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SOME UNDERLYING PRINCIPLES IN THE STRUCTURE OF THE NERVOUS SYSTEM[1]

IT has long been recognized that the fundamental problems of the nervous system are impossible of approach without keeping in view continually the finer structure of the parts concerned. Nervous organs are not relatively homogeneous bodies as, for instance, glands are, but are intricate systems of conducting paths and end-stations and in this respect are unlike the other organs of the body. This contrast appears clearly in many deficiency tests. If a portion of a gland, such as the pancreas or the liver, is removed, the loss may be quickly covered by the increased activity of that part of the organ which is left, but the ablation of even a small portion of a nervous organ is often followed by serious and permanent defects, which no amount of activity on the part of the adjacent tissue can make good. Thus the destruction of a small group of the receptive cells in the retina results in a scotoma, which the activity of the adjacent cells is incapable of remedying. Hence it appears that in the nervous system specialization may be said to have reached even to the cells themselves. Such a degree of differentiation is to be found in no other organ of the body, except perhaps the reproductive glands, whose sperm cells and egg cells, with their highly individualizing capacities, are separately quite as unique as are many nerve cells. It is, therefore, not sur-

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[1] Address of the vice-president and chairman of Section F, American Association for the Advancement of Science, Pittsburgh, December 31, 1917.

prising that neurologists have devoted much of their energy and time to discovering the disposition and arrangements of the cells in nervous organs.

Notwithstanding the fact that the cell doctrine as applied to animals was enunciated by Schwann as early as 1839, it was not till more than half a century later that a clear and consistent idea of the nerve cell was arrived at. The slowness with which this result was attained was due to the unusual form and complicated structure of this element. Nerve fibers, according to Stieda (1899), were probably first really seen and figured by the Florentine physician Felix Fontana in 1781, but it was not till 1833 that Ehrenberg in the preliminary announcement of a monumental work on the fibrous structure of the central nervous organs, described certain corpuscles that proved to be what later investigators called ganglion cells. The connection of these two elements, vaguely intimated in 1838 by Remak and surmised in 1840 by Hannover, was first really demonstrated for invertebrates in 1842 by Helmholtz and for vertebrates in 1844 by Kölliker who showed that fibers with a medullary sheath, and therefore unquestionably nervous, were directly connected with ganglion cells. From the time of these discoveries it became necessary to assume that in some way or other ganglion cells were an essential element in the nervous system. Their association with ganglionic masses and other deeper organs led naturally to the view that they were the real centers of nervous activity, the fibers being regarded as elements of conduction merely. Hence arose that infinite collection of diagrams of nervous mechanism devised by the neurologists and copied by the physiologists and psychologists of some two generations ago and consisting usually of an afferent fiber leading from the periphery to a centrally situated ganglion cell from which in turn an efferent fiber stretched out to a muscle or other like end-organ.

But the nervous system is not constructed upon so simple a plan. In 1847 Wagner showed that the ganglion cells in the electric lobes of the torpedo exhibited two types of processes. These were subsequently designated as protoplasmic and nerve-fiber processes by Deiters (1865), who attempted to support the generalization that every ganglion cell possessed both types of processes.

Not only did complications grow in these directions, but in 1855 Leydig discovered in the ganglionic bodies of spiders what appeared to be a finely granular material which he called punctate substance. Similar material was also shown to be a considerable constituent in the gray matter of the vertebrate nervous system. Hence, in addition to nerve fibers and ganglion cells, a third kind of material was shown to be present in many nervous organs.

This material, as was subsequently demonstrated by Gerlach (1871) and others, consisted in reality of very fine fibrils which when seen in section appeared as minute points; hence Leydig's name for it of punctate substance. From these very fine fibrils nerve fibers were seen to take their origin and thus arose the dispute over the direct and the indirect origin of nerve fibers, that is, their origin directly from ganglion cells or indirectly from these cells through the intervening fibrillar substance.

The confusion to which this discussion led was cleared up and swept away by the introduction of the Golgi method of silver impregnation, a method that yielded preparations so marvelously clear and sharp that for the first time the relations of nerve fibers, ganglion cells, and fibrillar material seemed within grasp. Although this method was described as early as 1873, it did not come into general use till nearly a decade and a half later. Nevertheless, as soon as it was generally applied, it yielded such important results that in May, 1891, Kölliker could substantiate the claim that every nerve fiber in the body was at some part of its course directly connected with a ganglion cell, and in June of the same year Waldeyer, on the basis of conclusions drawn largely from Golgi preparations, promulgated the theory of the neurone, the first consistent account of the nerve cell.

