in several rows, but their ends always reach the surfaces of the plate, and, when that closes to become a tube, the cell axes are disposed radially. Part of the protoplasm liquefies and disappears; the remainder, consisting of the cell wall and an intracellular network, remains as a highly refractive, easily

stained metaplasm. Thus the cells change their shape and character, being centrally rod-like and columnar, united at

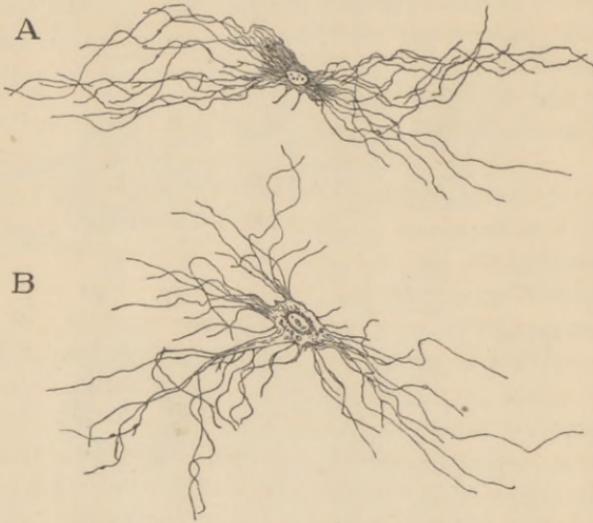


FIG. 3.—Neuroglia cells (Obersteiner). A. From human spinal cord. B. From ependyma of lateral ventricle.

their ends by their edges, peripherally forming a dense reticulum. From this peculiar formation they are called

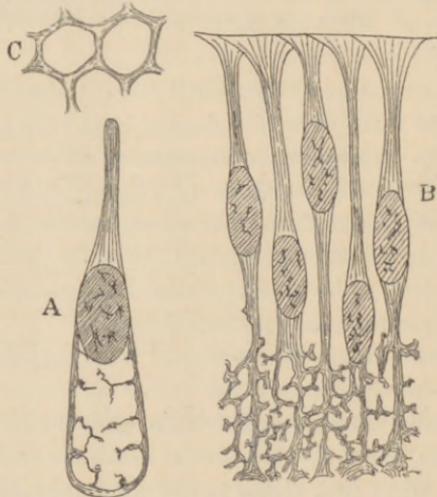


FIG. 4.—Formation of spongioblasts (His) A. Single spongioblast showing the liquefaction of the protoplasm and development of the reticulum. B. Arrangement of the spongioblasts in a lattice-like tissue or myelospongium. *a*, internal limiting membrane; *b*, columnar or mantle layer; *c*, velum confine. C. Surface view of the internal limiting membrane.

spongioblasts, and the entire lattice-like tissue composed by them is termed myelospongium.

There can now be distinguished three zones in this myelospongium of the medullary tube: one about the central canal, formed by the united central ends of the spongioblasts, one occupied by their nuclei, and one by the peripheral reticulum. These are respectively termed the internal limiting membrane, the columnar or mantle layer, and the velum confine. The first forms the *substantia gelatinosa centralis*, the second the neuroglia of the gray matter, the third the neuroglia of the white matter.

When the Golgi method is used, it is found that the silver salt is more readily reduced by the neuroglia than by the other tissues, so that by stopping the process at the proper point it is possible to mark out its elements with precision. For convenience of handling, the cords of the embryos of small animals are preferred. The spongioblasts proliferate and crowd together about the central canal, each developing a bristle-like process on its free surface, which thus becomes what has been usually designated as "ciliated epithelium." The columnar processes become more and more attenuated as the cord increases in size, still passing through the entire thickness from central canal to pia mater. (See Fig. 5.) Special aggregations of these processes form septa, of which the posterior median septum is one. The peripheral ends unite to form the outer investment of the cord under the pia mater.

After a time the continuity of the processes with the cell bodies can no longer be demonstrated. They break away at either end, numerous secondary processes are developed, and a typical neuroglia cell is thus formed. The primitive condition persists, however, in fishes, reptiles, and batrachians, also in certain regions of birds and mammals, as the retina (fibers of Müller) and the olfactory mucous membrane.

Thus the vexed question of the nature and origin of this tissue appears to be finally set at rest. The result is due principally to the labors of His and Lenhossék. The latter observer has traced all the changes in the spinal cord of the human embryo.

*Neuroblasts and Nerve Cells.*—The germ cells, the other

class of epithelial elements of the medullary plate, do not lag behind in development, but appear, on the contrary, to show an extraordinary activity. Originally occupying the inner stratum next the free surface of the epithelium, they

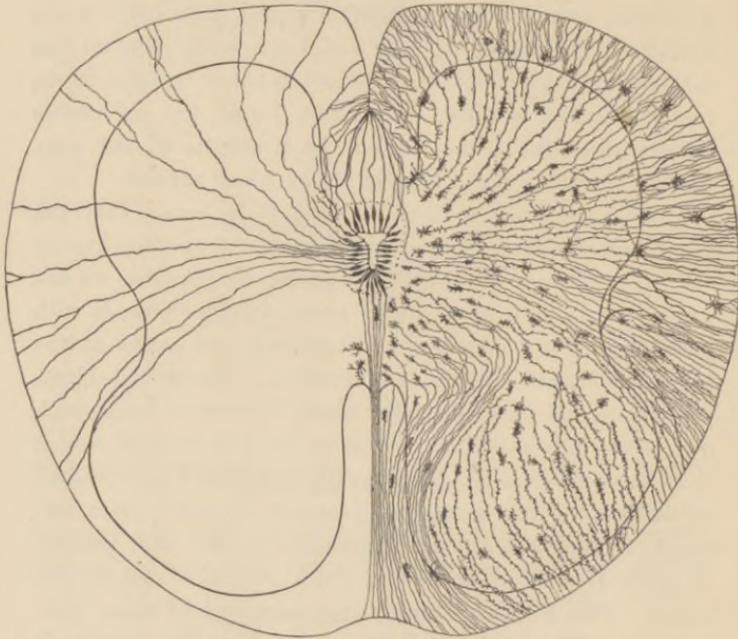


FIG. 5.—The spongioblastic framework of the spinal cord (Lenhossék). Cord of a human embryo, 14 ctm. long, impregnated by the Golgi method.

first begin to change their shape, becoming pointed upon one side and finally pyriform (Fig. 6, A, B). These are the apolar cells described by early observers—a transitory condition only. The pointed end continues to grow until it develops as an extended process of the cell, which, with its rounded head and tail-like appendage, strikingly resembles a tadpole, and also reminds one very much of the spermatoblasts of the seminal tubules that are developed in a similar manner (Fig. 6, C). The young cell is now called a *neuroblast*, and commences to migrate from its original seat (Fig. 7). As the myelospongium has now become fully developed, they pass outward between its columns. The velum confine appears to oppose an obstacle to their further outward progress, and upon reaching it they turn

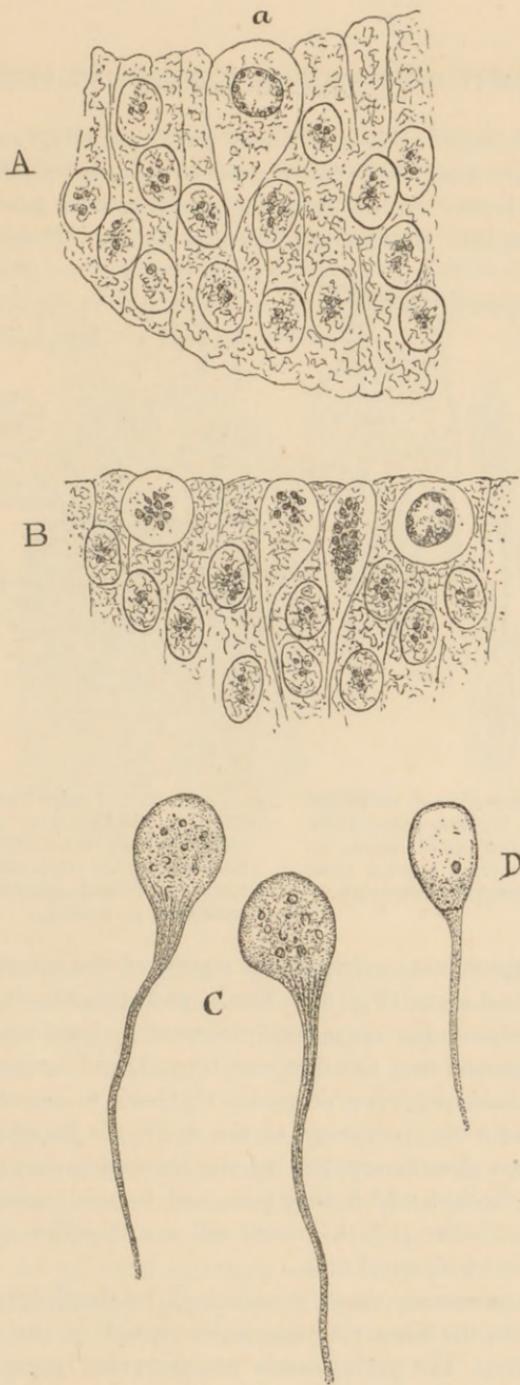


FIG. 6.—Development of neuroblasts (His). A. Epithelium from the medullary canal of the rabbit soon after it has closed. Between the epithelial cells lies a germ cell, *a*, which has become pyriform. B. Epithelium from the closed medullary canal of the cat. Between the epithelial cells lie four germ cells, two of which are still spherical; the others have developed processes that extend outwardly. C. Neuroblasts from the embryo of a salamander. D. Neuroblasts from an embryo trout.

their processes aside and direct them ventrally, forming a secondary zone within the mantle layer, called by His the arcuate layer. At this stage the processes have a tendency to collect into bundles, as shown in Fig. 8. These finally

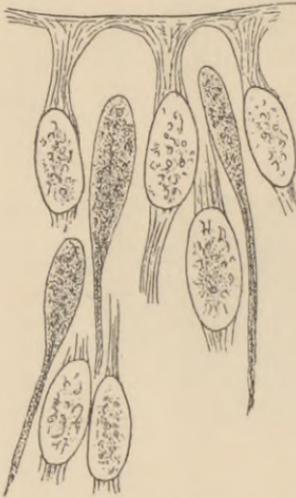


FIG. 7.—Migration of neuroblasts (His). Young neuroblasts from the spinal cord of a human embryo moving outward along the spongioblastic network.

