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By G. H. PARKER

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THE ORIGIN OF THE NERVOUS SYSTEM AND ITS APPROPRIATION OF EFFECTORS

I. Independent Effectors[1]

By G. H. PARKER

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THE physiological unit in the operations of the nervous system is the reflex. Broadly understood, this consists of the chain of consequences that begins with the reception of a stimulus on the surface of the animal and, leading through the central nervous organs, ends in the excitation of a reaction by some such organ as a muscle. The term reflex is made to apply nowadays to nervous operations involving conscious states as well as to those that are carried out unconsciously. In its greatest simplicity the conventional reflex involves at least two nervous cells or neurones and some form of reacting organ such as a muscle-fiber. The first neurone, as exemplified in the nervous structure of such an animal as the earthworm, is often the body of a sense-cell on the surface of the animal and the sensory nerve-fiber to which this cell body gives rise and which leads to the central nervous organ. The second neurone is a nerve-cell whose body lies within the central nervous organ and whose process, a motor nerve-fiber, extends from the central organ to the muscle-cells which it con-

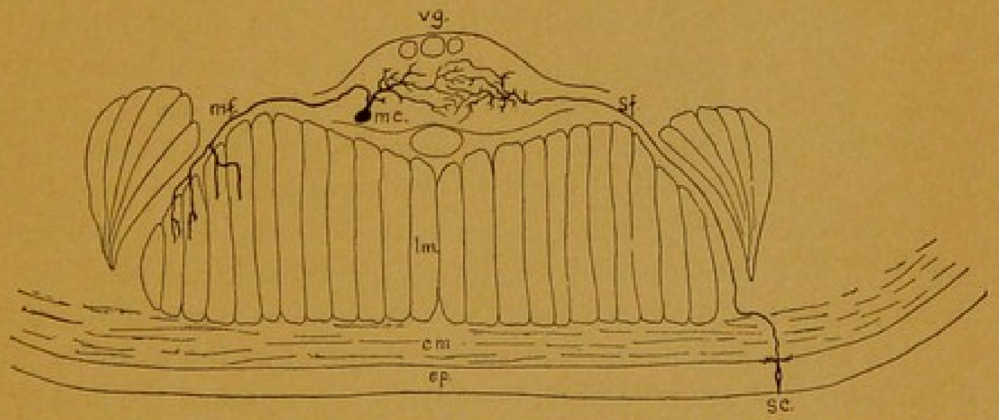

Fig. 1. Transverse Section of the Ventral Nervous Chain and surrounding Structures of an Earthworm (modified from Retzius). *cm*, circular muscle; *ep*, epidermis; *lm*, longitudinal muscle; *mc*, motor cell-body; *mf*, motor nerve-fiber; *sc*, sensory cell-body; *sf*, sensory nerve-fiber; *vg*, ventral ganglion.

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[1] The four articles in this series represent four lectures given at the University of Illinois between March 30 and April 3, 1909.

trols. The first neurone as it enters the central organ breaks up into a large number of delicate branches which are in physiological continuity with similar branches from the second neurone. It is over these delicate branches that the nerve-impulse passes from one neurone to the other and it is the structure of this system of branches that has been a matter of so much discussion within recent years. Anatomically, then, this simplest form of central nervous organ consists of motor cell-bodies and fibrillations from these bodies and from sensory neurones. Of course most central organs include additional neurones, such for instance as association neurones, which connect one part of the central organ with another and do not participate directly as sensory or motor constituents. The simplest conceivable reflex mechanism, however, does not include these, but only the sensory and the motor neurone as described. Such a chain reaching from the periphery of the animal through its central nervous organ to and including its muscles is usually regarded as the primary type of neuromuscular mechanism.

From a physiological standpoint this simplest type of reflex mechanism falls into three parts. The first of these is the sense organ or receptor, which, as its name implies, receives the external stimulus; the receptor is also the seat of the production of the nerve-impulse. The second is the central nervous organ or, as it may be called, the adjustor, which is concerned with directing the impulse toward the appropriate end-organ and with modifying it in accordance with the particular reaction to be obtained. The third and last is the effector or organ brought into action by the impulse, such as a muscle or gland. Thus a simple reflex may be said to involve at least three special classes of mechanisms: receptors, adjustors and effectors. These mechanisms, however, do not correspond exactly to the three histological elements already named, for, though the receptive function is an activity limited entirely to the first neurone in such an animal as the earthworm, and the effector is the muscle-fiber, the adjustor is a part of the first as well as of the second neurone and is made up of at least the fine fibrillar material contributed by these two neurones to the central nervous organ. The neuromuscular mechanism even in this its simplest type has probably not sprung into being fully formed, but it has had without doubt a slow and gradual growth. It is one of the objects of these articles to trace as far as possible the steps in this growth.

It is to be noted that every reflex mechanism is in the nature of a physiologically continuous span of living substance which reaches from the receptive surface on the one hand to the effector organ on the other. At no point in this span can there be a real interruption, for a physiologically continuous thread of protoplasm must connect the two extremes. It is, therefore, conceivable that a reflex mechanism might exist in the body of a protozoan and in fact there is experimental evidence to show that in certain infusorians the superficial protoplasm is somewhat differentiated as a receptive surface and that this protoplasm also serves as a conducting organ whereby, for instance, the activity of certain groups of specialized cilia in these animals is coordinated. These conditions, however, are found within the substance of a single cell and are so remote from those of a true nervous mechanism that, interesting and significant as they are, they had better be termed neuroid than nervous. They show at best that the protoplasm of the protozoan harbors operations that may develop in the multicellular animals into reflex processes rather than that the protozoans possess these processes, and that we must look among the simplest metazoans for the beginnings of a true neuromuscular mechanism.

In making a quest for the first stages in the development of the nervous system, it is important to keep in mind the relative significance of the three physiological elements already pointed out: the receptors, the adjustors and the effectors. A little reflection will show that these three are not likely to prove all of primary significance.

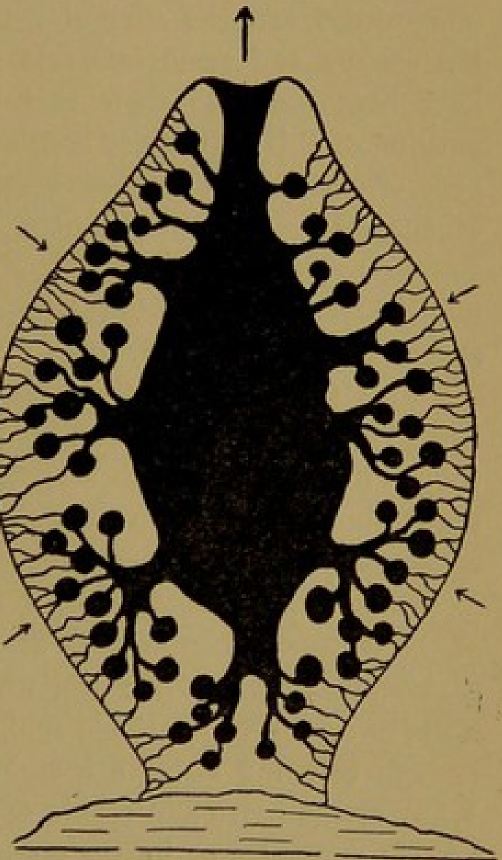

Fig. 2. Diagram of the Canal System of a Calcareous Sponge (modified from Haeckel). The lateral inlet pores receive water from the exterior, as shown by the arrows on the sides; the osculum at the apex discharges water to the exterior.

A receptor or sense organ alone would be of no service whatever to an animal; it would resemble a telephone receiver disconnected from the rest of the system. In a similar way the adjustor or central organ is useless without at least some other element in the reflex apparatus. The only mechanism sufficient in itself is the effector, which, if it can be brought into action by direct stimulation, may accomplish something serviceable to the animal. It is therefore improbable that we shall find multicellular animals that possess either receptors or adjustors without effectors, but it is conceivable that primitive metazoans may have effectors without other parts of the typical neuromuscular mechanism.

In a search for the earliest traces of the neuromuscular mechanism, we may turn first to those very primitive metazoans, the sponges. The body of one of the simpler sponges is a more or less goblet-shaped, multicellular mass, whose surface is covered with an enormous number of minute pores; these lead into tubes which in turn communicate with a relatively large central cavity that opens to the exterior by an aperture of considerable size, the osculum. In a living undisturbed sponge, water is continually passing into the lateral pores, through the tubes and central cavity, and out at the osculum. This current is produced by means of numerous cells, the choanocytes, which are provided with vibratile lashes and are variously distributed through the internal chambers and tubes of the sponge. Apparently these choanocytes work incessantly, and the current generated by them carries food, etc., to the sponge and removes waste products. Although frequent efforts have been made to show that nervous structures occur in sponges, nothing of this nature has been conclusively demonstrated and it is now generally believed that these animals are without differentiated nervous organs, either sensory or central. Nevertheless, sponges are capable of a certain amount of response. Merejkowsky (1878) observed that when he pricked with a needle the inner face of the osculum of *Rinalda,* this aperture quickly closed, not to open again for several minutes. The same reaction occurs with the lateral pores of many sponges (Vosmaer and Pekelharing, 1898). This power of closing the pores seems to be the only means by which a sponge may check the current which ordinarily flows through its canals, for, as already mentioned, the choanocytes apparently lash the water incessantly.

When a search is made for the organs concerned with the closing of the pores and oscula, they are found to consist of rings of elongated contractile cells or myocytes, which surround these apertures. These rings of cells form veritable sphincters and their action is often efficient enough to bring about a complete temporary closure of the aperture. Whether the pores and oscula open by the counteraction of radial, contractile myocytes or by the simple elasticity of the surrounding tissue does not seem to have been determined.