According to this well-known doctrine the ganglion cell of the older workers is really the nucleated body of the true nerve cell, or neurone, whose processes may be of two kinds: short, branching, protoplasmic extensions, the dendrites; and long, unbranched, nerve-fiber processes, the neurites. As all nerve fibers were believed to be thus related to nerve cells they were at once classed as a special type of cell process. Further, the fibrillar material of the central gray, the punctate substance, which was regarded by Gerlach (1871) as a continuous network, was now looked upon as the ultimate branches of the dendrites and neurites, the means by which one neurone is put into communication with another. Hence this material was believed to be broken up into appropriate neuronic systems separated one from another by an infinitude of minute interruptions, which, however, were capable of physiological continuity through what is known as a synapse. Thus each neurone, or true nerve cell, was believed to possess a certain amount of independence from its neighbors though physiologically united to them at least by transmitting contact. This in brief is the conception of the neurone, or true nerve cell, a conception that has been most prolific in its consequences not only as a means of understanding the structural relations of nervous elements but of interpreting their degeneration as originally outlined by Waller (1850), their regeneration as worked out by subsequent investigators, and their development as first clearly described by His (1886).

This conception, however, was not based on what can be seen in Golgi preparations only; it was confirmed and supported by a great array of results such as have been obtained by Ehrlich's methylen-blue treatment and by the host of new metal-impregnation methods modelled more or less on the original Golgi procedure.

In considering the activity of the typical vertebrate neurone, it is generally recognized that the nerve impulse enters this element through its dendrites and, after traversing its cell body, emerges from it through its neurite. This is very clearly seen in the motor neurones of the spinal and the cranial nerves (Fig. 1). Here the dendrites of the given neurone are in close relation with the neurite processes of other neurones (*d*) from which they receive nerve impulses that are passed on through their own cell body and over its neurite to be discharged finally into the attached muscle fibers (*m*). As in such series the dendrites serve as a receptive mechanism and the neurite as a discharging one, it may be claimed that the neurone exhibits a kind of cellular polarity in which the dendrites

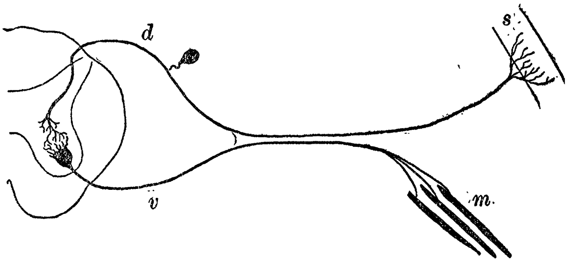

FIG. 1. Diagram of the primary neurones of the spinal cord; the dorsal neurone (*d*) extends from the skin (*s*) to the central gray of the cord, the ventral neurone (*v*) from the central gray to the muscles (*m*).

mark one pole and the neurite the other. This idea of the polarity of the neurone seems to have originated with van Gehuchten (1891), but on its announcement it was immediately taken up, amplified and strongly advocated by many other neurologists, especially by Ramón-y-Cajal (1891) and by Retzius (1892). Even now it holds a place in good text-books such as Herrick's Introduction to Neurology (1915), but it has never been without its serious opponents.

Barker (1899) in his account of the nervous system pointed out numerous and serious exceptions to it. The intermediate neurones of the vertebrate retina (Fig. 2, *i*) receive impulses by one system of processes and discharge them by another; yet the discharging processes have none of the structural peculiarities of neurites, but closely resemble the receiving processes, which are indistinguishable from dendrites. Again the sensory neurones of the spinal and the cranial nerves (Fig. 1, *d*) have their cell bodies on their length and not terminal, but their distal processes, which by definition should be dendrites, are from the standpoint of structure in all respects neurites, as are their proximal processes. Hence arises the difficulty that in some instances dendrites, though usually receptive in function, may discharge, and neurites though usually discharging in function, may receive. These and other like causes make it clear that any attempt to define neuronic polarity on the basis of dendrites and neurites is foredoomed to failure, for whatever may be the explanation of the difference between the two classes of processes, it is not necessarily connected with the direction in which they transmit impulses. This conclusion, moreover, is supported by what is known of invertebrates. Here it is commonly quite impossible by any of the structural tests used in vertebrates to distinguish dendrites from neurites. In fact the processes at the two poles of the cell seem to be essentially similar and both tend to resemble dendrites.