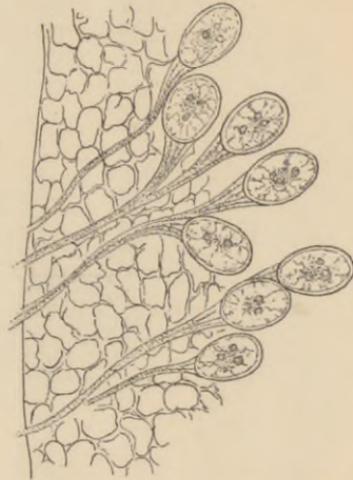


FIG. 8.—Bundles of neuroblasts (His). Young neuroblasts from the spinal cord of an embryo chick collecting into bundles along the velum confine at a locality where the longitudinal and arcuate fibers are wanting.

pierce the velum confine in the region of the anterior root of a spinal nerve (Fig. 9). The neuroblasts remain within the cord, develop secondary processes by budding in the same manner that the first was formed, and become *nerve cells*; their primitive processes continue to extend until they reach the periphery of the body, are invested with medullary sheaths supplied by the connective tissue of the region through which they pass, and become *nerve fibers*. The nerve fiber and the nerve cell are therefore parts of the same histological unit.

When nervous tissue is examined by the Golgi method we obtain the same precision as was noted in the case of neuroglia. The protoplasmic processes no longer appear as truncated stumps, but each is seen to break up into an arborescence of almost inconceivable delicacy. Some of the discoveries made are quite unexpected. Axis-cylinder

processes are found on all cells, even those of the posterior horn. Golgi was able to make out two classes of cells: one with a long axis-cylinder process, which he connected especially with the motor cells of the anterior horn, another with short axis-cylinder process, which he supposed to be characteristic of the posterior horn, but which recent observers find in all parts of the cord.

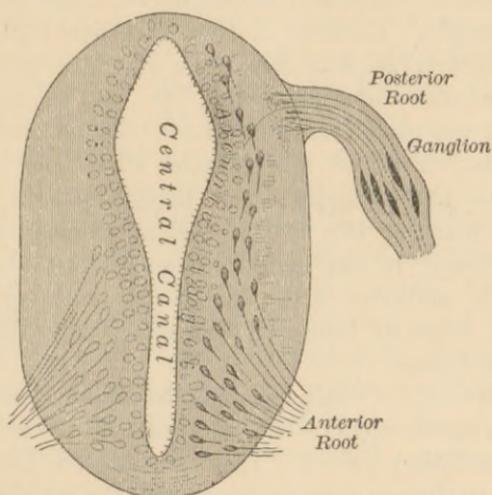


FIG. 9.—The formation of nerve roots (Edinger). Section through spinal cord of a human embryo.

While the axis cylinder process can be distinguished from the protoplasmic processes by its more direct course and simple appearance, it is yet found that it sooner or later branches, frequently giving out a few laterals at a short distance from the cell, and always terminating, as do the protoplasmic processes, in a tuft of filaments. For the motor cells these tufts are found at a considerable distance upon the motorial end plate of a muscle fiber. Indeed, as the neuroblast grows, its terminal process has an enlarged extremity—the “cone of growth”—upon which may be observed some slight elevations, representing the rudimentary terminals. It would therefore appear that the independence observed in the developing neuroblasts is preserved in the adult tissue.

But the neuroblasts we have been considering belong mainly to the anterior roots, which since the time of Sir

Charles Bell we recognize as motor or efferent. What shall be said of the posterior roots by which afferent impulses reach the cord?

*Æsthesioblasts and the Posterior Roots.*—At the time of the closure of the medullary groove a thickened portion of the epithelial lining remains just at the seam, constituting a band known as the neural crest. (See Fig. 1, C.) This becomes segmented, moves outward, and forms the spinal ganglia. Kölliker in 1844 first noted that these ganglia contain unipolar cells from which he supposed a single medullated fiber proceeded. In 1847 the significant discovery was made that in fishes the cells of these ganglia are bipolar, giving off a medullated fiber from opposite ends. In 1875 Ranvier found that the single fiber of Kölliker branches into two at a short distance from the cell (T fiber). It was then discovered that the ganglion cells in the embryos of the higher vertebrates agree with those of fishes in being bipolar, and finally His found transition forms.

These cells, for which I propose the term *æsthesioblasts*,\* assume a spindle shape while yet a part of the epithelium of the medullary groove. They resemble the neuroblasts in the formation of their processes, but the precocious development of a secondary process makes them bipolar. At first these are opposite—the cell is oppositipolar—then, as the cell body is pushed aside, the processes approach each other (geminipolar), and finally, as they become blended in a single prolongation of the body, unipolar. It is not likely that these changes of arrangement involve any differences of function.

One of the processes of an *æsthesioblast* seeks the periphery and terminates in fibrils that are either lost in the cuticular tissues or end in an expansion (tactile corpuscle, Pacinian corpuscle, end-bulb of Krause) surrounded by connective tissue. The other process grows centrally, and its final destination is one of the most significant of the recent discoveries.

The posterior roots of the cord have long been a great

\* Lenhossék calls them *ganglioblasts*. This term could not, however, be properly applied to the cells of a similar character found in the olfactory membrane and in the retina.

puzzle to neurologists. Clear and definite demonstrations of their central terminations and their behavior with respect to the other components of the cord have been wanting. Anatomists have therefore been obliged to rely upon evidence adduced from other sources. Waller, in 1852, discovered that when a nerve fiber is cut, one of its ends degenerates, and that this degeneration can be easily followed in a series of consecutive sections. Often it is the distal portion that degenerates, but not always. For example, the cutting of a spinal nerve beyond the ganglion causes a total degeneration of the distal end, while a section of the posterior root between the ganglion and the cord causes an almost total degeneration of the central end. In either case the long processes of the cells are severed from the cell body which probably controls their nutrition. After section of a posterior root degenerations are found in the posterior columns of the cord on both sides. Further experiments led to the discovery that lesions of the white matter of the cord cause degenerations in different directions—some *ascending*, as in the posterior columns, others *descending*, as in certain portions of the lateral columns. Certain tracts of the white matter could thus be separated with some precision.

This was supplemented by the embryological researches of Flechsig, who, in 1872-'76, found that some groups of the white fibers of the central nervous system always receive their myelin sheath earlier than others. By this means the results obtained by degenerations were supplemented and controlled. The aid of physiology and comparative anatomy was also invoked. As stimulation of certain cells produced definite movements, a continuity of path between cell and muscle was assumed; in some lower animals tracts were found comparatively larger or smaller than those of man, often correlated with special differences of function.

Combining the information derived from these indirect sources with the results of direct observation, the following views have been held as to the posterior roots (see Fig. 10): On entering the cord they separate into two bundles—one median, large-fibered, myelinating early, related to muscular movements; another lateral, small-fibered, myelinating

late, related to cutaneous and visceral sensibility. The first bundle passes inward to the posterior columns, thence sending some fibers that pass upward and perhaps downward, and are connected with muscular co-ordination and equilibrium; also others that pass forward to the anterior horn and are concerned in reflex movements. Some may also pass to the gray matter of the opposite half of the cord.

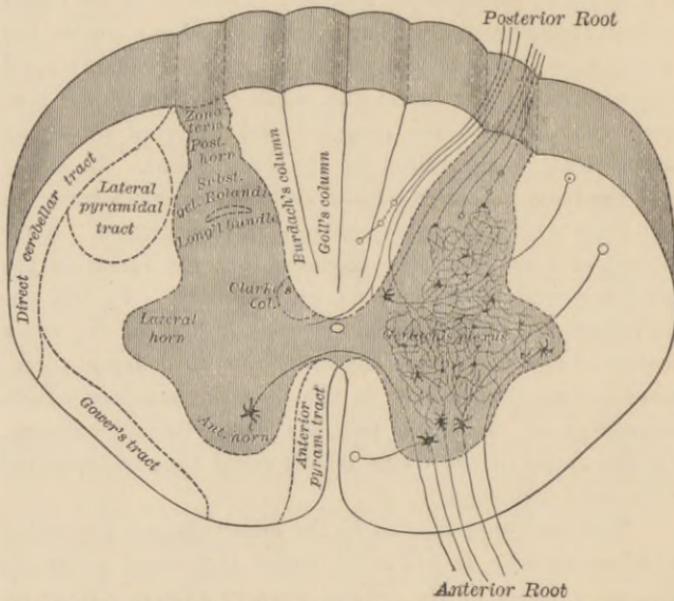


FIG. 10.—Diagram showing views formerly prevalent with regard to the course of nerve fibers within the spinal cord.