Since these sphincters lie very close to the epithelium that bounds the surfaces of the pores or oscula and in fact probably often form a part of this very epithelium, and since no nervous mechanism is known to be connected with them, it seems very probable that they are brought into action by direct stimulation and that the sponge is a metazoan in which there are functional effectors unassociated with receptors or adjustors. Thus the sponge would represent the first stage in the differentiation of a neuromuscular mechanism, *i. e.,* one in which the effector in the form of a primitive muscle-cell is the only element present. In my opinion it is around these contractile cells that the nervous organs of the higher metazoans have developed and I therefore believe that these effector elements are the most primitive members in the typical neuromuscular mechanism.

That there is absolutely no trace of nervous activity in sponges is probably not true, but their extreme inertness shows that this function is certainly in a most primitive state and corresponds at best probably only to that sluggish form of reception and transmission that Kraft (1890) demonstrated for ciliated epithelium and that is probably characteristic of other epithelia. Taking all in all, the only element of the neuromuscular mechanism that is really present in sponges is the effector as represented by the sphincters of the pores and oscula.

If independent effectors occur in sponges, it is not unlikely that they may be present in the higher animals, and as possible examples of these the sphincter pupillae of the eye in vertebrates and the heart-muscle may be considered. The sphincter pupillæ is a ring of muscle imbedded in the iris and surrounding the pupil in the eyes of most vertebrates. Its contraction would naturally reduce the size of the pupil and thereby diminish the amount of light that enters the eye. In the higher vertebrates it is well known that this reaction has the character of a simple reflex in which the retina is the receptor, with the optic nerve as its transmitting organ, and the stem of the brain is the adjustor from which the oculomotor nerve transmits peripherally to the effector, the sphincter pupillæ. In the lower vertebrates, particularly in the fishes and amphibians, it has long been known that the sphincter pupillæ will react in a characteristic way even in extirpated eyes. This fact has been explained by those who cling to the idea of a reflex as due to intraocular nervous connections between the retina and the sphincter. But Steinach (1892) demonstrated the contraction of the pupil in the extirpated eyes of lower vertebrates from which the retina had been removed and moreover he showed that when a minute beam of light was thrown on a part of the sphincter, that part contracted first and was followed later by the rest of the muscle, an observation recently confirmed by Hertel (1907) in the eyes of higher vertebrates, including man. It therefore seems quite certain that the sphincter pupillæ of the vertebrate eye, though usually controlled by nerves, is a muscle that can be directly stimulated and in this respect is an independent effector like the sphincters of the pores in sponges.

A second case of independent muscle action in the higher metazoans is the heart-muscle. This muscle for a long time past has been the occasion of much discussion. In the vertebrates it is still an open question whether the beat of the heart is primarily nervous or muscular in its origin and the neurogenic and the myogenic theories of heart action have had a lengthy history (Engelmann, 1904; Howell, 1906). To Harvey we owe not only the discovery of the circulation of the blood, but the first true ideas of the action of the heart, for he showed that the active phase of the heart-beat was during contraction, not during expansion, as had been generally supposed, and that the heart was in reality a muscular force pump. Harvey seems likewise to have had the idea, though perhaps not very clearly expressed, that the heart-beat was dependent upon the heart-muscle and not upon some extra-cardiac mechanism. In this sense he may be regarded as the founder of the myogenic theory. Later Willis pointed out that the stomach, intestine, and heart received nerves from the brain and he believed that the movements of these parts were controlled by such nerves; he therefore may be looked upon as the originator of the neurogenic theory. To account for the fact that the heart would continue to beat for some time after its removal from the body, it was assumed by the neurogenists that the branches of the nerves left in the substance of the heart when this organ was cut from the body were sufficient to maintain the heart-beat for some time, but Haller opposed this view and declared that the heart-muscle itself was directly stimulated by the blood that coursed through it. The older form of the neurogenic theory, however, was entirely swept away by the discovery of the brothers Weber that the vagus nerve when stimulated, instead of increasing the heart-beat brought this organ to a standstill. At about this time Remak described nerve ganglia within the substance of the heart and these have been accepted by the modern neurogenists as the nervous mechanism for the heart-beat. The fact that it is practically impossible to get adult, vertebrate heart-muscle free from nerve-cells has left the problem of the heart-beat in these animals in a situation difficult for experimental approach. That the heart-muscle in vertebrates is always a continuous one, the auricles and ventricles being connected by at least a slender bridge of muscle, favors the myogenic theory, as does also the fact that the beat can be reversed in that the ventricle can be made to contract first and the auricle afterwards. In fact the general proposition, clearly expounded by Gaskell (1900), that the vertebrate heart is a muscular tube over which a myogenic wave of contraction proceeds from the posterior to the anterior end, has much in its favor and yet there are facts enough to show that the neurogenic interpretation of the action of the adult vertebrate heart is not an impossibility.

The unfavorable conditions that surround the study of the vertebrate heart have forced investigators to seek evidence concerning the nature of the heart-beat in other animals and as a result two remarkably clear sets of cases have been obtained. The first of these is the heart of the king-crab, *Limulus*. The heart of this animal, as Carlson (1904) has pointed out, possesses the unique feature of a complete anatomical separation of nervous and muscular parts. The heart itself is a long, segmented, muscular tube situated near the dorsal line of the animal. On the dorsal face of the heart is a median nerve-cord containing ganglion-cells and connected with two parallel lateral nerve-strands that lie near the sides of the heart. This whole nervous mechanism may be dissected off from the heart, leaving this organ in other respects intact.

If a vigorous *Limulus* is opened from the dorsal side and the heart exposed, it will be seen to contract at the rate of about twenty beats per minute, and this is likely to continue under the conditions of simple exposure for some twelve to fifteen hours. If now the median nerve-cord and the lateral strands are dissected away, the heart comes to a standstill and never again shows a natural beat, though a stimulus applied directly to its substance will cause it to contract. If instead of removing the nerves, the median and lateral strands are cut through at any plane, care being taken not to injure the underlying heart-muscle, the two regions of the heart thus established beat independently and coordination of the heart as a whole is lost. If the nervous connections are left intact but the muscular heart is completely cut across in several places, the whole organ continues to beat in complete coordination. It is quite clear from these observations that the heart-beat of *Limulus* is absolutely dependent upon an extra-cardiac nervous mechanism and that this beat is carried out in exact accordance with the neurogenic theory. Since the artificial stimulation of a cardiac nerve in *Limulus* is followed by tetanus in the region of the heart under the control of this nerve, the conclusion is justified that the heart-muscle of *Limulus* is comparable rather with the skeletal muscles of this animal than with the so-called organic muscles, for skeletal muscles show tetanus when thus stimulated.

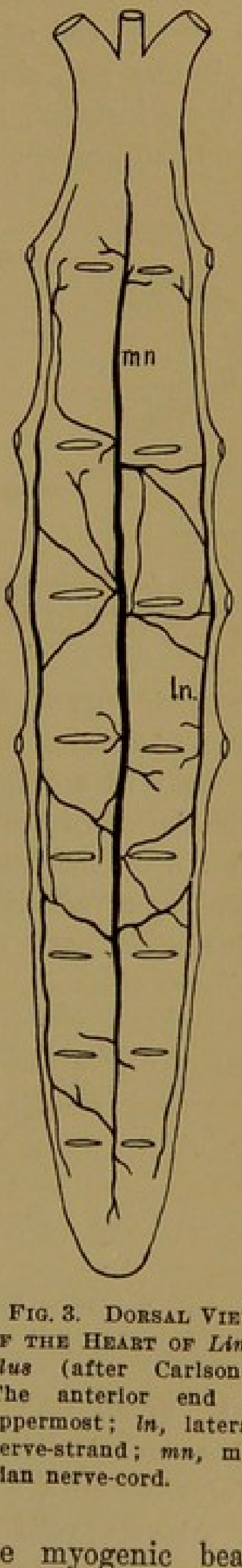

FIG. 3. DORSAL VIEW OF THE HEART OF *Limulus* (after Carlson). The anterior end is uppermost; *ln*, lateral nerve-strand; *mn*, median nerve-cord.

As Carlson himself remarks, however, the fact that the heart-beat of *Limulus* is neurogenic does not prove that the heart in other animals necessarily functions in a like way. In fact it is comparatively easy to point to another example in which the evidence for the myogenic beat is just as strong as that already presented for the neurogenic beat. This example is the tunicate heart. The tunicate heart, as for instance that of *Salpa,* is a muscular tube over which peristaltic waves run from end to end. As is well known, the direction of these waves reverses from moment to moment, running for a short interval toward the visceral end of the heart, advisceral waves, and then toward the respiratory end, abvisceral waves. In *Salpa africana-maxima,* to take a single instance, according to Schultze (1901), after 16 abvisceral waves had passed over the heart in some 20 seconds, a resting period of 2 seconds ensued, whereupon 18 advisceral waves occupying 25 seconds preceded another resting period, etc. When the heart is removed from the body of a *Salpa,* it continues to beat with characteristic reversal. Stimulation of the central nervous ganglion of a normal *Salpa* has no effect upon the heart-beat, and though a removal of this organ is followed by a reduction in the rate, the same reduction is to be observed when other parts of the body than the central nervous organ are cut out. Small fragments of the heart of *Salpa* also beat rhythmically when entirely isolated, a fact recently confirmed by Hunter (1903) on *Molgula,* and a most careful search of these fragments has failed to reveal nerve-cells or nerve-fibers. It seems therefore clear that the rhythmic heart-beat of the tunicates is myogenic in origin. This seems also to be true of the embryonic, vertebrate heart, for His (1891) has shown that this organ beats at a time when no trace of nervous tissue can be discovered in it.