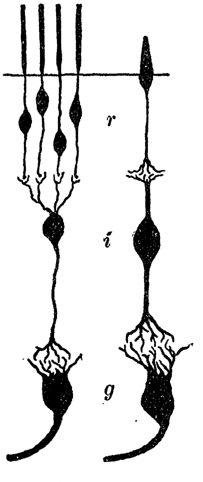

Fig. 2. Diagram of the chief nervous elements in the vertebrate retina; rod- and cone-cells (*r*), intermediate cells (*i*), and ganglion cells (*g*).

But in my opinion the chief reason the hypothesis of neuronic polarity as ordinarily stated meets with serious difficulties is not because of the complications that arise when dendrites and neurites are involved, but because nervous activity is commonly described in reference to the cell body of the neurone. Certain parts of the neurone are said to transmit toward the cell body or cellulipitally and other parts are said to conduct away from this body or cellulifugally. But polarity established upon this basis is surely upon very insecure ground, for it involves the assumption that the cell body of the neurone is the center of nervous activity, an assumption which has come down to us from the past, but in support of which little can really be said.

To be sure neurofibrils have been abundantly identified in the cell body of the neurone, but they have never been shown to extend in any particular way to the structure that is most characteristic of the cell body, namely, the nucleus. Structurally, therefore, there is no special reason for assuming that the nucleus and its surrounding cytoplasm constitute a special nervous center. Moreover, as Bethe (1897, 1898) and Steinach (1899) have shown, certain neurones may continue to function for some considerable time after the removal or destruction of their cell bodies, thus demonstrating very clearly that these bodies are not a necessary part in the internal nervous mechanism of the neurone.

But not only can it be shown that the cell body with its contained nucleus is not essential to the nervous organization of the neurone, it can also be shown that this part has a very definite, specific and non-nervous function of its own. It has come to be an admitted fact in cytology that the nucleus of a cell is in some very direct way essential to the normal metabolism of that element, for when a cell is cut into pieces the non-nucleated fragments are incapable of further growth and invariably die, whereas the nucleated part may regenerate and continue to live. To this rule the nerve cell seems to be no exception, for when a nerve fiber is separated from the rest of the neurone, it invariably undergoes degeneration and death. The nucleated part meanwhile usually remains intact, and is the part from which a new nerve fiber will grow out if one is formed at all. Thus the nucleated and non-nucleated parts of the neurone act in the same way as the corresponding parts of an ordinary cell do and hence it is concluded that the nucleus of the neurone, like that of the ordinary cell, is a structure essentially concerned with metabolism. In this way only is the nucleated part of the neurone necessary to nervous processes. The older neurologists were certainly quite mistaken when they regarded what they called the ganglion cell as the center of nervous activity. It is the metabolic or trophic center of the neurone, but, though it may be invaded by neurofibrils, it is not a seat of special nervous function. Hence how misleading and erroneous is it to discuss the nervous polarity of the neurone as though it centered on the cell body of that structure!

The polarity of the neurone is best described in the statement that nerve impulses are received at one end of it and discharged at the other. From this standpoint polarity is not necessarily associated with dendrites and neurites or with the cell body, but depends upon the positional relations of the neurone as a whole, especially in reference to the rest of the animal's body, including, in particular, other neurones. If one end of a neurone forms a part of a sensory surface, that end naturally serves as the receptive end and the opposite one becomes the region of discharge. If the neurone is imbedded in central nervous organs, its polarity is apparently determined by the nature of the synapses. Thus, though an impulse can be transmitted in either direction within the limits of a single neurone, it can pass from one neurone to another only in one direction. This principle is well illustrated by the Bell-Magendie law as extended by the observations of Gotch and Horsley (1891), Mislawski (1895), Veszi (1909) and others. When a stimulus is applied to the central end of the cut dorsal root of a spinal nerve (Fig. 1), the ventral root exhibits an electrical change and the muscles connected with it contract showing that a nerve impulse has passed through the cord from the dorsal to the ventral side. When on the other hand the central end of a ventral root is stimulated, no change of any kind whatsoever can be discovered in the dorsal root, showing that the same path can not be traversed in the reverse direction. As intraneural conduction is well known to occur in both directions this interruption is believed to be interneural, that is, synaptic; hence the conclusion that the synapse is a valve-like mechanism that permits the passage of an impulse in one direction only. The polarity of a deep-seated neurone then is determined by its synapse.