The second bundle passes to the gray matter and is lost in the column of Clarke, the scattered cells of the posterior horn, or turns upward and downward in a fascicle of white fibers lying in the gray near the substance of Rolando.

The actual terminations have been carefully investigated by Ramón y Cajal, of the University of Barcelona, using the Golgi method of staining. His discoveries have been amply confirmed by Kölliker, Lenhossék, Van Gehuchten, and others. It is found that the great majority of the fibers of the posterior roots divide dichotomously on entering the cord, sending one branch upward and another downward. These branches form the bulk of the posterior columns (Fig. 11). From them at short intervals collateral twigs

are given off at right angles. These enter the gray substance of the cord and break up into delicate fibrils, each fibril, however, remaining distinct and ending free, either by filaments or minute enlargements. The plexus imagined by Gerlach has no existence; there is instead an intimate felt-like interlacing of filaments—the *neuropilem* of His.

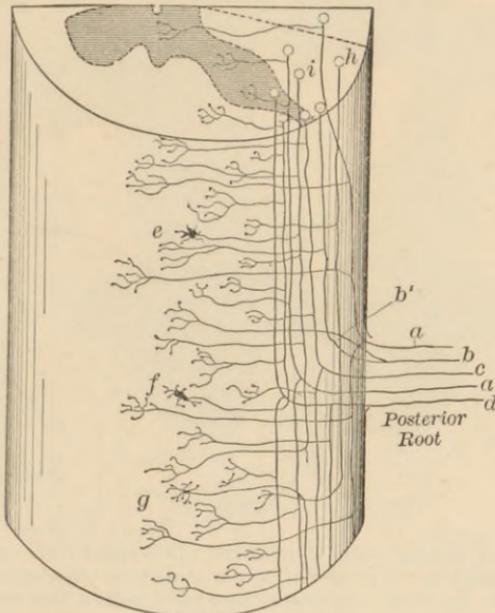


FIG. 11.—Root fibers and collaterals. *a, b*, fibers that pass upward and downward in posterior columns, sending collaterals to anterior horn; *b'*, collateral given off from main trunk before division; *c*, fiber that passes upward and downward in the terminal zone, sending collaterals to posterior horn; *d*, fiber that passes upward and downward in the longitudinal bundle, sending collaterals to posterior horn; *e*, cell that sends an axis-cylinder process to posterior columns, where it bifurcates, proceeding upward and downward and sending collaterals to posterior horn; *f*, cell that sends process to cerebellar tract; *g*, cell that sends process downward; *h, i*, fibers from roots or cells at a higher level, descending and giving off collaterals.

The area of distribution of a single nerve fiber is therefore much greater than had been heretofore imagined, as it supplies by its collaterals many different levels of the cord, passing perhaps as far as the medulla oblongata. The posterior columns of the cord are mainly composed of the ascending and descending branches of the fibers; the collaterals take for the most part the directions formerly described for the nerve fibers proper—viz., a reflex bundle to

the anterior column that ramifies about the motor cells, another to the column of Clarke, forming a rich felt-work about its cells, a few fibers to the posterior horn of the opposite side, and many fibers that break into terminals within the posterior horn (Fig. 12).

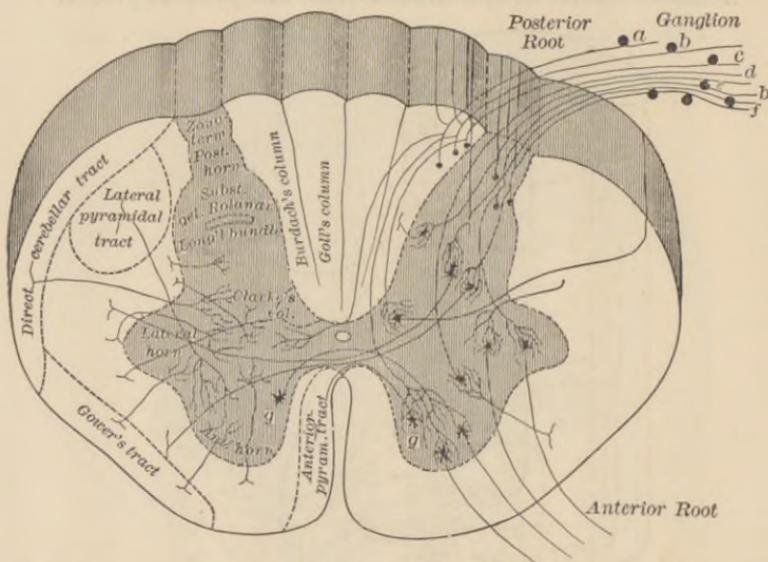


FIG. 12.—Diagram showing course of collaterals within spinal cord. *a*, fiber sending collateral to opposite side of the cord by way of posterior commissure; *b*, fiber sending collaterals to anterior horn constituting a reflex path; *c*, fiber sending collateral to the column of Clarke; *d*, efferent fiber from cell of anterior horn; *e*, fiber sending collateral to cell of posterior horn that forms a secondary path on the same side of cord; *f*, fibers sending collaterals to cells of posterior horn that form a secondary path on opposite side of cord; *g*, *g*, commissural cells. On the left of the drawing numerous collaterals are seen that belong to fibers that lie in the antero-posterior columns which are derived from cells lying at other levels.

There is a small fascicle apparently derived from cells of the anterior horn that passes to the posterior roots. This is probably an efferent bundle and constitutes an exception to the rule which makes the posterior roots exclusively afferent.

*The Neurons.*—On comparing the development of the anterior and posterior roots it will be seen that they are composed of essentially similar elements developed in a similar manner. Waldeyer has given to these elements the name of neurons. Each is composed of (1) a nerve cell with (2) its protoplasmic processes, (3) its axis-cylinder process passing into a nerve fiber, and (4) its final

termination in a branching tuft. In the case of the anterior root the neuron has short protoplasmic processes and a long axis-cylinder process; in that of the posterior root the protoplasmic process is long, extending to the periphery and collecting impulses from without like the terminals of a nerve of special sense; the axis-cylinder process

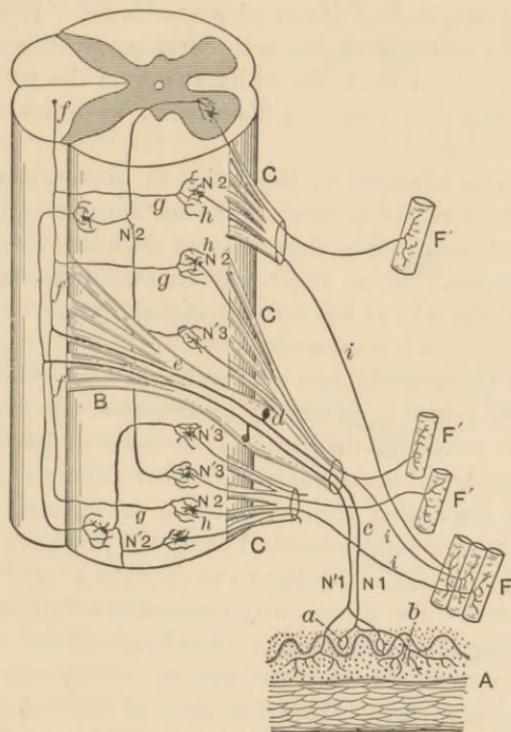


FIG. 13.—Neurons of reflex paths of spinal cord. A. Skin. B. Posterior nerve root. C, C, C. Anterior nerve roots. F, F'. Muscle fibers. The simple reflex path is composed of neuron, N, 1, that arises from the periphery by terminal filaments either in an end bulb, *a*, or free between the cells, *b*, and proceeds by a cellulipetal fiber, *c*, to the aesthesioblast, *d*, in the ganglion of the posterior root of a spinal nerve, thence by a cellulifugal process, *e*, which bifurcates, *f*, *f*, in the posterior columns of the cord, sending collaterals, *g*, *g*, *g*, that break into terminals about cells of the anterior horn belonging to neurons, N, 2. These neurons are composed of short cellulipetal processes, *h*, *h*, *h*, from which spring cellulifugal axis-cylinder processes, *i*, *i*, *i*, that pass to the peripheral muscles through the anterior roots and break into terminal filaments in the motorial end plate. The compound reflex path is composed of a similar collecting neuron, N' 1, one or more correlating neurons, N' 2, and distributing neurons, N' 3.

is short, almost immediately dividing and subdividing (Fig. 13). Lenhossék has recently made an important discovery

that appears to show that both of these originate from a single primitive type. In the earthworm there are no organs like the spinal ganglia, and the sensory cells or æsthesioblasts are scattered throughout the epidermis, presenting short collecting filaments externally and sending to the central nervous system long processes that finally bifurcate like the æsthesioblasts of a vertebrate. It appears that in the course of phylogenetic development the æsthesioblasts have been gradually withdrawn from the periphery, this causing their collecting filaments to be drawn out into long processes.

The idea advanced by Golgi that the protoplasmic processes subservise the nutrition of the cell appears to be without foundation. Many circumstances show that they transmit impulses. In no other way can we understand the action of the cells of the spinal ganglia or those belonging to the organs of special sense.