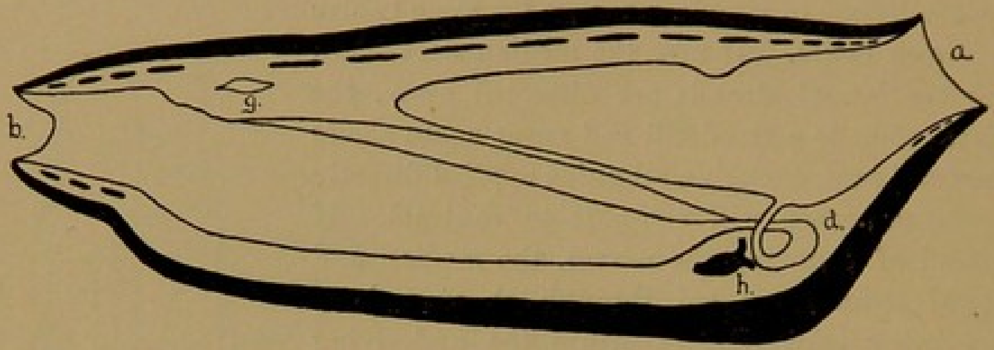

FIG. 4. SECTION OF A *Salpa* (modified from Herdman), showing the positions of the atrial aperture (*a*), branchial aperture (*b*), digestive tube (*d*), ganglion (*g*) and heart (*h*).

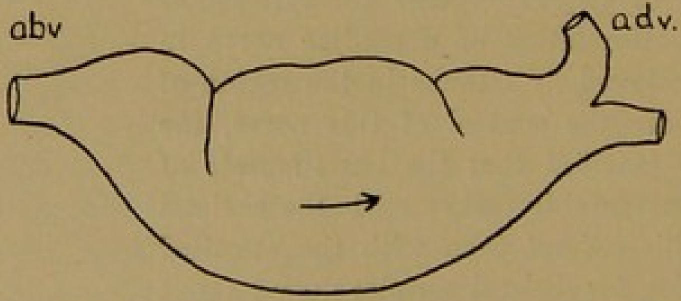

FIG. 5. HEART OF A *Salpa* (modified from Schultze), showing advisceral waves. *abv,* abvisceral end; *adv,* advisceral end.

From this general discussion it is quite evident that the cardiac muscles of different animals act in very different ways and that while some, like the heart of *Limulus*, have a neurogenic beat, others like that of the tunicates have a myogenic beat.

From this rather lengthy digression we may return to the question raised in the earlier part of this lecture, namely, the possibility of the existence of physiologically independent muscles. This I believe to have been demonstrated in part at least in the sphincter pupillæ of the lower and perhaps all vertebrates, and wholly so in the tunicate heart and the embryonic vertebrate heart. The complete freedom of such muscles from nervous control and their dependence on direct stimulation for normal action is a repetition of a process that, in my opinion, characterized all primitive muscles such as we now meet with in the sphincters of sponges. Such muscles as these sphincters I believe to represent the original and primitive elements around which the other members of the neuromuscular mechanism, the sense organs and the central nervous organs, subsequently developed. In my opinion then, effectors in the form of muscles preceded in an evolutionary sense the receptors and adjustors, and formed the centers around which these organs developed later.

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THE ORIGIN OF THE NERVOUS SYSTEM AND ITS APPROPRIATION OF EFFECTORS

II. Receptor-effector Systems

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THE second step in the development of the neuromuscular mechanism is represented by the receptor-effector system, a condition fairly realized in such cœlenterates as the sea-anemones and the jellyfishes and probably recurring in the digestive tubes of the higher metazoans. As an introductory example we may turn to the sea-anemones.

Most sea-anemones (Fig. 1) are cylindrical animals attached to some firm object by their aboral disks and carrying on their oral disks a ring of tentacles surrounding the mouth. This aperture leads inward through a short gullet to a large, somewhat divided, digestive cavity, the gastro-vascular space, which extends throughout the whole interior of the animal even to the tips of its tentacles and is the only cavity within the sea-anemone. The body of the animal is made up of walls of extreme thinness; these walls consist of two layers of cells, an outer one next the sea water, the ectoderm, and an inner one next the gastrovascular space, the entoderm. These two layers are separated by a tough, non-cellular sheet, the supporting lamella.

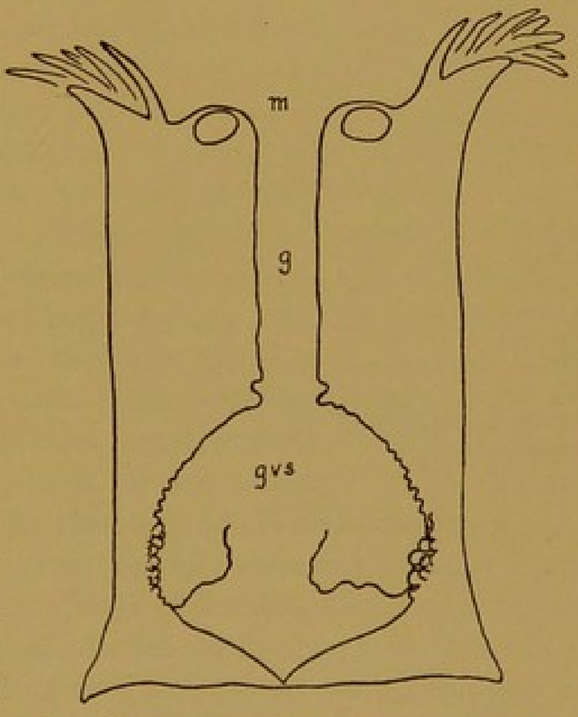

Fig. 1. Longitudinal Section of a Sea-anemone (*Metridium*); *g*, gullet; *gvs*, gastrovascular space; *m*, mouth; *t*, tentacles.

Unlike sponges, sea-anemones are very responsive to changes in their environment. If a fully expanded *Metridium* is disturbed by mechanical agitation, it will quickly retract its oral disk, discharge through its mouth the water contained in its gastrovascular cavity, and finally cover its tentacles and mouth by puckering in the oral edge of its column. In this contracted state it may remain hours at a time, and when it eventually expands it does so by relaxing its muscles and refilling its body with sea water. A beam of strong sunlight, if thrown upon an expanded *Metridium* several feet under water, will usually call forth the same contraction as mechanical stimulation does.

When the exterior of a *Metridium* is tested locally, its receptiveness for certain stimuli is found to be quite diverse. The animal makes no movements when dissolved food-substances are cautiously discharged upon the external surface of its column, though this very area is sensitive to mechanical stimulation. Precisely the reverse is true of the lips; these organs are easily stimulated by dissolved food-products, but no reaction occurs even when they are punctured by a needle. Both mechanical and chemical stimulation, however, are effective on the tentacles and vigorous responses can be called forth from even distant parts of the body by the application of either of these forms of stimuli to the tentacles. Since these reactions, as just intimated, often involve responses in very different parts of the animal from those to which the stimulus is applied, it follows that we are dealing with a process justly regarded as nervous, for transmission in this case is not accompanied with any observable motion. The surface of a sea-anemone may then be pictured as a true receptor surface partly differentiated in different regions for particular classes of stimuli, but not so far specialized that it can be described as made up of sense organs.

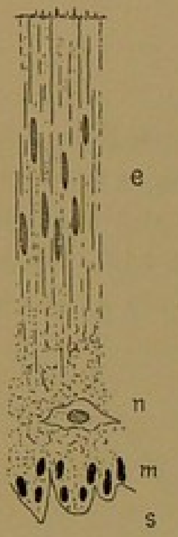

FIG. 2. ECTODERM FROM THE TENTACLE OF A SEA-ANEMONE (*Metridium*); *e*, epithelial layer; *m*, muscular layer; *n*, nervous layer; *s*, supporting lamella.

An examination of the structure of the ectoderm (Fig. 2) will do much to make clear the mechanism by which the reactions of sea-anemones are carried out. The ectoderm of these animals is a modified epithelium in which three definite layers can be distinguished. The outermost of these forms more than half the thickness of the total layer and is a true columnar epithelium. It contains, in addition to ordinary epithelial cells, gland-cells and nettle-cells, and, what is of more importance to us, sense-cells. These sense-cells are long, narrow bodies whose distal ends are armed with a sensory bristle which, under ordinary conditions, projects into the surrounding sea water and whose proximal ends run out into finely branched, nervous processes which intermingle with similar processes from other cells. The complex made by the interweaving of immense numbers of these processes constitutes the second layer of the ectoderm, the nervous layer, and this layer often contains in addition to the large amount of fibrillar material derived from the sense-cells, numerous multipolar ganglion-cells whose processes add to the fibrillar material already mentioned. A careful study of this fibrillar material has recently been made with the result that a true nervous network has been demonstrated in hydroids (Wolff, 1904; Hadzi, 1909), siphonophores (Schaeppi, 1904) and sea-anemones (Wolff, 1904; Groselj, 1909). In the sea-anemones in particular this network appears to be a perfectly continuous and diffuse one, notwithstanding Havet's previous declaration (1901) to the contrary. The third layer is composed of parallel muscle-fibers that rest against the supporting lamella on one side and are in contact with the nervous network on the other side. The muscle-cells of this layer are much elongated, spindle-shaped cells. These three layers, the epithelial layer, the nervous layer and the muscular layer, constitute the structural elements in the ectodermic neuromuscular mechanism of a sea-anemone.

The nervous type of ectoderm just described covers practically the whole surface of a sea-anemone and has been designated as a diffuse nervous system in contrast to a centralized one. The fact that the nervous layer is more fully developed on the oral disk than elsewhere has given anatomical grounds for the assumption that this portion is a central nervous organ, but, as will be shown later, the physiological evidence in favor of this opinion is so slight that the designation of the nervous system as a diffuse one is more consistent with facts.

From the standpoint of our original analysis, it is quite plain that in the sea-anemones we are dealing with at least two elements of the typical neuromuscular mechanism, namely, receptors as represented by the sense-cells, and effectors as seen in the muscle-fibers. Whether the fibrillar material that intervenes between these two structures represents an adjustor or central apparatus will be discussed after the action of this nervous mechanism has been more fully described.