If we divest our minds of the assumed nervous significance of the cell body of the neurone and of all the misleading terminology of cellulipetal and cellulifugal conduction in relation to dendrites and neurites, we have left the simple proposition that neurones, though capable of double conduction within themselves, nevertheless conduct normally in one direction only. This is the real and sufficient basis for neuronic polarity. That it is partly dependent upon the synapse is quite obvious. For this and other reasons the synapse has been a matter of much concern to neurologists, but its extreme minuteness has been a baffling feature in its investigation. The researches of His (1886) supported by those of Harrison (1901) and others have shown that in many parts of the nervous system neuroblasts that give rise to contiguous neurones in adult neuronic chains may be in embryonic stages far separated and come together only after considerable growth. Of their initial separation there can be not the least doubt; the question that naturally arises concerns the extent of their final union as they establish synaptic relations. That this can not be complete has already been pointed out in discussing synaptic transmission, but precisely what the incompleteness consists in from a histological point of view is by no means easily determined. Bartelmez (1915) has had the opportunity of studying the synapse under conditions in which the elements were extremely coarse (the Mauthner's cells of fishes) and he finds, as might have been expected, no continuity, but delicate membranous separations. These membranes must be the parts concerned with synaptic activities and hence with the polarity of the neurone so far as it is dependent upon the synapse.

Thus after years of infinite pain and labor the neurologist of to-day can describe in terms of cells the nervous system of one of the higher animals as composed of an intricate association of neurones whose relations to the animal as a whole and to each other through synaptic contact have impressed upon these structures a definite form of polarity.

As this idea of the synaptic nervous system gradually unfolded itself to the more orthodox neurologists, there arose from another school of workers the diametrically opposite conception of the nerve-net. This new movement received its initial impetus chiefly from the work of Apáthy (1897), who maintained on the basis of preparations of almost incredible clearness that the nervous elements of many animals were bound together by a network of neurofibrils in which there was not the slightest evidence of interruption such as is implied in the synapse. This view in a way was a revival of the idea of a continuous network as maintained in a previous generation by Gerlach. The careful reader of Apáthy's papers will find it by no means easy to separate in them fact from speculation and consequently it is difficult to state in exact terms Apáthy's real contribution to this subject, but, however this may be, it is certainly true that the appearance of his publications excited others to a further investigation of the subject with the result that nerve-nets were proved to exist in a number of animals. They were definitely identified by Bethe (1903) in jelly fishes, by Wolff (1904) and by Hadzi (1909) in hydrozoans, and by Groselj (1909) in sea-anemones. In fact the coelenterate nervous system seemed to be nothing but a nerve-net. Von Uexküll's physiological studies led to much the same conclusion concerning the nervous system of echinoderms. Prentiss (1904) in a brief summary gathered together the evidence to show that nerve-nets were at least components of the nervous systems of worms, arthropods, mollusks and even vertebrates (Fig. 3) where they were especially associated with the blood vessels (Dogiel, 1893, 1898; Bethe, 1895, 1903; Leontowitsch, 1901; Cavalié, 1902; Prentiss, 1904), including the heart (Dogiel, 1898; Hofmann, 1902; Bethe, 1903). Moreover, it is now regarded as probable that there is a nerve-net associated with the musculature of the vertebrate digestive tube. Thus nerve-nets were identified from the cœlenterates to the vertebrates and some of the more ardent advocates for this type of nervous organization went so far as to assume that it was the only type of nervous structure really extant and that the evidence for a synaptic system rested upon artifacts that obscured the real relations of cell to cell. But this extreme position has not been justified by further research. It is now generally admitted that the conceptions of a synaptic system and of a nerve-net are not opposing ideas, but represent two types of nervous organization, both of which may exist side by side in the same animal (Herrick, 1915; Bayliss, 1915). Judging from the fact that the nerve-net is apparently the exclusive type of nervous organization in the cœlenterates and that it becomes progressively less and less evident the higher one ascends the animal series, it seems fair to conclude that the nerve-net is the more primitive type and that in the course of evolution it has given way more and more to the synaptic system which has finally come to be the dominating plan of nervous organization in the higher animals. From this standpoint one of the higher metazoans might perfectly well possess both types of nervous structure: nerve-nets having been retained in its more conservative portions and synaptic structures having been developed in its more progressive parts. Thus the nerve-net may be regarded as phylogenetically older than the synaptic system.