This transmission does not involve, as was formerly supposed, an unbroken continuity of structure. It would appear that certain of the terminal filaments of the neurons are excitable to stimuli received either from the outside world or from other neurons, and that the impulses or currents thus formed are conveyed along the processes toward the nucleus of the cell, being, to use Ramón y Cajal's term, *cellulipetal*; from thence they proceed as *cellulifugal* currents along other processes to other terminals and these in turn may stimulate other neurons by contact only, either being applied closely about the body of the cell or interlacing with its arborescent filaments. To the cellulipetal currents the protoplasmic processes are assigned, while the currents of the axis-cylinder processes appear to be exclusively cellulifugal.

It should be remarked that a comparative study of the nerve cells shows that it is probable that the differentiation which we find in higher and adult animals between the protoplasmic and the axis-cylinder processes is a matter of gradual development. In the earthworm Lenhossék and Retzius have found cells that show all varieties of form, from a unipolar cell branching out into widely ramifying processes to a bipolar cell, in which there are two processes of the same character and the same ramification,

and a multipolar cell which has one axis-cylinder process (Fig. 14).

The primitive neuron appears, then, to be merely a multipolar, remarkably differentiated cell, whose processes may receive stimuli from without or excite other similar cells by contact with them.

It should be remarked that both of these functions agree fully with what we have long known with regard to cells. The endings of the nerves of special sense have always been supposed to be excited by external stimuli, and it has been known that a motor nerve conveys impulses to a muscle by means of contact alone in its motorial end plate.

It is conceivable that an impulse received from without by means of a neuron should be transmitted at once to other neurons within the substance of the cord, and thence referred immediately to a muscular fiber. No doubt this frequently occurs, for this would account for the simplest forms of reflex movement. Yet it is probable that in most cases the matter is more complex than this, and that there are certain *secondary* neurons interposed. These may refer the sensation to neurons presiding over special groups of muscles which may be either on the same side or on opposite sides of the body. Recent investigations seem to make it probable that most of the impulses that cross the median line are carried by secondary paths of this character. It is now denied that any fibers from the cells of the anterior horn cross to the nerve roots of the opposite side, and while a few fibers of the posterior roots are found to cross,

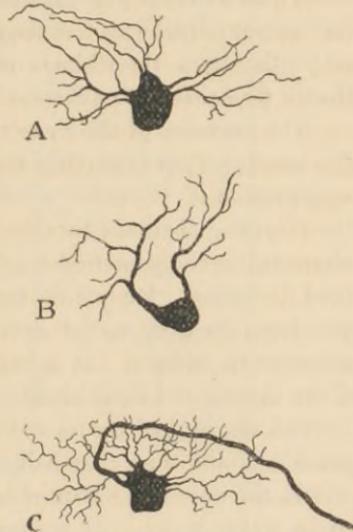


FIG. 14.—Ganglion cells of the earthworm (*Lumbricus*) as shown by the Golgi impregnation (Retzius). A. Protoplasmic processes undifferentiated. B. Bipolar cell, two groups of equally differentiated processes. C. Protoplasmic and axis-cylinder processes fully differentiated.

yet they are insignificant. Yet, as is well known, both motor and sensory impulses do actually cross. This is effected by a large number of so-called *commissural* cells found in all parts of the cord. These are cells having a short axis-cylinder process which they send to the opposite half of the cord, there terminating in the usual arborescence or passing into the white matter in one or more branches, thence proceeding to different levels.

The branches of the fibers of the posterior roots pass for the most part into the posterior columns. What, then, is the constitution of the other white columns of the cord? On investigating them they are found to be of the same general character as the posterior columns, being composed of vertical fibers that give off at short intervals collaterals that penetrate the gray matter and there terminate in the usual arborescent manner. It is impossible to actually trace these fibers throughout their whole extent, because they soon pass beyond the field of the microscope; but there can be no reasonable doubt that they belong to cells that are situated within the nervous centers either above or below the section under examination. As lesions of some portions of the cortex of the brain are followed by degenerations within the substance of the cord, it appears that some of the cells at least must be referred to that part of the system. We will therefore proceed to consider the anatomical constitution of the cortex for the purpose of ascertaining whether there are any elements there which would justify the conclusion that they are connected with the cord.

*Cortex of the Cerebrum.*—It has long been known that a considerable portion of the cortex is occupied by large cells of a triangular outline, presenting a pointed extremity toward the exterior. These, the pyramidal cells of authors, are of great size in the so-called motor regions of the cortex—that is to say, in the central convolutions—the region which if injured causes the descending degenerations above referred to. Since the publication of Golgi's chief work\* it has been known that these structures have wide-reaching connections, and Ramón y Cajal and Van Gehuchten have much extended our knowledge.

\* *Sulla fina anatomia degli organi centrali del sistema nervoso.* Milano, 1885-'86.

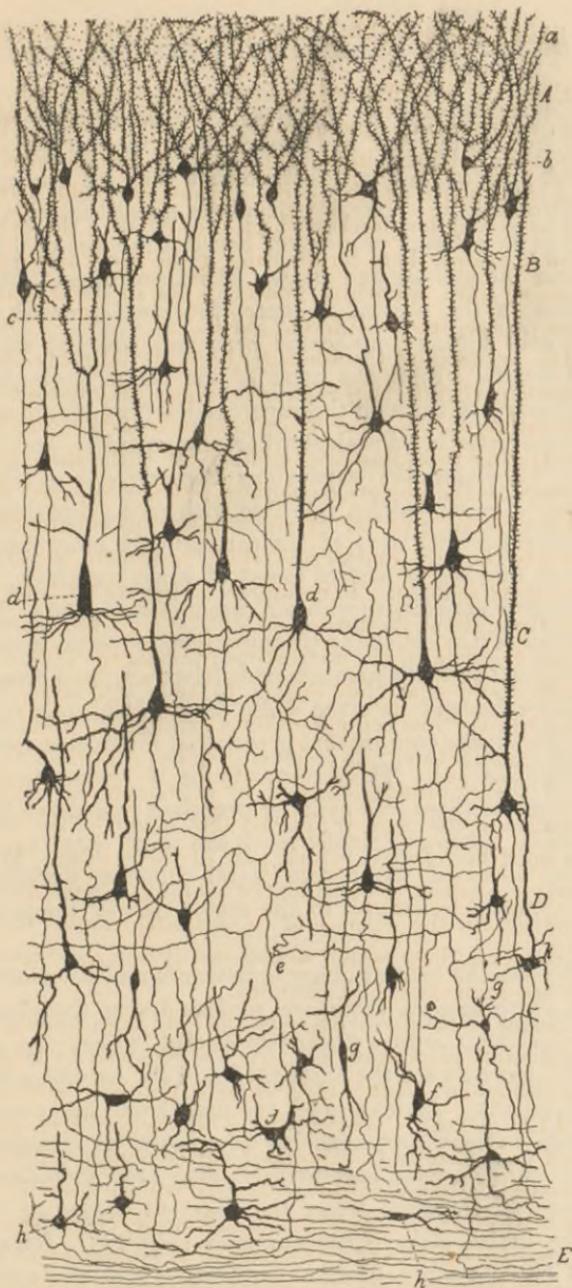


FIG. 15.—Section of the cerebral cortex (Ramón y Cajal). From the supra-ventricular region of a young mouse. A. Molecular layer. B. Small pyramidal layers. C. Large pyramidal layer. D. Layer of irregular corpuscles. E. White matter. *a*, panicles of the pyramids; *b*, smallest and most superficial of the pyramids; *c*, axis cylinder from a small pyramid; *d*, large pyramid; *e*, its axis cylinder; *f*, cell with ascending axis cylinder; *g*, similar but smaller cells; *h*, cells found in the white matter; *i*, rounded cell that sends its axis cylinder toward the white substance; *j*, cell with short axis-cylinder process.

The largest of these cells may reach  $40 \mu$ , or about  $\frac{1}{800}$  of an inch, in breadth, and the length of the cell body may be four or five times as great, so that they are among the largest cells in the body. It has been noted that there appears to be a direct proportion between the size of a nerve cell and the number and length of its processes. This is justified in the present instance, for there proceed from these cells highly complicated processes, some of them of great length. From the apex of the cell a protoplasmic stem passes up through the superficial layers of the cortex and terminates in an arched arborescent panicle, each composed of plume-like expansions barbed with secondary spines. These panicles interlace with each other throughout the superficial layer of the cortex in the most intricate manner, forming a perfect forest of branches which, however, never anastomose with each other (see Fig. 15). From the sides of the cell body protoplasmic processes arranged in the usual tuft-like manner extend laterally, and from below there descends into the white fibers of the zona radiata an axis-cylinder process that gives off at intervals a few collaterals (Fig. 16). There seems to be no reason to doubt that many of these axis-cylinder processes pass down in the pyramidal tracts and finally reach the spinal cord as some of the fibers of the antero-lateral columns, distributing their terminal collaterals to the motor cells of the anterior horn.

Besides the extraordinary appearance and peculiar situation of these cells there are reasons drawn from embryology and from comparative anatomy that indicate the probability that they are the chief agents in the psychic activity of the cortex. As we ascend the scale from the lower vertebrates to man an increasing complexity of structure is found in these cells, and there is also seen a similar progressive development when the different stages of their growth in the embryo are observed (Fig. 17). Ramón y Cajal has therefore given to these structures the name of *psychic cells*.