The feeding habits of the sea-anemones throw considerable light on the physiology of their nervous structures. If particles of meat are dropped on the tentacles of an expanded *Metridium,* they become entangled in the mucus on these organs and are quickly delivered to the mouth, where they are swallowed. If fragments of clean filter-paper soaked in sea water are similarly dropped on the tentacles, they are usually discharged from the edge of the oral disk without having been brought to the mouth. Thus the animal appears to discriminate between what is good for food and what is not. If, however, pieces of filter-paper soaked with meat juice are put on the tentacles, they are usually swallowed as though the sea-anemone had been deceived. On the basis of these simple experiments a still more striking combination can be devised. If a sea-anemone is provided alternately with pieces of meat and pieces of filter-paper soaked in meat juice it will in the beginning swallow in sequence both materials, but after ten or a dozen trials it will regularly swallow the meat but usually discard the filter-paper. Thus it would appear that the sea-anemone had detected the deception practised on it in the beginning and had learned to circumvent the experimenter. But further observations show how erroneous this interpretation is. If the experiment just described is performed on a limited group of tentacles on one side of the oral disk and, after the animal has arrived at the stage of discriminating between meat and paper, the experiment is repeated on another and distant group of tentacles, it is found that these tentacles and the part of the mouth next them will accept both meat and paper as the first group did and the same process as was used on this group must be repeated on the second group in order to bring it to the stage of discrimination. Thus it is clear that, however we may regard these acts, *Metridium* shows no marked power of making the experience of one part of its body serve another; in other words, it shows no decided evidence of a central nervous organ.

This conclusion is in substantial accord with the recent results obtained by Fleure and Walton (1907) from experiments on *Actinia* except that they believe that the repeated trials on the tentacles of one side of the circle had in this form a slight influence on those of the other. This influence, however, was so slight that they declared that experience of this kind certainly did not become the possession of the animal as a whole.

Not only is there in these reactions absence of any strong evidence in favor of well-marked central nervous functions in anemones, but it is very doubtful if we are justified in regarding the local reaction just described as a true discrimination. Jennings (1905) has suggested that sea-anemones possess sensations of hunger and that as the experiment proceeds the animal's hunger diminishes and it finally discards when less hungry what it at first accepted. But Allabach (1905) has shown that the same so-called discrimination is arrived at if the sea-anemone is not allowed to swallow anything, but is robbed of meat and paper alike by having these materials picked out of its gullet just as they are about to be swallowed. In fact it seems quite clear that this process of apparent discrimination is in no sense due to centralized nervous functions, but is merely the result of exhaustion. At the beginning of each experiment the receptors are stimulated by the strong juices of the meat and the weaker juice of the paper. As they run down in efficiency, they come to a stage where they no longer react to the weaker stimulus of the paper and respond only to the meat. At this stage apparent discrimination takes place.

Not only do these experiments show no evidence of central nervous functions, but they indicate a decided looseness of nervous articulation. The activity of one side of the body of the sea-anemone has very little, if any, influence on the other side. Moreover, the fact of intimate local relations between nerve and muscle, as seen in the anatomy of these animals, supports the idea of neuromuscular independence instead of centralized relations. This is well exemplified in the reactions of the tentacles. If a tentacle of *Metridium* is stimulated by food, it turns and twists irregularly and then points toward the mouth. If the same tentacle is cut off and held filled with water so that its original relations in the animal as a whole can be kept in mind, it will be found to react to food as it formerly did, in that it will finally turn toward that side which was originally next the mouth. Hence we may conclude that the tentacle has within itself all that is necessary by way of neuromuscular mechanism for its characteristic reactions and is not dependent for these on such other parts of the sea-anemone as have been regarded as central nervous organs. Physiologically as well as anatomically the sea-anemone seems to possess a diffuse rather than a centralized nervous system, and its neuromuscular mechanism consists of receptors and effectors connected by a nervous net which is composed partly of the nervous processes of the receptor cells and partly of similar processes from ganglion cells.

The type of neuromuscular mechanism found in the sea-anemones probably also recurs in the digestive tube of vertebrates. This view is supported not only by the action of the intestine, but also by its structure (Fig. 3). Omitting for the moment the outer serous layer and the inner mucous layer of the intestine, both of which have little or nothing directly to do with its neuromuscular mechanism, there are left the outer or longitudinal muscular layer, followed internally by a nervous layer, Auerbach's plexus, which in turn is followed by the cir-

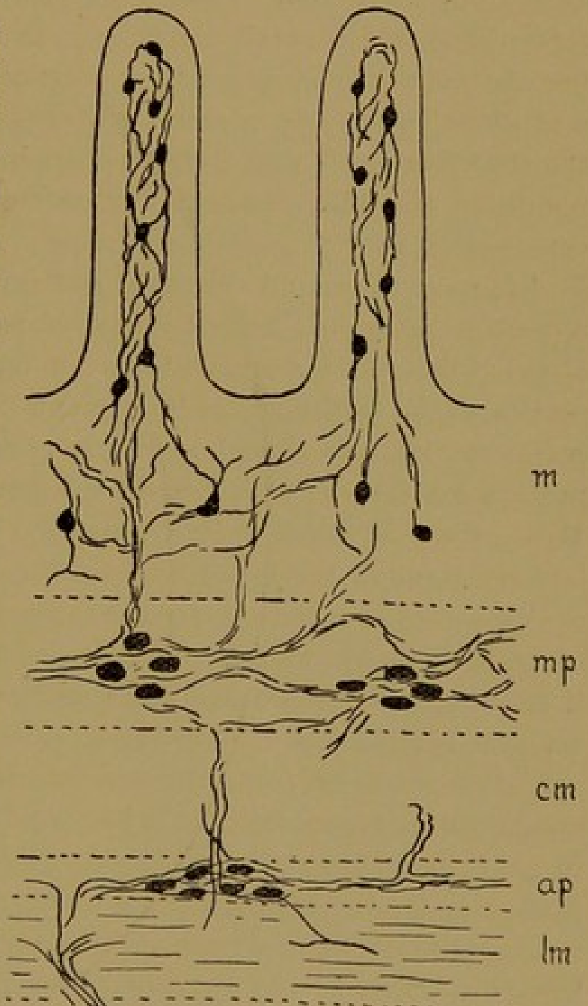

FIG. 3. LONGITUDINAL SECTION OF THE INTESTINAL WALL OF A VERTEBRATE, showing the nervous and muscular constituents; *ap*, Auerbach's plexus; *cm*, circular muscles; *lm*, longitudinal muscles; *m*, mucous layer; *mp*, Meissner's plexus; *s*, serous layer.

cular muscles on which rests a second nervous layer, Meissner's plexus. Each plexus, so far as is known, is a true nervous net as intimately related to the adjacent muscle fibers as is the case of the sea-anemones. In fact one of the muscle layers and the adjacent plexus in the intestine reproduce very accurately all the essentials of the neuromuscular mechanism of a sea-anemone except the epithelial sense-cells.

Not only is there this anatomical similarity between the neuromuscular mechanisms of the sea-anemone and of the vertebrate intestine, but there is also a physiological similarity as seen in the movements of the digestive tube. The essentials of these movements are well exemplified in the small intestine. In this part of the digestive tube the characteristic movements are segmentation and peristalsis. Segmentation consists in a series of temporary, ring-like constrictions in the intestinal wall that come and go in such a way that the enlarged region of the tube between any two constrictions is the site of the constriction next to appear, and so on. As a result of segmentation, the food is most thoroughly churned and mixed. Peristalsis is a wave-like movement whereby the food is carried posteriorly through the intestine. Usually these two movements go on together in such a way that the peristalsis is combined with segmentation in that the latter becomes somewhat unsymmetrical and cuts each food mass into two unequal parts the larger of which is on the posterior side of the constriction. Hence the food is not only churned but is at the same time moved posteriorly through the intestine.

The small intestine receives nerve-fibers from two extraneous sources, the vagus and the splanchnic nerves, and it might be supposed that these were essential for the movements of the intestine. But as Cannon (1906) has demonstrated, both sets of nerves may be cut, and yet after recovery from the immediate effects of the operation segmentation and peristalsis will be found to go on in the digestive tube in an essentially natural manner. It is thus clear that the vertebrate intestine, like the tentacle of a sea-anemone, contains a complete neuromuscular mechanism within its own wall, and though there is no histological evidence of the presence of receptors reaching from the mucous surfaces of the intestine to the nervous nets within, yet there are sound physiological grounds for assuming the presence of such organs. In that case the type of neuromuscular mechanism in the intestine would be practically identical with that in the sea-anemone.

A second example of a receptor-effector system in cœlenterates is seen in the jellyfishes. In these animals as contrasted with the sea-anemones, locomotion is a well-developed activity, and it is the neuromuscular mechanism concerned with this function that must be considered. The structures involved in locomotion are well exemplified in *Aurelia* (Fig. 4). This common jellyfish possesses on the edge of its bell eight clusters of sense-organs. Each cluster contains an ocellus, two sensory pits that are probably concerned with the chemical sense, and a sense-club which may be a pressure organ. The sensory portions of all these organs are modified ectoderm and from these portions nerve-fibers pass out as radiating bundles to the ectoderm of the subumbrellar surface. Here they merge into a nervous net which overlies the ectodermic musculature as in the sea-anemones. This musculature forms a circular sheet concentrically disposed with reference to the symmetry of the jellyfish. When the bell of an *Aurelia* is pulsing, the movement is carried out by the more or less general contraction of this circular band of muscle, which is brought back to its original position on relaxation by the elasticity of the gelatinous mass of the bell. The locomotor muscle, then, is a gigantic sphincter that works against an elastic resistance.