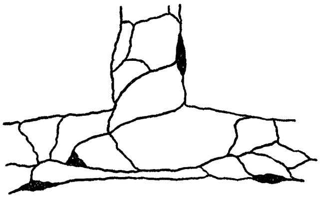

FIG. 3. Outline of a nerve-net from a vertebrate blood-vessel (after Prentiss).

If this view of the relation of nerve-nets and synaptic systems is correct, there ought to be found in the animal series evidences of transitions from one type to the other. Herrick (1915) has stated very clearly the essential differences between these two types in the declaration that in nerve-nets there are no synapses and no polarity, both of which characterize the more differentiated type. The many illustrations that have been used to show the structure of nerve-nets from the cœlenterates to the vertebrates exhibit continuous diffuse nets without the least suggestion of synapses. Some of the best of these examples are from the subumbrellar surfaces of jellyfishes. Here, too, conduction has been studied for a long time and it has been shown through the work of Romanes (1877) and others that transmission in these regions is as diffuse and general as would be expected from the structure of their nets. Probably the only evidence of polarity that these nets exhibit is seen in the temporary condition that has been claimed for them by von Uexküll, namely, that impulses flow for the moment more freely through them into stretched regions than into unstretched regions. Aside from this momentary state they are probably quite unpolarized in their transmitting capacities.

From such a condition as this it ought to be possible to trace the transition stages that have led to the synaptic nervous system, and, in fact, examples of this kind are not difficult to find. As a first step in this direction we may examine the tentacles of sea-anemones. These organs were shown by Ránd (1909) to exhibit in their responses to stimulation a marked polarity. If a stimulus is applied to the tip of a tentacle, the whole tentacle usually shortens. If it is applied to any other point on the tentacle, this organ shortens as a rule only from the point stimulated to the base, the distal portion of the tentacle remaining unchanged. Hence it may be concluded that transmission does not proceed from any region in the tentacle freely in all directions, but only towards its base; in other words, the tentacle exhibits polarity. As this polarity disappears on treating the tentacle with chloretone or other anesthetizing agents, it is clear that it is a nervous polarity. The neuromuscular mechanism of the tentacle is well known to consist of peripheral sense cells whose deep ends are much branched constituting a nerve-net that is applied to the longitudinal muscle cells of the tentacular ectoderm. The polarity of the tentacle depends upon a peculiarity in the structure of the sense cells as pointed out by Groselj (1909), namely, that most of the fibrous prolongations from the deep ends of these cells, instead of spreading out in all directions, extend down the tentacle towards the base. Hence, when the sense cells are stimulated, nerve impulses are generated, which, in consequence of the direction of the cell fibers, are conducted into the proximal portion of the tentacle, where they call forth the contraction of the longitudinal muscle cells. Here then is the first evidence of permanent nervous polarity such as is so clearly shown in the neurone. It occurs in a nerve-net without synapses, but so organized that its fibrous constituents, instead of being diffusely arranged, have a predominating trend in one direction.

Judging from the nature of the responses, polarized nerve-nets occur in many other places. Thus the stalk of the giant hydrozoan, *Corymorpha,* has recently been shown to transmit nervous impulses more freely on its length than transversely, a condition that immediately suggests a locomotor waves that pass over the foot of a creeping snail are believed with good reason to depend upon the presence of a nerve-net, in which case the net must be strongly polarized, for these waves are limited in almost every instance to a single direction. In a similar way the peristalsis of the vertebrate digestive tube implies a polarized net in the wall of that structure.

Thus the primitive, diffuse, or apolar, nerve-net may be imagined to undergo the first change toward a synaptic system by becoming polarized, a process that may be described as due to a lengthening of its fibers in one direction, whereby transmission in that direction predominates over transmission in any other. The cells whose processes exhibit this change are the ordinary sense cells and nerve cells of the nerve-net. They may be looked upon as the forerunners of neurones, protoneurones so to speak, and from them have arisen by further differentiation the highly specialized nerve cells of the synaptic system. Thus we can picture to ourselves the initiation of that process which resulted in the production of longer and longer transmission tracts such as we find in the central nervous organs of the higher animals, whereby nerve cells once near neighbors come to be widely separated. In their ontogenetic recovery of connections thus temporarily lost they seem to have failed to reestablish a complete union. This feature of partial recovery, at first a mere incident of growth, contained within it a germ of first importance, for out of it was differentiated the synapse, a device that reinforced the original polarity of the nerve cell and established a new range of nervous possibilities from which have evolved those highly organized adjustments that make the abode of man's intelligence, his cerebral cortex, so different from the nerve-net of his digestive tube.