These elements are scattered throughout the cortex in the pyramidal layers of Meynert. Those lying superficially are small and their panicles are short, and there is a regular increase in size and length of panicles as we proceed deeper,

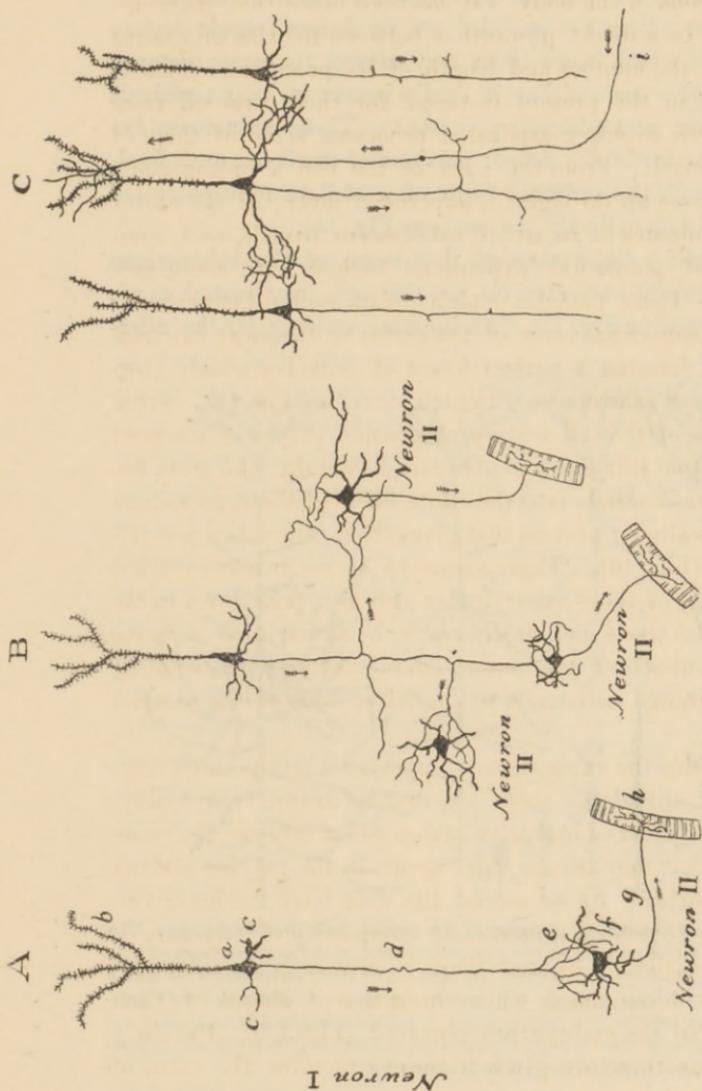


Fig. 16.—Psychic cells and their connections. A. The simplest form of connection. *a*, psychic cell forming with its processes, *b*, *c*, *d*, a neuron of the first order; *b*, cortical plicae, cellulipetal; *c*, lateral processes; *d*, axis-cylinder process forming a portion of the pyramidal tract; *e*, terminal filaments embracing *f*, a cell of the spinal cord which forms a neuron of the second order, sending an axis-cylinder process, *g*, in the anterior root of the spinal cord to break into terminal filaments within the motorial plate of a muscle, *h*. B. Connection of a psychic cell with more than one secondary neuron by means of the collaterals of its axis-cylinder process. C. Connection of psychic cells with each other by means of their collateral processes. Communication of stimuli by means of cellulifugal process, *i*, coming up from the zona radiata.

until some reach the enormous length shown in the cell at the right in Fig. 15.

In Meynert's fourth layer (layer of mixed or polymorphous cells) the psychic cells appear to undergo certain reductions. Here the panicles are no longer found; a stem like that which bears them may extend for some distance toward the surface, but it finally breaks up into terminals like other protoplasmic processes. These reductions become greater in the deeper portions of the layer, until finally we reach the ordinary form of a stellate multipolar cell with an axis-cylinder process (see Fig. 15).

Ramón y Cajal suggests that some of the interactions that take place between the psychic cells may be such as are represented in Fig. 18. An impulse arriving by the affer-

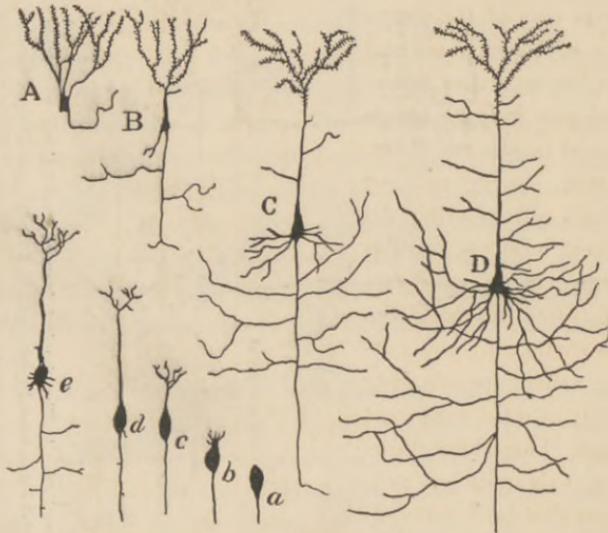


FIG. 17.—Phylogeny and ontogeny of the psychic cells (Ramón y Cajal). The upper series of cells shows the psychic cell in different vertebrates. A. Frog. B. Newt. C. Mouse. D. Man. The lower series shows the stages of growth that a single cell passes through. *a*, neuroblast with axis-cylinder process just commencing; *b*, panicle commencing; *c*, panicle and axis-cylinder process more advanced; *d*, collaterals of axis cylinder appearing; *e*, collaterals of the cell body appearing.

ent fiber E is conveyed by its terminal filaments to the panicles of the psychic cells lying in the superficial layers of the cortex. These transmit it downward and at the same time affect by their collaterals the cells situated in deeper layers,

as C and D. These finally discharge into the efferent fibers of the central white matter, G, and these may convey the impulses by means of their own collaterals, F, to other cortical cells, or they may carry it down to lower levels.

Although the psychic cells are the principal elements of the cerebral cortex, there are others that should be mentioned. Throughout the superficial layer there are scattered sparsely a few cells of peculiar types. There are at least two classes of these: First, fusiform or irregularly-shaped cells with processes of great length given off from either end and passing horizontally (Fig. 19, A, B, D, E). In some cases, as in cell A, several axis cylinders belong to the same cell, usually arising from its processes. Such multiplication is not known to occur elsewhere in the human body, and reminds one of the nerve cells of batrachians and reptiles, several of whose processes may be transformed into nerve fibers. Second, polygonal or stellate cells sending divergent varicose ramifications in every direction, some reaching the free surface of the cortex, others penetrating deeply into the subjacent layers. These have, however, axis-cylinder processes that have no tendency to descend, but run either horizontally or toward the surface.

Below the pyramidal layers cells are found that send their axis-cylinder processes upward (Fig. 15, *f*, *g*), also others that have short axis-cylinder processes like the commissural cells of the spinal cord (Fig. 15, *j*).

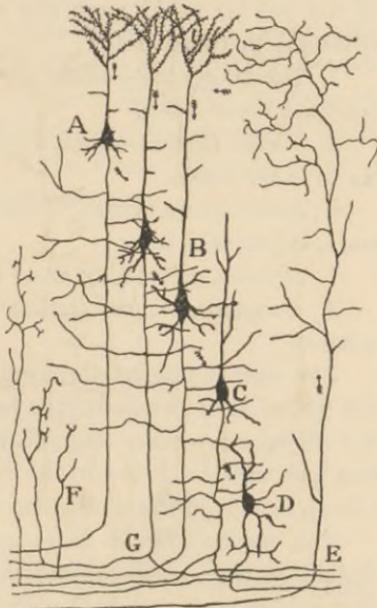


FIG. 18.—Cortical currents (Ramón y Cajal)  
 A. Small pyramidal cell. B. Giant pyramidal cell. C. Pyramidal cell that has lost its panicle. D. Stellate cell. E. Terminal fibril coming from cells situated in other centers. F. Collaterals of the white substance. G. Axis cylinder bifurcating in the white substance.

The fibers constituting the white matter of the hemispheres may be classified as follows :

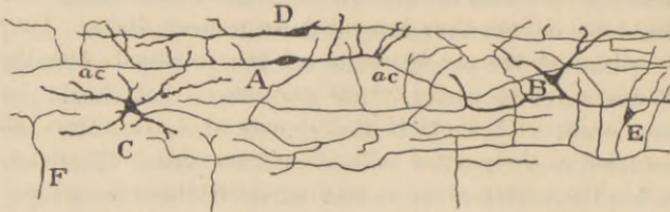


FIG. 19.—Cells of first cerebral layer (Ramón y Cajal). A. Fusiform cells with two horizontal axis-cylinder processes, *ac*. B. Triangular cells. C. Polygonal cells with a single axis-cylinder process. D. Fusiform cell with a horizontal axis-cylinder process. E. Small cell with a bifurcated axis-cylinder process.

*a.* PROJECTION FIBERS—those which project the impulses of the outside world upon the sensorium or the reverse. Divisible, therefore, into :

1. *Cortico-afferent*—those carrying impulses to the cortex from lower levels.
2. *Cortico-efferent*—those carrying impulses from the cortex to lower levels.

*b.* ASSOCIATION FIBERS \*—those which correlate cortical areas, subdivided into :

1. *Arcuate*, correlating areas of the same hemisphere.
2. *Commissural*, correlating areas of opposite hemispheres.

The cortico-afferent fibers are not easily made out, as the cell bodies must necessarily lie beyond the field of vision. Yet there are certain large-fibered terminals (E, Fig. 18) that pass up from below to the outer layers, that appear to belong to cells in the cerebellum or the medulla.