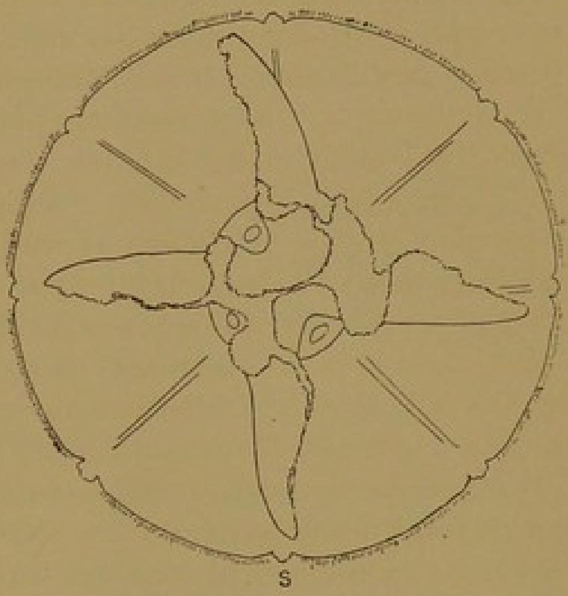

FIG. 4. *Aurelia*, subumbrellar surface; *s*, cluster of sense-organs.

The significance of the various parts of the neuromuscular mechanism in such an animal as *Aurelia* can be determined by experiment. If the eight sense-bodies are removed, the animal will no longer pulse spontaneously, though its muscles may be made to contract by direct stimulation. If all but one sense-body are removed, the bell will pulse with regularity and by artificially stimulating the single remaining body a wave of muscular contraction can be sent over it. It is therefore evident that the sense-bodies act like extremely delicate triggers and thus touch off the contractile mechanism. In this respect, then, the jellyfish is more highly developed than the sea-anemone, for the latter possesses no such specialized and delicate receptors.

The wave of contraction that passes over a bell when one of its sense-bodies is stimulated, may be either a purely muscular phenomenon or may be the result of nervous transmission through the nervous net whereby one region after another of the musculature is brought into action. The fact that this wave is not checked when the bell is cut even in a most irregular way provided the subumbrellar epithelium is still continuous, favors the nervous rather than the muscular interpretation. But stronger evidence on the nervous side than this has come from an entirely different direction. Mayer (1906) has shown that the subumbrellar epithelium of *Cassiopea* after removal will readily regenerate, and that in regeneration the nervous net forms earlier than the muscles. By taking jellyfishes at the appropriate stage in regeneration, it was found that a stimulus applied to one side of a regenerated area was followed by a muscular response on the other side of this area without any observable movement in the area itself. Hence transmission through the regenerated region must have been by nervous means, doubtless by the nervous net.

In jellyfishes the nervous net will transmit apparently in any direction and in this respect it is in strong contrast with the central nervous organs of the higher metazoans, where, especially in the vertebrates, a polarized condition generally prevails. Thus in the spinal nerves of vertebrates, it is easy to send impulses through from a dorsal root to a ventral one, but impossible to send them in the reverse direction. Apparently the cord contains some structure on its path of conduction that is valve-like and allows impulses to pass in one direction only. Such a condition does not exist in the nervous net of the jellyfishes.

FIG. 5. NEUROMUSCULAR CELL (black) in place in a columnar epithelium.

The neuromuscular organs of the cœlenterates have been considered by so many investigators as the most primitive in the animal kingdom that it is not inappropriate to consider at this place the relations of some of the older views on this subject to those expressed in these articles.

The discovery by Kleinenberg (1872) of the so-called neuromuscular cells (Fig. 5) in *Hydra* led this investigator to the belief that these cells represented a complete neuromuscular apparatus in that each cell-body could be regarded as a receptor and its fibrous portion as an effector. By growth and cell division, according to Kleinenberg, separate receptors and effectors would be differentiated simultaneously from such single cells.

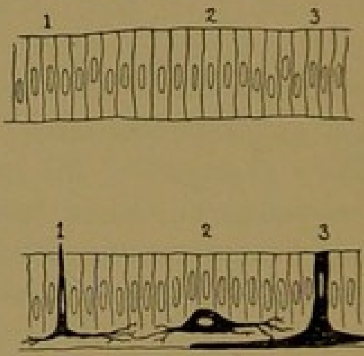

FIG. 6. DIFFERENTIATION OF NEUROMUSCULAR CONSTITUENTS FROM AN INDIFFERENT EPITHELIUM. The upper figure represents an indifferent condition containing three cells which subsequently (lower figure) differentiate into a sense-cell (1), a ganglion-cell (2), and an epithelial muscle-cell (3).

The simultaneous differentiation of nervous and muscular elements (Fig. 6) was also accepted by the brothers Hertwig (1878), but in their opinion the two types of tissue did not arise from a common cell as claimed by Kleinenberg, but from separate cells which became simultaneously differentiated, some to form nerve-cells (sense- and ganglion-cells) and others to form muscle-cells. This view has come to be commonly accepted by the majority of investigators.

The independent origin of the nervous system and its secondary connection with the musculature has been advocated by Claus (1878) and by Chun (1880), but a nervous system without effectors is, as Samassa (1892) and Schaeppi (1904) declare, scarcely conceivable.

The opinion about the origin of nervous and muscular tissues as expressed in these articles is opposed to the various theories stated in the preceding paragraphs in that muscular tissue is regarded as the ancestral tissue and nervous tissue is supposed to have formed secondarily and as a means of bringing muscular tissue into action with greater certainty than direct stimulation would do. According to this view the primitive state of the neuromuscular mechanism is to be seen in such animals as sponges, which possess muscles but no true nervous organs; and the neuromuscular or, better, epithelial-muscular cells of the cœlenterates represent these primitive effectors to which have been added a diffuse system of receptors as seen in the sea-anemones or a specialized system as in the jellyfishes. In both instances the receptors and effectors are related through a nervous net.

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THE ORIGIN OF THE NERVOUS SYSTEM AND ITS APPROPRIATION OF EFFECTORS

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III. CENTRAL NERVOUS ORGANS

IN dealing with the differentiation of nervous organs, the earthworm affords a good example of a simple type of well-centralized nervous system. The central nervous organs in this animal (Fig. 1) consist of a brain or cerebral ganglion situated anteriorly and dorsal to the buccal cavity, right and left œsophageal connectives extending from the brain ventrally to the ventral nerve-cord which stretches as a segmented organ from near the anterior end of the worm over its ventral line posteriorly to the tail. The segments in the ventral cord agree in number and position with those of the worm's body and from each segment three pairs of nerves pass out to the integument and muscles of the adjacent region.

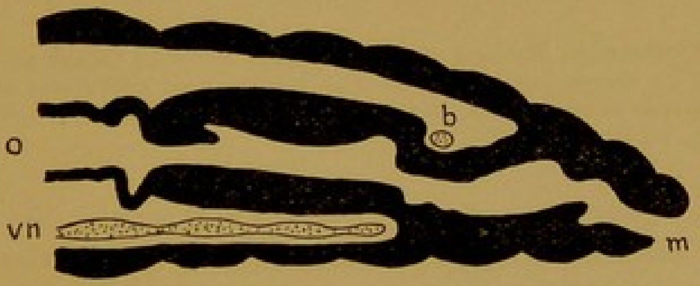

FIG. 1. HEAD OF AN EARTHWORM IN LONGITUDINAL SECTION. *b*, brain; *m*, mouth; *o*, œsophagus; *vn*, ventral nerve-cord.

The essential nervous elements of the ventral cord can be made out in transverse sections (Fig. 2). In such sections the integument will be seen to be filled with sense-cells, each of which ends peripherally in a sensory bristle and gives rise centrally, in addition to a few subepithelial processes, to a single nerve-fiber which passes inward between the muscles and enters the ventral ganglion by one of its three nerves; finally this fiber spreads out in the fibrillar substance or neuropile of the ganglion. This cell-body in the integument with its processes including the nerve-fiber constitutes a primary sensory neurone. These neurones usually do not spread beyond the ganglion with which they are directly connected, but in exceptional cases they may extend into the ganglion anterior or posterior to this one.

In the ventral and lateral portions of each ganglion are numerous large nerve-cells from which coarse processes extend through the neuropile, fibrillating as they pass to terminate as motor nerve-fibers in the muscles of the adjacent part of the body. These cells with their processes constitute the primary motor neurones of the earthworm and, like the sensory neurones, they may be present in any one of the three nerves of a segment. Their longitudinal extent is probably not much beyond a single segment.

The primary sensory and motor neurones not only give rise to the nerves of the earthworm, but they contribute a larger part of the substance of each ganglion. As stated in the first article, they form when together the necessary elements for the simplest, conventional reflex-arc. How they are related to one another in the neuropile is not conclusively settled, but, judging from the work of Apáthy (1897) and others, the connection here as in the nervous net is one of direct continuity.

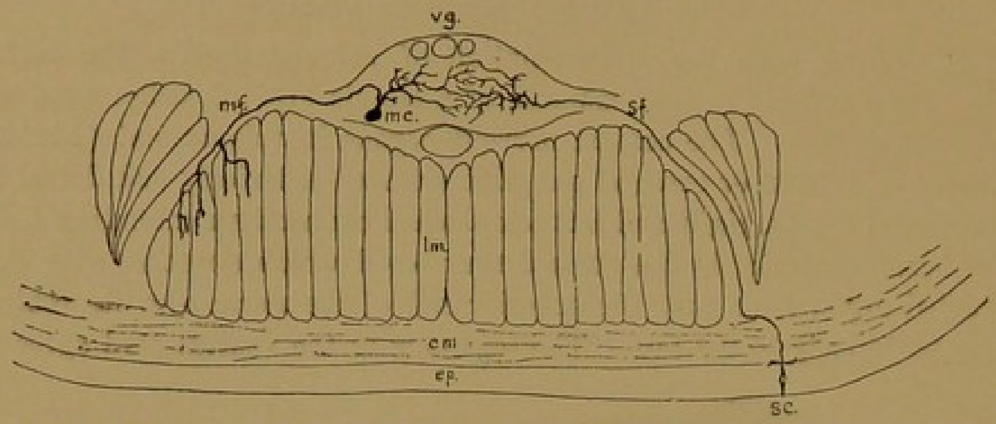

FIG. 2. TRANSVERSE SECTION OF THE VENTRAL NERVOUS CHAIN AND SURROUNDING STRUCTURES OF AN EARTHWORM. *cm*, circular muscles; *ep*, epidermis; *lm*, longitudinal muscles; *mc*, motor cell-body; *mf*, motor nerve-fiber; *sc*, sensory cell-body; *sf*, sensory nerve-fiber; *vg*, ventral ganglion.