It will be interesting as new discoveries are made in this field of research to follow in detail the transition from the nerve-net to the synaptic system. At present little is known about this subject, but a very suggestive and interesting contribution has been made to it by Moore (1917). It has long been known that strychnine greatly heightens the reflex excitability of many animals and it has been commonly assumed that this action is due to the reduction under the influence of this drug of the synaptic resistances. This being the case strychnine may be used as a test for the presence of synapses. From this standpoint Moore's results are of extreme interest, for he has found that the drug has no effect on the neuromuscular responses of cœlenterates, a slight one on echinoderms, and a much greater one on crustaceans and mollusks, a series that leads up to the well-known condition in vertebrates and suggests in its continuity that the effects are dependent upon the appearance and degrees of differentiation of the synapse.

Although the nucleated portion of the nerve cell, be it a protoneurone or a neurone, is the trophic center and not the nervous center of this element, the migrations that this part undergoes in the course of evolution are not without interest. Two lines of movement are observable, one seen in the receptive cells and the other in those of the nerve-net proper.

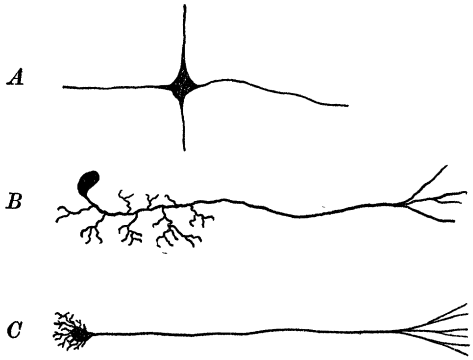

FIG. 4. Motor nerve-cells; *A*, motor cell from the nerve-net of a cœlenterate; *B*, motor neurone from an earthworm; *C*, motor neurone from a vertebrate. In examples *B* and *C* the central ends of the cells are toward the left.

In the primitive protoneurones of the nerve-net in cœlenterates (Fig. 4, *A*) the cell body with its contained nucleus is almost always centrally located, its processes being in direct connection with those of other like elements. In nerve-nets that exhibit polarization and thus begin to take on the character of differentiated nerve centers, the cell bodies are nearer the receptive than the discharging ends. This is best seen where the process has more nearly reached completion as in the central nervous organs of worms, arthropods and mollusks (Fig. 4, *B*). Here the cell bodies, usually unipolar, are attached to the transmitting axis of the neurones near their receptive poles, and this condition foreshadows the final stage of this process as seen in vertebrates where the cell bodies are almost invariably at the receptive ends of centrally situated neurones (Fig. 4, *C*). Thus, in the evolution of the protoneurone of the nerve-net into the neurone of the specialized central organ, the cell body migrates from a central position to a polar one at the receptive end of the neurone.

The second type of migration is quite the reverse of that just described. It is seen in the sense cells of the nerve-nets and in those cells that are derived from them and that are associated with the more differentiated sensory surfaces of the higher animals. This type of migration was long ago pointed out by Retzius (1892) and his account needs only to be supplemented by what is now known of the cœlenterates in order to bring it thoroughly up to date. In the cœlenterates the sense cell, or receptive protoneurone, has its cell body at its receptive end whence its fibrous prolongation reaches into the nerve-net (Fig. 5, *A*). Much the same condition is found in the earthworm, though in many other worms the cell body has moved to a deeper position, leaving only a process of the cell in connection with the sensory surface. In mollusks this inward migration of the cell body is still more pronounced (Fig. 5, *B*.) And finally in vertebrates (Fig. 5, *C*), the cell body of what has now become the primary receptive neurone has migrated so far inward as to come to lie much nearer to the central nervous organ than to the peripheral receptive surface from which it started. Thus in the two types of cells, peripheral and central, the directions of migration are opposite, for while in the primary sensory neurone the cell body has moved away from the receptive pole, in the central neurone it has moved to that pole.