The cortico-efferent fibers appear to proceed from all regions of the cortex, passing through the corpus striatum to converge in the cerebral peduncles. They arise as axis-cylinder processes from all the varieties of the psychic cells, large pyramids, small pyramids, and those without panicles.

\* Meynert confines this term to fibers associating areas of the same hemisphere, or those termed in the text *arcuate* fibers. He supposed that the commissural fibers connected identical or homogeneous areas of the opposite hemispheres. This is now known not to be the case, all fibers being associational in the sense of connecting heterogeneous areas.

Most of them pass to the pyramidal tracts of the medular and spinal cord. Collaterals from these fibers may pass either to the corpus callosum (C, Fig. 21) or to neighboring convolutions, thus becoming association fibers. They usually communicate by means of fine collaterals with the cellular elements of the corpus striatum.

The arcuate fibers (Fig. 20) may also arise from all varieties of the psychic cells. They are extremely numerous in the higher animals, sending their terminals and collaterals into every region of the cortex. The fasciculus arcuatus is almost entirely made up by their trunks. In adult forms their complication is so great as to make it beyond our power to disentangle them; it is therefore necessary to investigate them in the embryos of small mammals, where the whole may be brought within the limits of the microscopical field. The whole system offers a remarkable analogy to the fibers and collaterals found in the columns of the spinal cord. The shortest fibers of this class are those belonging to the commissural cells of the deeper layers of the cortex, while some of the longer fibers are those of the spindle cells of the superficial layer.

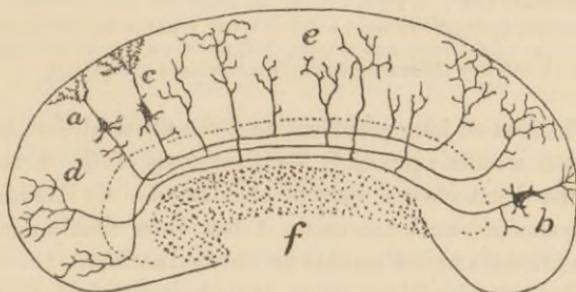


FIG. 20.—Arcuate fibers (Ramón y Cajal). Diagram of an antero-posterior section of one of the hemispheres of the cerebrum to show that arrangement of the fibers associating the frontal and occipital lobes. *a*, psychic cell of the frontal lobe sending fibers to terminate in the occipital lobe; *b*, psychic cell of the occipital lobe sending fiber to terminate in the frontal lobe; *c*, psychic cell of frontal lobe whose axis-cylinder process bifurcates; *d*, terminal tuft; *e*, collaterals to parietal lobe; *f*, corpus callosum cut across.

The commissural fibers (Fig. 21) may pass to the opposite side either in the corpus callosum or in the anterior commissure. The fibers of the corpus callosum have long been noted for their fineness, and this is found to arise from the

fact that many of them are collaterals from axis-cylinder processes. These may arise either from the arcuate fibers or from the efferent projection fibers. It is not known whether any afferent fibers send collaterals to the opposite side. Besides these, there are certain commissural fibers derived directly from the small pyramids of the cortex.

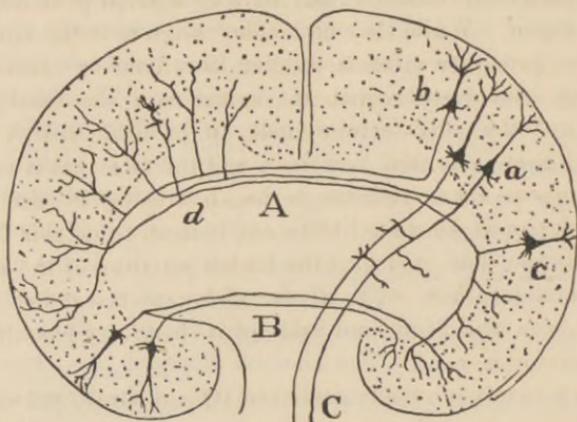


FIG. 21.—Commissural fibers (Ramón y Cajal). Diagram of a cross section of the hemispheres showing the arrangement of the fibers connecting the areas on opposite sides. A. Corpus callosum. B. Anterior commissure. C. Peduncular fibers. *a*, psychic cell of the pyramidal tract that sends a collateral to the opposite side; *b*, psychic cell whose axis-cylinder process bends at a right angle and is widely distributed on the opposite side; *c*, psychic cell with bifurcating axis-cylinder process; *d*, terminals.

The idea so long prevalent that the fibers of the corpus callosum associate precisely identical areas of the cortex in opposite hemispheres must be abandoned. By examining the brains of small mammals it has been clearly demonstrated that a single fiber may be widely distributed throughout the opposite side. It is, in fact, doubtful whether, in any case whatever, such a union of identical areas really occurs.

The fibers of the cortex myelinate late, none receiving their medullary sheath until the ninth month of fetal life. Those of the central convolutions are the first to receive it, then those of the occipital lobe. The former appear to be connected with the motor functions, the latter with the functions of visual memory.

*The Cerebellum.*—If the new discoveries give promise of leading to a rational knowledge of the elements of the

cerebrum, what shall be said of the cerebellum, that organ which has caused so much conjecture and concerning which so many contradictory views have been expressed that Eckhardt said that it would be much more satisfactory if we knew nothing at all about it?

Anatomists since the time of Gall have been struck with its remarkable relations and have considered it an important organ. While they no longer assign to it the control of the procreative functions, yet its union, by means of clearly defined paths, with the spinal cord, the basal ganglia, and the cortex cerebri, make it probable that it performs some essential function; and the fact that it exists throughout the vertebrate series, increasing in size and complexity as we ascend the scale, indicates that this function is one connected with the higher activities of the nervous system. Yet, with all the elaborate researches that have been made, our knowledge of its histology has hitherto been meager.

Its cortex is usually described (Quain, Gray, Schwalbe, etc.) as composed of two layers—an outer clear gray or molecular layer, and an inner reddish-gray or granular layer. At the junction of these two layers are found the large, flask-shaped cells called the cells of Purkinje. It has been known for some time that these cells send branches toward the periphery, and that an axis-cylinder process from them is directed toward the fibrous center of the convolution.

When stained by the Golgi method, these cells remind one of the psychic cells of the cerebrum in their size and general arrangement. Yet there are some striking differences. From the large, spheroidal cell body there are given off two or more trunk-like processes, which branch quite extensively and have upon them spines like those upon the panicles of the psychic cells. This ramification does not extend in all directions, but is, as Obersteiner has aptly said, like that of an espalier fruit tree—expanded in two dimensions only, so that when a section is taken across a convolution the processes show as large and fan-like (Fig. 22, *a*), while a section lengthwise of the convolution shows only an edge not occupying more space than the width of the cell body (Fig. 23, *d, d*). The cells lie in a single narrow stratum of the cortex. From the lower portion of each

a well-marked axis-cylinder process is given off from which collaterals pass to ramify about the processes of neighboring cells, probably assisting to correlate the action of these elements.

Two other classes of cells are in intimate relation with the cells of Purkinje. First, small, stellate cells of the outer layer (Fig. 22, *b, b*), whose axis-cylinder processes run transversely—that is to say, parallel to the plane of ramification

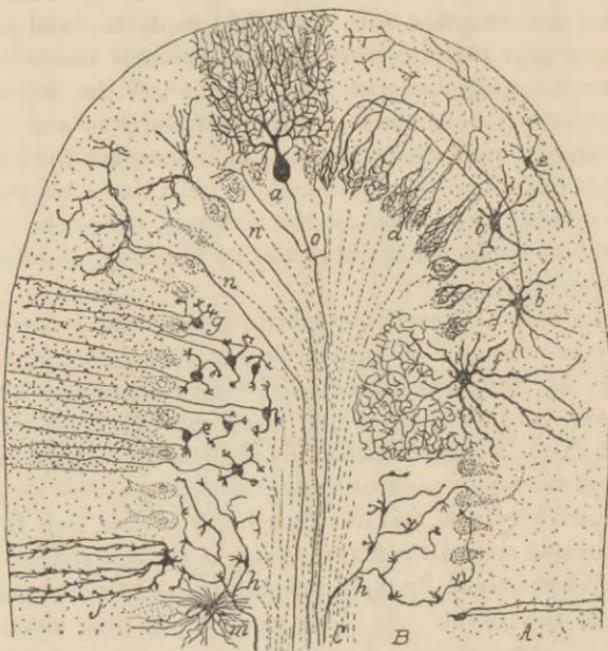


FIG. 22.—Transverse section of a convolution of the cerebellum. A. Molecular layer. B. Granular layer. C. White substance. *a*, Purkinje's cell, front view; *b*, small stellate cells of the molecular layer; *d*, descending terminals that surround the cells of Purkinje; *e*, superficial stellate cells; *f*, large stellate cells of the granular layer; *g*, granules with ascending axis-cylinder processes bifurcating at *i*; *h*, mossy fibers; *j*, neuroglia cell with radial processes; *m*, neuroglia cell with diverging processes; *n*, scendant fibers; *o*, axis-cylinder fiber of a cell of Purkinje sending collaterals to adjacent cells.

of Purkinje's cells, giving off collaterals that pass downward and break into fine tufts, enveloping the body of those cells in a fine basket-like reticulum, the *Endkorben* of Kölliker. These cells correlate with themselves the Purkinje cells of a single transverse system.