Besides the motor and sensory neurones, the central nervous organs of the earthworm contain a considerable number of so-called association neurones. These are nerve-cells with longer or shorter processes that connect parts within the same ganglion or run from one ganglion to another. They give rise to no fibers that extend into the nerves and hence they are strictly limited to the central nervous organs. Their longitudinal extent is seldom over more than one or two segments.

Since the sensory, motor, and association neurones thus far described make up the bulk of the ventral nerve-cord of the earthworm and since none of these have a longitudinal extent of more than a few segments, it follows that the cord must be conceived as made up of an immense number of overlapping short neurones which in this collective way stretch over its hundred and twenty or more segments. But the nerve-cord of the earthworm is not composed exclusively of short neurones. In its dorsal portion are three giant fibers which, though their nature has been even recently disputed, are without much doubt nervous organs. The middle and largest of these fibers extends almost the whole length of the ventral cord and, according to Friedländer (1894), has unquestionable connections with ganglion-cells. The two lateral fibers, though smaller, have much the same extent as the median one and are also directly connected with cells. Both sets of fibers connect by branches with the neuropile of the successive segments. Thus the ventral cord of the earthworm may be described as composed of three long neurones and an immense number of overlapping short neurones.

This peculiarity in the structure of the cord makes itself manifest in the movements of the worm. Undoubtedly the slow waves of muscular activity that move over the worm from head to tail as it creeps along are dependent upon the interlocked short neurones, whereas the sudden drawing together of the worm as a whole, when it is vigorously stimulated, is very probably the result of impulses spread through the long neurones.

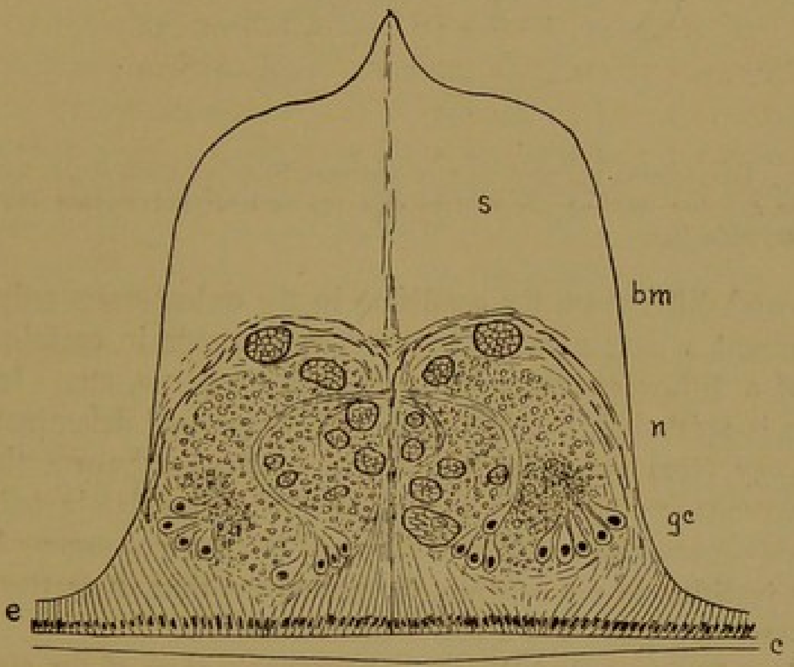

FIG. 3. TRANSVERSE SECTION OF THE VENTRAL NERVOUS CORD OF *Segalion* (modified from Hatschek). *bm*, basement membrane; *c*, cuticula; *e*, epidermis; *gc*, ganglion-cells; *n*, nerve-fibers and neuropile; *s*, space occupied by vacuolated supporting tissue.

The absence of degenerated fiber-tracts in the ventral cords of earthworms that have been cut in two and the rapidity with which nervous regeneration takes place in these worms are conditions that very likely depend upon the almost entire formation of the cord from systems of short neurones.

At first sight the central nervous apparatus of the earthworm seems to be widely different from the neuromuscular mechanism of the cœlenterates, but the difference in reality is not so pronounced. To begin with, the whole nervous mechanism of the cœlenterate is within an epithelial layer, whereas the central nervous organs of the earthworm are solid masses of nerve-cells, fibers, and neuropile entirely distinct from any epithelium. But this condition is apparently a recent acquisition on the part of the earthworm, for in another annelid, Sagalion, the ventral cord (Fig. 3) and the brain are still a part of the superficial ectoderm and differ from the condition in the cœlenterates only in that they represent a concentration of nervous elements in certain regions instead of a diffuse condition as in the sea-anemones, etc. In *Nereis* the brain is epithelial, but the cord by a process of delamination has broken away from the integument, and in the earthworm the whole central nervous system, brain as well as cord, has delaminated. It is chiefly this concentration and separation of the nervous organs from the skin that justifies, in my opinion, the statement that an earthworm has central nervous organs and a sea-anemone has not.

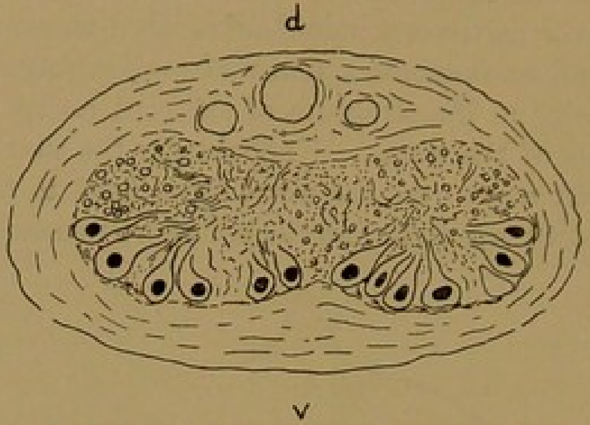

FIG. 4. TRANSVERSE SECTION OF THE VENTRAL NERVOUS CORD OF AN EARTHWORM, showing the ganglion-cells on the ventral side (*v*) and the nerve-fibers and neuropile on the dorsal side (*d*).

The fact, however, that the central nervous system of the earthworm has developed on the lines of the cœlenterate, has left its mark in the distribution of nervous materials in the ventral cord of this animal. In the ectoderm of the cœlenterate the cell-bodies of the nervous mechanism are nearer the exterior of the animal than are their processes, the fibrillar mass, and the same is true in the ventral ganglia of the earthworm (Fig. 4); here the cell-bodies are on the ventral side of the ganglion, *i. e.*, next the integumentary epithelium, and the neuropile and nerve-fibers are on the opposite or dorsal side of the ganglion. This peculiarity in the distribution of nervous materials is apparently true for most higher metazoans.

Another point of comparison between the nervous mechanism in cœlenterates and in the earthworm is the presence of nerves in the latter and their absence in the former. As already pointed out, the nerves in the earthworm are bundles of independent fibers which course more or less together between their end-organs and the central apparatus.

The fibers in a nerve have no necessary functional relations one with another, but are brought together chiefly by convenience of passage. They are characteristic of those animals in which sense organs and muscles have become well differentiated and widely separated from the central organs, and are not to be confused with elongated bundles of nervous elements such as are to be met with in some cœlenterates and many echinoderms, for though these may represent early steps in the evolution of nerves, they still retain so many evidences of functional interrelation among their elements that they are to be classed rather with nervous nets than with nerves.

The differentiation of nerves as thus defined implies an increased interrelation of neurones in the central apparatus as compared with the condition in the more primitive nervous net. The nature of this growing interrelation has been well expressed by Sherrington (1906) in his principle of the common path. This principle implies that each sense organ may be connected through the central organ with every effector and conversely any effector may receive through the central organ impulses from any sense-organ. In consequence the central organ must contain many common paths which are momentarily used, now for this, now for that combination of particular receptors and effectors. This condition without doubt obtains in earthworms as it does in higher animals, and is a feature that can hardly be said to exist in the nervous nets of the cœlenterates.

It is also probable that the nervous mechanism in cœlenterates differs from that in the earthworm in its capacity as a nervous transmitter. Attention has already been called to the fact that transmission in the nervous net of a cœlenterate may occur in almost any direction and that in the central nervous organs of vertebrates it is very definitely limited and may in fact flow in only one of two apparently possible directions. So definite a restriction can not be asserted for the earthworm but, as Norman (1900) has shown, significant differences do obtain. If an earthworm that is creeping forward over a smooth surface is suddenly cut in two near the middle, the anterior portion will move onward without much disturbance whereas the posterior part will wriggle as though in convulsions. This reaction, which can be repeatedly obtained on even fragments of worms, shows that a single cut involves a stimulation which in a posterior direction gives rise to a wholly different form of response to what it does anteriorly; in other words, transmission in the nerve-cord of the worm is specialized as compared with transmission in the nervous net of the cœlenterate.

There is good reason to believe that the cerebral ganglion or brain of the earthworm is in a measure degenerate. Certainly if we turn to such an annelid as *Nereis* we find in place of the small mass of ganglionic cells and fibers that represent the brain in the earthworm a much more extensive organ connected with a considerable number of sense organs none of which are present in the earthworm. Eight peristomial tentacles, a pair of palps, a pair of antennæ and, two pairs of eyes are found connected by nerves with the brain of *Nereis* and represent a condition in strong contrast with the unspecialized state in the earthworm. Yet both the earthworm and *Nereis* show much the same traits when deprived of their brains (Loeb, 1894). Each worm is immensely reduced in activity somewhat as a jellyfish is after the removal of its sense-bodies, and one is justified in concluding that the head of even the earthworm is an especially sensitive region through which many slight environmental influences that might not be able to affect other parts of the body gain access at this point to the neuromuscular mechanism. That such a condition should obtain at the anterior end of a bilateral animal has long been recognized as appropriate, for this is the part of the animal that in normal locomotion first reaches the new environment. But I am not acquainted with any discussion as to the mutual relations of the nervous parts at the anterior end of an animal so far as their origins are concerned. If what has been said in these lectures is true, namely, that sense-organs in general precede central nervous organs in evolution, then the brain of the worm has developed at its anterior end because the chief sense-organs were originally there, and not *vice versa,* a statement that I believe to hold for the growth of the brain in all animals. Intricate and marvelous as the brain of the higher animals is, it is, in my opinion, the product of a group of sense-organs that in evolution preceded it in point of time.