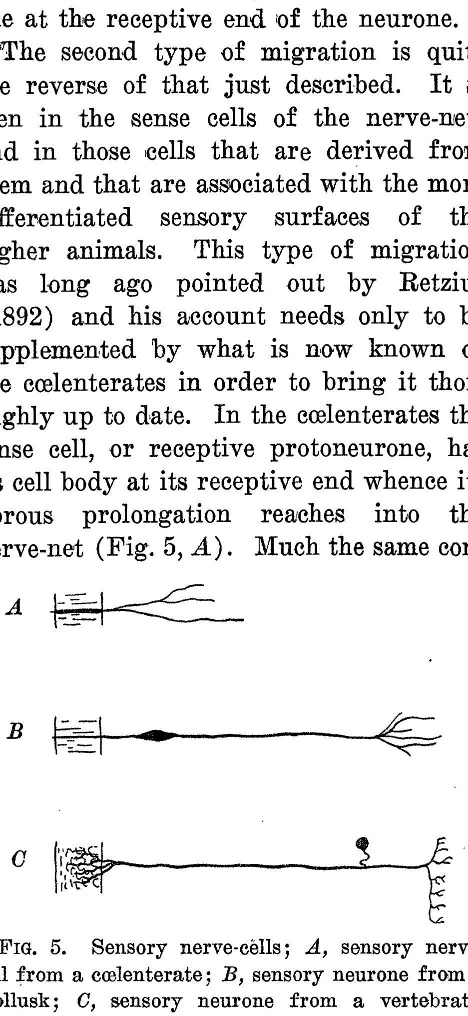

Fig. 5. Sensory nerve-cells; *A*, sensory nerve-cell from a cœlenterate; *B*, sensory neurone from a mollusk; *C*, sensory neurone from a vertebrate. In each example the peripheral end of the cell is toward the left.

These migrations, in my opinion, are not to be interpreted as direct expressions of nervous changes in the neurone, as would probably have been surmised by the older school of neurologists. They are the migrations of the trophic center of the cell and they probably find their explanation in the changed metabolic needs of the evolving neurone rather than in its immediate nervous changes. Something of what these relations are may be gathered from the conditions presented by the receptive neurones of the chemical senses of vertebrates. Of these the most primitive are the olfactory neurones in which the trophic center is at the receptive end of the cell (Fig. 6, *A*) reproducing in this respect the conditions found in the integument of sea-anemones and of earthworms. Next in sequence are the receptive neurones of the common chemical sense (Fig. 6, *B*) in which the trophic center has migrated far inward toward the central organ, a strictly vertebrate condition. The last members of the series are the receptive neurones of the sense of taste (Fig. 6, *C*), which are like those of the common chemical sense, except that they have appropriated distally certain integumentary cells, often called secondary sense cells, that constitute a taste bud.

These three types of chemical sense organs, genetically related in the order just given, show most interesting physiological differences. Some few substances, like ethyl alcohol, stimulate all three, but at strikingly different concentrations (Parker and Stabler, 1913). If the dilution that will just stimulate the most sensitive of the three, the olfactory neurones, is expressed as unity, the concentration necessary to stimulate the terminals of the common chemical neurones is 80,000 and of the gustatory apparatus 24,000. Hence it appears that when the trophic center is at the receptive end of the neurone, as in the olfactory organ, that end is thousands of times more sensitive than when this center has migrated away from it, though it can recover some of its lost sensitivity by appropriating to itself neighboring cells whose nuclear activity may make good in some measure that which was lost by the inward migration of its own trophic center. Why these centers in the course of phylogeny should have migrated from their original superficial positions inward over much of the length of their neurones is difficult to say. Possibly it may have been due to the advantages of increased nutritive opportunities in these deeper situations or to the establishment of a second and deeper receptive surface for other systems of neurones.

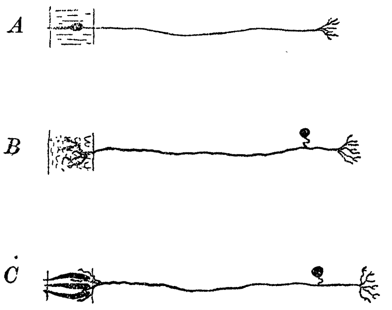

FIG. 6. The primary neurones of the three chemical senses of vertebrates; *A*, olfactory; *B*, common chemical; *C*, gustatory. In each example the peripheral end is toward the left.