Second, the granular cells of the inner layer, elements concerning which there has been much dispute, Henle and Merkel considering them as lymphatic elements, Gerlach and Kölliker holding that they are of a connective-tissue character, while Obersteiner thought that they were special elements peculiar to this tissue. They are now known to be small polyhedric nerve cells with short protoplasmic processes ending abruptly in tufts, and with axis-cylinder processes that ascend into the outer layer and there divide, T-like, into branches that run parallel to the convolutions, at right angles to the plane of ramification of the cells of Purkinje. These *parallel fibers* (Fig. 23, *b*), as they are called, run for long distances, connecting the Purkinje cells of different transverse systems. They seem finally to terminate freely.

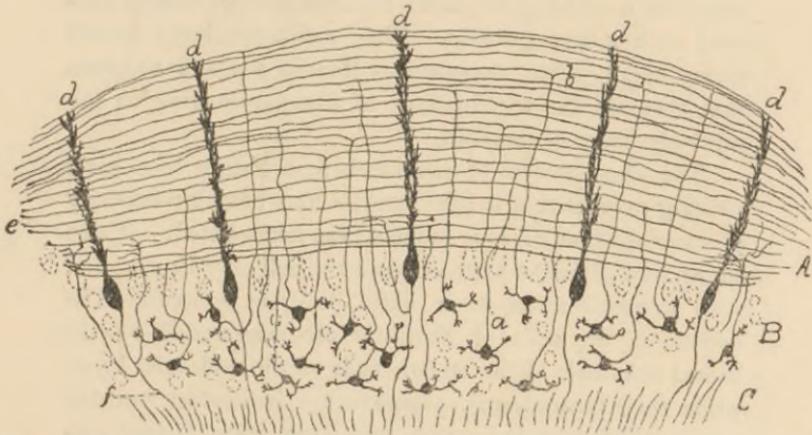


FIG. 23.—Longitudinal section of a convolution of the cerebellum. A. Molecular layer. B. Granular layer. C. White substance. *a*, ascending axis-cylinder process of a granule; *b*, bifurcation of that process to form a parallel fiber; *d*, *d*, *d*, Purkinje's cell seen in profile; *e*, granular terminations of the parallel fibers; *f*, axis-cylinder process of a cell of Purkinje.

Cells of still another class are found here and there in the inner layer—the so-called large, stellate cells (Fig. 22, *f*). These send their protoplasmic processes far toward the surface, while their axis-cylinder processes give off innumerable collaterals that divide and subdivide into finely interlacing branches that occupy nearly the whole of the molecular zone around the granules.

It is difficult to come to any definite conclusion with

regard to fibers coming from other regions, as their length is so great that even in the smallest animals there is no possibility of tracing their course from the cells of origin to their termination. Two kinds of terminals are found, both of a very special character.

The afferent fibers for the cells of Purkinje pass up from the medullary substance into the molecular layer and there divide into branches that apply themselves to the corresponding ramifications of the Purkinje cells, ascending among them, as Ramón y Cajal says, like a liana among the branches of a tropical tree. For this reason he named them the climbing or scandent fibers (*fibras trepadoras*).

The afferent fibers for the granular cells of the inner layer are thick and richly ramified. At short distances they present tufts of short diverging branches that terminate freely. This gives them the aspect of a branch covered with mossy growths. They are accordingly named mossy fibers (*fibras musgosas*). Ramón y Cajal suggests that they are the terminations of fibers belonging to the cerebellar tract of the cord.

The whole system of the cerebellum shows in a most striking manner that it is by contact and not by continuity of structure that nervous impulses are transmitted. It also shows that different parts of the same cell may be supplied with terminal fibers from quite different sources. The bodies of the cells of Purkinje are surrounded by the basket terminals of the stellate cells of the molecular layer, while their protoplasmic processes are in contact with the scandent, afferent fibers that arise from more distant portions of the nervous system.

Such being the general plan of constitution of the nervous centers and of the nerves arising therefrom, there still remains to be considered the nervous structure of the organs of special sense—the nose, the eye, and the ear. It is well known that the olfactory bulb and the retina are, morphologically speaking, portions of the brain. In many lower animals the bulb is seen to be a distinct lobe projecting from the hemispheres and provided with its own special ventricle, and in the embryo the retina is found to be the invaginated end of a stalk-like outgrowth from the older portion of the fore-brain. We might

therefore expect to find in these organs an arrangement somewhat similar to that of the cerebral cortex.

The ear has a somewhat different history, and is rather to be compared to a peripheral sense organ that has been gradually withdrawn from the surface, like the spinal ganglia.

*Olfactory Organ.*—The active cortical agents are represented here by large bifurcated elements called mitral cells

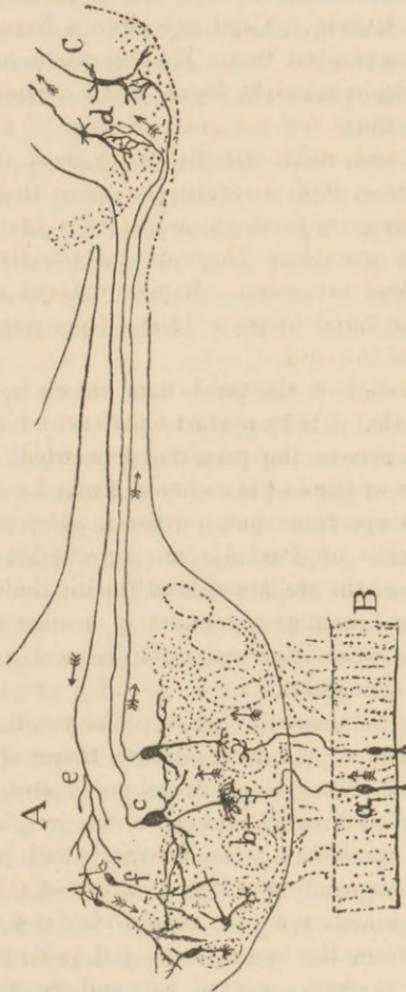


FIG. 24.—Olfactory bulb (Ramón y Cajal). Diagram showing the course of nervous currents. A. Olfactory bulb. B. Mucous membrane. C. Hippocampal region of the cerebrum. a, bipolar cell of the mucous membrane; b, glomerules; c, mitral cells; d, cells of the cortex cerebri; e, centrifugal fibers; f, amacrine cells.

(Fig. 24, c). These lie in the olfactory bulb in the so-called intermediate or nerve-cell layer. Like the psychic

cells and the cells of Purkinje, these send toward the periphery a trunk that breaks up into a tuft of convoluted and varicose processes and give off an axis-cylinder process which extends centrally and ends in the hippocampal area of the general cortex. The olfactory sensations are brought to these by means of true bipolar æsthesioblasts situated in the olfactory membrane. These present externally one short process for collecting sensations, while from the opposite end a process leads centrally to end in a convoluted tuft that closely intertwines with the similar tuft on the peripheral process of a mitral cell. These intertwining varicose tufts form the *olfactory glomeruli*, which have hitherto puzzled anatomists so much.

It will be seen that the æsthesioblasts preserve the primitive form found in invertebrates throughout the surface of the body. The olfactory membrane is therefore to be compared to a spinal ganglion in which the elements have become spread out superficially. The investigations of His with reference to their development fully confirm this.

Neuroglia cells in considerable numbers are found about the æsthesioblasts. They appear to perform an insulating function and preserve the primitive form which has been spoken of as occurring in the embryonic spinal cord.

Besides the apparatus just described, which appears to be solely for the purpose of receiving and transmitting sensations, other cells are found which, with their connections, appear to constitute a regulating or correlating apparatus. These—the amacrine cells (Ramón y Cajal)—are situated within the deeper or so-called granular layer of the olfactory bulb, and have this special peculiarity, that they have no process presenting the appearance of an axis-cylinder process. They are small and polyhedral, having a tuft-like expansion directed centrally and a peripheral stem that sends out plume-like processes that come in contact with the lateral expansions of the mitral cells. The centrally directed processes are in contact with the terminals of centrifugal fibers that come in along the olfactory tract.

Certain stellate cells scattered here and there throughout the granular layer appear to be large-sized modifications of the granular cells and to have similar connections.

It will be seen from Fig. 24 that the path of the sensory impulses is quite simple. Received upon the æsthesioblasts at *a*, they are transmitted to the glomeruli at *b*, thence to the mitral cells *c*, and finally taken up by the hippocampal region at *d*. The regulating mechanism passes from the central organs through the fiber *e*, thence to the granular cells *f*. In either centripetal or centrifugal path but two neurons are employed.

*The Retina.*—The nervous apparatus of the retina is highly specialized and the homology of the different structures with those found in the cortex is by no means clear. In this case the æsthesioblasts appear to be the rods and cones which are situated upon that surface of the cerebral outgrowth which was originally free and ventricular, therefore a part of the primitive medullary groove. These, like æsthesioblasts elsewhere, are bipolar cells with a specialized cellulipetal expansion for collecting impulses, and another cellulifugal for distributing them to other cells. These nuclei are contained in the so-called layer of visual cells and their cellulifugal expansion is found in the external plexiform layer. The latter differs somewhat for the two classes of cells, the rods ending in small spherules, the cones breaking up into laterally expanded tufts (Fig. 25).

The great cells of the ganglionic layer correspond apparently to the psychic cells of the cortex, as they send an axis-cylinder process brainward along the optic nerve and throw out collecting expansions. There is, however, interposed between them and the æsthesioblasts an apparatus which apparently has for its object the assorting of sensations derived from special cells. This apparatus occupies the internal granular layer, and is composed of, first, a series of bipolar cells that take up impulses from the rods and cones and deliver them to the ganglion cells; second, a series of laterally extended cells (Fig. 26) that correlate elements of different localities.