The annelids then possess a neuromuscular mechanism in which there are not only primary organs such as muscles, and secondary organs, the sense-organs, but also tertiary organs, central nervous organs. These central organs intervene in position between the receptors and effectors and in the annelids are composed almost exclusively of short overlapping neurones. It is probable that in the sea-anemone these neurones are represented by the so-called ganglion-cells of the nervous layer, but I would not go as far as Havet (1901) and designate these cells in cœlenterates as motor cells, for though some of them undoubtedly connect with the muscle-fibers, others may be purely association neurones. I believe further that in the sea-anemones the fibrils from many sense-cells connect directly with muscle-fibers without the intervention of ganglion-cells.

As an example of a central nervous system built upon the annelid type but with increased complication, we may turn to the arthropods. The central nervous system of these animals, like that of the annelids, consists of a dorsal brain, œsophageal connectives, and a ventral, segmented cord. These organs have been formed by a process of delamination as in the earthworm and exhibit the same fundamental arrangement of cellular elements as is seen in this animal, *i. e.*, the ganglion-cells are on the side of the cord next the exterior, and the neuropile and nerve-fibers next the interior.

The chief fundamental point of difference in the nervous systems of the annelids and arthropods consists in the great number of long neurones in the latter as compared with the former. In the crab, as demonstrated by Bethe (1897), many of the primary sensory neurones extend over half the length of the ventral cord instead of being limited to a few segments as in the earthworm, and the same is true of the primary motor neurones. Moreover, the association neurones have shown an extensive growth. Although in the crab there are some neurones limited to one or two segments, as is the rule in the earthworm, the great majority extend over many segments and often through the whole length of the nervous system. In this way the central nervous organs of these animals are locked together much more closely than are those in the worm and exhibit consequently in their physiology a unity that the worms do not possess. This nervous unity, moreover, has developed to such a degree in the higher arthropods that we may with reason ascribe to such animals as the insects a primitive form of intellectual life not unlike that found in the vertebrates. The structural basis for this seems to me to be foreshadowed in the few long neurones of the worm which, as I have just pointed out, come to be the common type in the arthropods. The type of central nervous system with long neurones also characterizes the other higher invertebrates such as the mollusks, etc.

The central nervous system of the vertebrates and of certain other closely allied forms like the tunicates, is usually put in strong contrast with that of the higher invertebrates. The most striking feature in this contrast is the fact that the vertebrate nervous system is tubular and the invertebrate solid. As is well known, the central nervous organs in vertebrates develop from an ectodermic tube that has been infolded from the median dorsal surface of the animal. This simple nerve-tube with nervous connections, but otherwise almost unmodified, exists to-day in that primitive vertebrate amphioxus. In the higher vertebrates the posterior portion of this tube becomes uniformly thickened and forms the spinal cord, the central canal of which gives evidence of its tubular nature. The anterior portion undergoes still more profound changes than the posterior part in that its wall thickens very differently in different regions and expands in several lobe-like outgrowths, giving rise thus to the brain whose ventricles represent the original cavity of the nerve-tube.

Notwithstanding the striking difference between the central nervous organs of vertebrates and invertebrates, they show certain fundamental similarities and the first of these has to do with the distribution of nervous materials. Since the nerve-tube from which the central nervous organs in vertebrates are developed is infolded ectoderm, it follows that the inner surface of the tube represents a portion of the outer surface of the animal. This inner surface even in the adult central nervous system is always covered by an epithelium as the exterior of the animal is, and the nervous materials which surround it are related to this epithelium in a characteristic way. This relation can be most easily seen in any transverse section of the spinal cord. Beginning at the central canal of such a section (Fig. 5) and proceeding through the substance of the cord to the opposite face, one passes first an epithelial layer, then gray substances composed of nerve-cells, neuropile, etc., and finally white substance made up of nerve-fibers. Precisely this sequence is met with in the central nervous system of any primitive invertebrate such as *Segalion*, where, as already pointed out, in passing through the thickness of the central nervous organ from the exterior to the interior one meets first external epithelium, then ganglion-cells and fibrillæ corresponding to the gray substance of vertebrates, and finally nerve-fibers corresponding to the white substance of these animals. Thus the nervous materials of the vertebrate spinal cord are distributed through that structure on a plan similar to that found in invertebrates, and this plan, though considerably modified, also holds good for the vertebrate brain. So far as these particulars are concerned, the vertebrate central nervous system differs from that of the higher invertebrates chiefly in that in separating from the integument it has carried with it its epithelial mother-tissue instead of leaving this tissue behind.

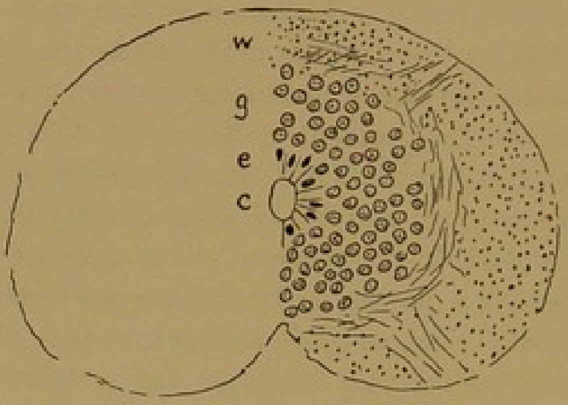

FIG. 5. TRANSVERSE SECTION OF THE SPINAL CORD OF A VERTEBRATE (SALAMANDER). *c*, central canal; *e*, epidermis; *g*, gray substance composed of ganglion-cells and neuropile; *w*, white substance or nerve-fibers.

Not only are the materials of the vertebrate central organs distributed on a plan that is best understood from the standpoint of the invertebrates, but the primary neurones of vertebrates are also most clearly interpreted from this point of view. The primary motor neurones of vertebrates (Fig. 6) resemble very closely those of invertebrates, for their cell-bodies are within the central nervous mass and their neurites extend as motor nerve-fibers to the skeletal muscles. The primary sensory neurones also agree with those of the invertebrates except that their cell-bodies instead of being in or near the integument, as in most invertebrates, have migrated centrally and thus form the dorsal ganglia. At least this appears to have occurred in all vertebrate sensory nerves except the olfactory, which still retains the usual invertebrate condition.

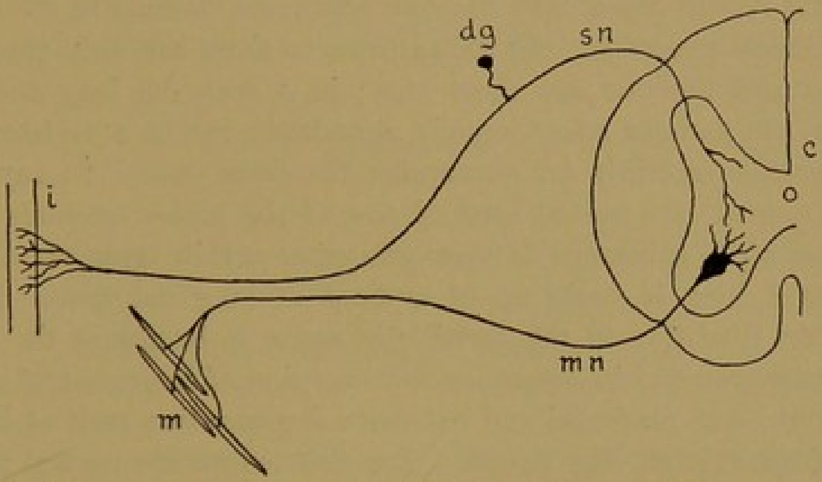

Fig. 6. Diagram of the Primary Neurones of the Vertebrate Nervous System as seen in Transverse Section. *c*, spinal cord; *dg*, dorsal ganglion; *i*, integument; *m*, muscle; *mn*, motor neurone; *sn*, sensory neurone.

Association neurones, which were met with in the invertebrates, are abundantly present in the vertebrates.

How the neurones in vertebrates are related to one another has been a matter of much dispute. Whether the gray substance of the central organs in these animals contains a true nervous net as seems to be the case in many invertebrates or whether their neurones retain greater individuality and are related morphologically only through contact, is not yet settled. That many embryonic neurones, or neurocytes, are in the beginning widely separated from others with which they are ultimately closely related is true and gives color to the belief that they may never fuse anatomically, though physiologically they do become continuous. The fact that nervous transmission through central organs in adult vertebrates is slow, open to exhaustion, and restricted to one direction as contrasted with transmission through nerve-fibers, is strong physiological evidence of a special central mechanism of interrelation between neurones such as Sherrington (1906) has pictured in the synapse. That no special anatomical condition has thus far been discovered that answers to this physiological requirement can in no sense be taken as an objection to it. That the vertebrate central nervous system is in many of its parts a synaptic organ can not be doubted, but that all its parts are synaptic is not yet proved. Possibly this is a feature characteristic of only the more specialized parts of the vertebrate central organs and entirely absent from the invertebrate, but whether this difference really exists or not must remain for future investigation.