If, as seems to be the case, the proximity of the trophic center greatly enhances the sensitivity of the receptive pole of a neurone, it is easy to understand why in the differentiation of the protoneurones of the nerve-net into the central neurones of the synaptic system the trophic center should migrate toward the receptive pole of the neurone. Such a step is only another aspect of that whole series of changes that give the synaptic system its high efficiency as compared with that of the nerve-net.

It might seem at first sight that the migrations that have been discussed are the cellular aspects of the general migrations of nerve centers that have been ably and interestingly expounded by Kappers (1907–1917) and his followers, under the head of neurobiotaxis. But these migrations, as a moment's reflection will show, are strictly concerned with nervous operations and have to do with the association of groups of neurones in connection with developing reflexes rather than with what may be called the inner life of the neurone. The neurobiotaxes, therefore, are not to be confused with those intraneuronic shifts whereby the trophic center of the nerve cell is placed in such a position as to administer most efficiently to the metabolic needs of the neurone. These shifts give evidence of the interrelation of the prime factors involved in the organization of every nerve cell, the metabolic and the nervous. Those two factors have been most important in shaping the evolution of this element, but they have not always received at the hands of investigators that separate attention which they deserve. It is one of the objects of this address to emphasize their separateness without, however, losing sight of their intimate interdependence.

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Harvard University

ROLLIN ARTHUR HARRIS

Dr. Rollin Arthur Harris, of the U. S. Coast and Geodetic Survey, died suddenly of heart disease on the twentieth of January, 1918, in the fifty-fifth year of his age. He was born in Randolph, N. Y., April 18, 1863, and received his early education in the public schools and high school of Jamestown, N. Y. In 1881 he entered Cornell University, receiving the degree of Ph.B. in 1885. He remained at Cornell, taking up graduate work in mathematics and physics. In 1886–7 he was a fellow in mathematics and in 1888 he received the degree of Ph.D. From 1889 to 1890 he was a fellow in mathematics at Clark University where he pursued special studies in mathematics and lectured on mathematical subjects.

He entered the Tidal Division of the U. S. Coast and Geodetic Survey as computer in 1890, through the United States Civil Service. After becoming familiar with the work, he began the preparation of a publication into which would be gathered the tidal information scattered in various journals and memoirs and in which the methods of tidal reduction and prediction would be coordinated. Dr. Harris threw himself into the work with enthusiasm. Because of his splended training in mathematics and his ability, he was specially fitted for the work, and the result, as embodied in the "Manual of Tides," which appeared in six parts in various reports of the superintendent of the Coast and Geodetic Survey, between the years 1884 and 1907, has placed our country well at the front in that branch of scientific enquiry. Taken as a whole the "Manual of Tides" is a monumental work of some 1,200 quarto pages of text and plate containing a large amount of original contributions, in a field cultivated by the most brilliant mathematicians.

It is gratifying to know that the "Manual of Tides" has received the recognition it merited from scientists the world over. Perhaps it may not be out of place here to quote the words of the eminent French mathematician Henri Poincaré. In his "Mécanique Céleste" he subjects the various tidal theories to searching analysis and sums up by saying that "it appears probable that the final theory will have to borrow from that of Harris a notable part of its essential features."

Dr. Harris published a number of articles in Science and other scientific journals on mathematical and tidal subjects. Mention should also be made of "Arctic Tides," a monograph published by the Coast and Geodetic Survey in 1911 which is a classic of its kind.

Personally, Harris was a man of modest bearing, somewhat reticent, but possessed of a pleasing sense of humor. He was an indefatigable worker with a high conception of the obligations of the scientist. He was a member of scientific societies, both local and national. He leaves a widow, Emily Doty Harris, whom he married in 1890.

His loss will be felt by his friends and colleagues of the Coast and Geodetic Survey and by the many scientific men, engineers and explorers in many parts of the world, who brought their problems to him and received the benefit of his wide knowledge in a peculiarly abstruse branch of science.

SCIENTIFIC EVENTS

DR. FEWKES AND THE BUREAU OF AMERICAN ETHNOLOGY

Mr. Frederick Webb Hodge, who has been the head of the Bureau of American Ethnology of the Smithsonian Institution since 1905, has resigned to accept a position in connection with the Museum of the American Indian, founded by George G. Heye, of New York City. Mr. Hodge's resignation, to take effect February 28, has been accepted with regret by the secretary of the Smithsonian Institution, with whom he has been associated in scientific work for many years. Mr. Hodge will be greatly missed by his associates and generally by the men of Washington's scientific colony, among whom he is well known.