The cellulifugal processes of the rod bipolars all appear to end at about the same level, but the cone bipolars represent the remarkable peculiarity of ending at definite and distinct levels in the internal plexiform layer. In mammals at least five such levels can be made out, and in birds seven (see Fig. 25).

The laterally extended cells are of several different varieties. Some lie within the external plexiform layer and connect the bases of the rods and cones. These, as described by Ramón y Cajal, have the usual short cellulipetal

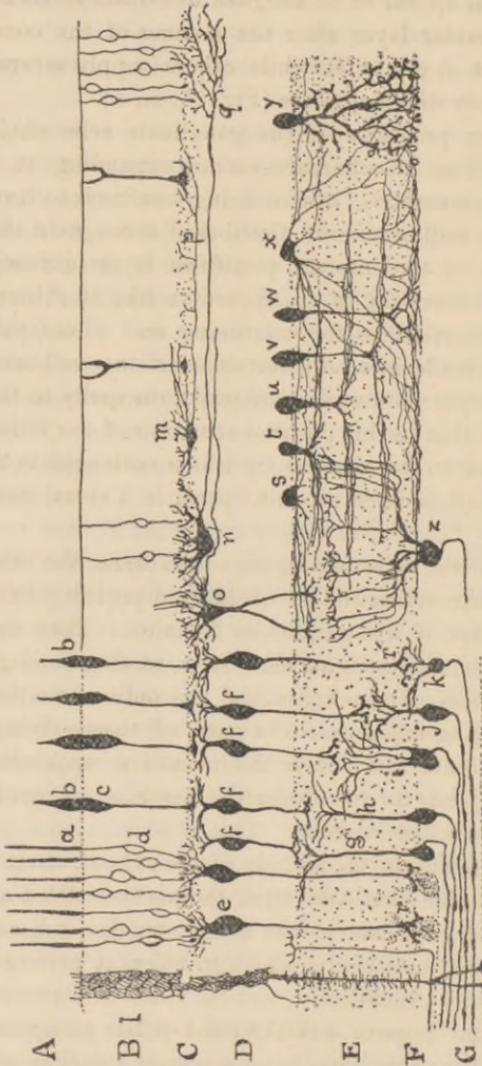


FIG. 25.—Cross section of the retina (Ramón y Cajal). A. Layer of rods and cones. B. External granular layer. C. External plexiform layer. D. Internal granular layer. E. Layer of ganglionic cells. G. Layer of nerve fibers.  $\alpha$ , rod;  $\beta$ , cone;  $\gamma$ , cone nucleus;  $\delta$ , rod nucleus;  $\epsilon$ , rod bipolar;  $f$ , cone bipolar;  $g$ ,  $h$ ,  $i$ ,  $j$ ,  $k$ , ganglionic cells branching at different levels of the internal plexiform layer;  $l$ , neuroglia cell or fiber of Müller;  $m$ , small or external horizontal cell;  $n$ , internal or large horizontal cell;  $o$ , same with descending processes;  $p$ , axis-cylinder process of cell  $m$ ;  $q$ , terminal tuft of cell  $n$ ;  $r$ , inferior ramification of the rod bipolar;  $s$ ,  $t$ ,  $u$ ,  $v$ , amacrine cells branching in distinct layers of the internal plexiform layer;  $x$ ,  $y$ , diffuse amacrine cells;  $z$ , bistratral ganglion cell.

processes and an extended axis cylinder which may give off collaterals or terminate as a varicose tuft (Fig. 25,  $a$ ,  $b$ ). Sometimes processes from these cells descend to the internal plexiform layer (Fig. 25,  $c$ ). But the most curious

and apparently the most important of these elements are the *amacrinal* cells similar to those of the olfactory membrane that form the deepest stratum of the internal granular layer.\*

Some of them appear to be assigned to certain levels of the internal granular layer after the manner of the cone bipolars (Fig. 24, *f, g, h, j, l*), while others supply several layers by obliquely directed fibers (Fig. 25, *m, n*).

The collecting processes of the ganglionic cells adapt themselves to these peculiarities—some expanding in a single layer (monostratal), others being confined to two (bistratal), while still others are distributed throughout the entire thickness of the internal plexiform layer (diffuse). It can easily be seen that in an apparatus like this there are marvelous possibilities for combining and co-ordinating impressions made upon the terminals of the *æsthesioblasts*. If color perceptions are assigned principally to the cones, it may be that in this peculiar structure of the retina we possess a clew to the method by which such sensations are sorted out and isolated so as to produce a visual concept.

Like those of the olfactory mucous membrane, the neuroglia cells of the retina (fibers of Müller) probably have an isolating as well as a sustentacular function. They also preserve the primitive spongioblastic type, passing through the entire thickness of the organ and expanding at either end into limiting membranes. The outer of these—being, as Minot has pointed out, near the primitive ventricular surface—corresponds to the *limitans interna* of the cord; the inner, to the *velum confine*.

In Fig. 26 are shown the courses of the currents excited by visual impressions received upon the retina. That affecting a cone, *a*, is transferred to a cone bipolar at *b*, and thence to the ganglionic cell, *c*, which transfers it by means of its axis-cylinder process, *d, e*, and its terminal filaments, *f*, to cells of the *corpora quadrigemina* or the geniculate bodies at *g*. These may refer it to a central ganglion at *j*

\* These are the spongioblasts of W. Müller. As His has applied this term to embryonic neuroglia cells, for which it seems more aptly fitted, it seems better to adopt the name in the text proposed by Ramón y Cajal.



elements, like the terminals of the sensory nerves that supply epithelium in other regions. The true *æsthesioblasts* lie in ganglionic masses, situated, for the cochlear nerve, in the *ganglion spirale*; for the vestibular nerve, in the little-known *intumescentia gangliiformis* of Scarpa (see Fig. 27) that is found in the internal auditory meatus.

The distribution of the processes is essentially the same in both cases. The cellulipetal process ramifies between and about the epithelial cells (see Fig. 28); the cellulifugal process passes brainward and, on reaching the central ganglia, divides like the processes of an *æsthesioblast* of a spinal nerve.

It would appear that we have here, as in so many cases in the cranial nerves, traces of an earlier phylogenetic condition. The *æsthesioblasts* have been withdrawn from the surface as in the case of the spinal nerves, but not to so remote regions. They show traces also of their primitive condition in that they remain bipolar, as in fishes, never assuming a unipolar type as in the spinal ganglia.

By this hasty review of the main features of the new discoveries it will be seen that we are entering upon an entirely new era in investigations of the nervous system. We experience something of the shock which an inhabitant of the temperate zone might feel if suddenly placed in the midst of an unknown tropical forest, surrounded on every side by new and strange forms. All the ideas that we have had concerning the development and interrelations of the structures must be revised. It is evident that we are as yet on the very threshold of inquiry; the entire nervous system must be re-examined, the history of every ganglionic center must be traced. This is rapidly being done, and we may expect that in the next few years important additions to our knowledge will be made, which

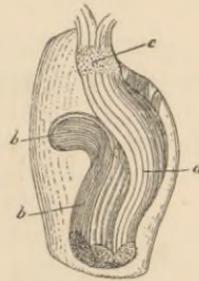


FIG. 27.—Auditory nerve in the internal auditory meatus (Schwalbe). *a*, vestibular nerve; *b, b*, cochlear nerve; *c*, ganglion of Scarpa (*intumescentia gangliiformis* Scarpæ).

will be unquestionably followed by practical results of great moment.

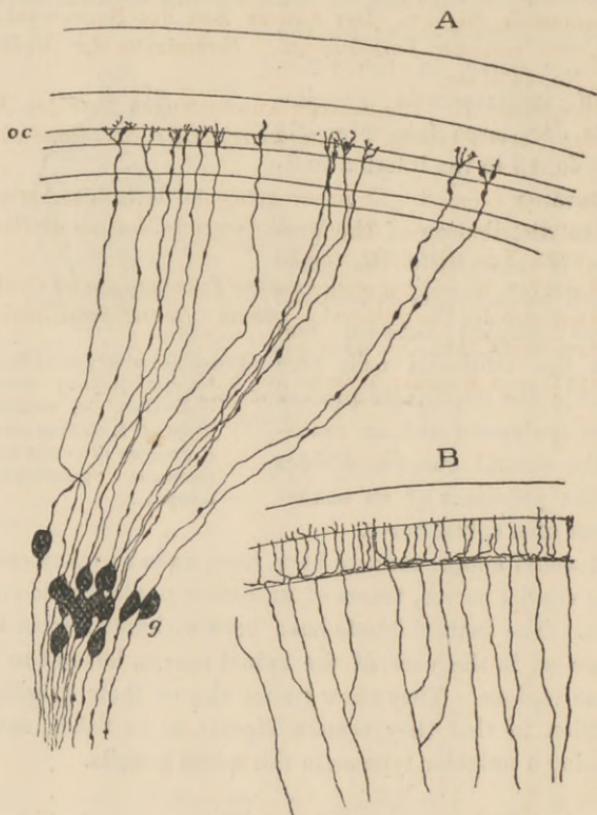


FIG. 28.—Terminations of auditory nerve (Retzius). A. Part of the lamina spiralis of a mouse four days old, showing bipolar ganglion cells springing from the ganglion spirale, *g*, and ending in the organ of Corti, *oc*. B. Part of the organ of Corti of a mouse showing branched nerve fibers.

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