Although it can not be said at present that a synaptic nervous system is the peculiar possession of the vertebrates, there are two important features in which the central organs of these animals differ from those of the invertebrates. In the first place, the central organs of vertebrates exhibit a large prepondernace of long neurones over short ones, and in the second place, they show an enormous increase in the number of association neurones. In an earthworm there are only three long neurones and the rest are short ones; in a crab the long and short neurones are perhaps about equally abundant; but in a vertebrate the long neurones certainly far outnumber the short ones. In any transverse section of the spinal cord of one of the higher animals almost all of the white substance in view excepting a thin layer surrounding the ventral horn is made up of systems of long neurones. In this respect the condition in the vertebrates seems to be almost the reverse of that in worms and in consequence transection of their central nervous organs results in profound and extensive degeneration such as is never met with in animals like worms. For this reason the central nervous system of the vertebrate, though giving much evidence of segmentation in its early stages of growth, is finally a physiological unit such as is realized in no other group of animals, a condition well evidenced by the fact that some of its most recent phylogenetic acquisitions, like the pyramidal tracts of the mammals, may consist of neurones that reach almost from one end of the system to the other.

The second feature that distinguishes the central nervous organs of vertebrates from those of invertebrates is the enormous development of association neurones. These neurones are present in worms, are numerous in arthropods, but are overwhelmingly abundant in vertebrates. Of the white substance seen in the transverse section of the spinal cord almost all except the dorsal columns represent association neurones. Judged from this standpoint there are certainly many more association neurones in the cord than all other kinds taken together. But the association neurones are not only the most numerous in the vertebrates; they also constitute the basis of the most significant evolution. The central nervous organs that show the most conspicuous progressive changes in the vertebrates are the cerebellum and the cerebrum, particularly their cortical portions, and when it is remembered that few or no primary sensory or motor neurones contribute to these two organs, but that they are made up of association neurones almost exclusively, it will be seen how enormously important these neurones become. The association neurones in the vertebrates are not only the organs of intricate nervous exchange, but in the region of the cerebral cortex they afford the material basis of the intellectual life. Thus in the vertebrates the primary sensory and motor neurones in number and importance are outstripped by the association neurones.

As thus sketched the development of the adjustor or central nervous element of the neuromuscular mechanism takes place in the region between the receptors and the effectors and in time after these two sets of organs have appeared. Its primary function is undoubtedly transmission involving the principle of the common path; secondarily it comes to be a repository of the effects of nervous stimulation whereby its principal function as a modifier of impulses is made possible.

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THE ORIGIN OF THE NERVOUS SYSTEM AND ITS APPROPRIATION OF EFFECTORS

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IV. THE APPROPRIATION OF EFFECTORS

IN the preceding articles in this series the origin and development of the neuromuscular mechanism has been broadly sketched in a succession of representative stages. The first stage was that of the independent effector, the muscle which was brought into action by the direct influence of environmental changes as seen in the pore sphincters of sponges. The second stage was that of the combined receptor and effector in which the receptors, in the form of diffuse sensory epithelia or specialized sense-organs, served as delicate triggers to set the muscles in action and thereby render the effectors responsive to a wider range of stimuli than they would be under independent stimulation. Finally, the third stage is seen in the complete neuromuscular mechanism in which a central nervous organ or adjustor has developed between the receptors and the effectors. This adjustor serves as a switchboard for nervous transmission and a repository for the effects of nervous activities.

This line of progressive differentiation from the muscle to the complete nervous system is complicated by the fact that in the more complete examples of the third stage the nervous system is found connected not only with such effectors as muscles, but with electric organs, chromatophores, glands, luminous organs, etc. If the history of the growth of the neuromuscular mechanism as it has been sketched in these articles is a correct one, the effectors just named must be regarded in the light of relatively recent acquisitions and in my opinion they illustrate an invasion and appropriation on the part of the nervous system of territory that was not originally under its control. This principle of appropriation results not only in the acquisition of totally new forms of effectors such as glands, etc., but also in gaining control over independently and newly developed muscles. Examples of this kind will be taken up first in discussing this question of nervous appropriation.

The differentiation of the central nervous organs is in large part a process that goes on hand in hand with the differentiation of the muscles. This is well seen not only in the higher invertebrates, but also in the vertebrates. The differentiation of a single muscle into a group of muscles and the consequent and corresponding changes in the nervous relations, both central and peripheral, are too well known to require comment. To this process must be added, I believe, the appropriation of totally new muscles. There is good reason to assume that the heart-beat in tunicates is of myogenic origin and the fact that the embryonic vertebrate heart pulses before it contains any nervous elements is strong evidence in favor of the view that the cardiac muscle of the primitive vertebrate was a muscle developed independently of nervous control. That that muscle in modern adult vertebrates is under a certain amount of nervous control is unquestionable, but this control is not of the kind usually seen in other neuromuscular combinations. The nerves that enter the heart are probably not ordinarily directly concerned with its beat, for, as already pointed out, this continues after they are cut. The function of these nerves seems to be that of modifying this beat and in this respect two classes of fibers may be distinguished: augmentors which increase the beat, and inhibitors which retard or even check it. This whole nervous mechanism has the appearance of having been superimposed upon a muscle that was originally non-nervously active, and I therefore regard the vertebrate heart as an example of an originally independent muscle secondarily brought under the influence of central nervous organs. Many other muscles, like the sphincter pupillæ, etc., have doubtless had a like history, but as they have not been investigated from this standpoint, the question of their exact relations to nervous control must remain for the present somewhat open.

In the vertebrates at least, nervous effectors include not only muscles, but also electric organs. These organs occur not infrequently among the fishes. They are best represented in the South American electric eel, the electric catfish of Africa and the torpedoes of the Mediterranean Sea and the Atlantic and Indian Oceans. They also occur less fully developed in certain skates, mormyres and the star-gazer. These organs are usually imbedded in a mass of the fish's muscle or they occupy such positions that they clearly replace muscles. Their histogenesis, as worked out particularly in the skates by Ewart (1888), shows conclusively that each electric plate is a modified muscle-fiber and in fact there seems to be good reason to conclude that all known electric organs, excepting possibly those of the electric catfish, are modified muscles. This is entirely consistent with what is known of the physiology of these two kinds of effectors, for muscles not only move parts, but generate through their activity a certain amount of electricity, while the electric organs have lost the power of producing molar movements and have enormously increased that of producing electricity. Electric organs, though often described as a special class of effectors, are in reality merely modified muscles and therefore can not be regarded properly as a new appropriation of the nervous system.

The chromatophores, on the other hand, are effectors which are in no sense derived from muscles. These organs enable many animals to make relatively sudden changes in their external coloration, and though they are present in many animals, they are most perfectly developed in the arthropods, mollusks and vertebrates. They are also present in the more complex types of eyes, where their movements serve to protect the receptive elements from exposure to excessive light or to open them to the full effects of dim light. The investigation of these organs dates from comparatively recent times and van Rynberk (1906), who has recently summarized our information about them, has shown that the accounts already given are in many respects contradictory. Hence what I shall have to say I shall draw mostly from those fields with which I am somewhat acquainted at first hand.

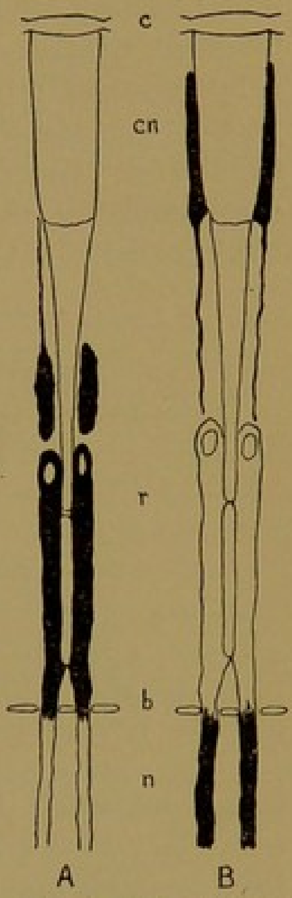

Fig. 1. Two Elements from the Compound Eye of a Shrimp, showing the distribution of pigment in the light (*A*) and in the dark (*B*). *b*, basement membrane; *c*, cuticula; *cn*, cone; *n*, nerve-fiber; *r*, retinular cell.

That some chromatophores are completely independent of nervous control even though they are most intimately associated with nervous mechanisms is well attested. The deeper part of the compound eye in the shrimp, *Palæmonetes,* contains a layer of cells, the retinular cells (Fig. 1), which though they carry rhabdomes and end proximally in nerve-fibers and are therefore unquestionably sensory cells, contain many dark pigment-granules which change positions in accordance with the illumination. From this standpoint these cells are true chromatophores. In an eye exposed to the light the pigment-granules occupy distal positions in these cells; in one in the dark they come to lie in proximal positions. The place occupied by the pigment in a given eye is entirely determined by the presence or absence of light in that eye, for the two eyes have no sympathetic relations. Moreover if a persistent shadow is cast on part of one eye, the condition characteristic for the dark is assumed by that part even though the pigment in the rest of the eye is in the position characteristic for light. These observations show the physiological independence of the chromatophores in different parts of the eye. These organs, though connected by nerve-fibers with the central nervous organs, are also in their action independent of such parts, for the movements of their pigment from the dark to the light position and the reverse go on in an essentially normal way even after these connections have been cut. Chromatophores then may carry out under direct stimulation somewhat complicated pigment-migrations in intimate relations to the successful action of such an organ as an eye, and yet with complete independence of central-nervous control.

Other chromatophores, like those in the skin of lizards, can be as clearly demonstrated to be under the control of nerves as those in the eyes of *Palæmonetes* have been shown to be free from this control. The integumentary color changes in lizards are often extremely complicated processes, especially in such forms as the chameleon, but they include as a fundamental principle the inward and outward migration of dark pigment-granules within certain large unicellular chromatophores (Fig. 2). When these pigment-granules pass out into the processes of the chromatophores, they give to the surface of the lizard a dark or even black aspect. When they migrate inward to the body of the chromatophore, which is often hidden in pigment masses of some particular color, they thus allow the ground-color behind them to assert itself. By this simple inward and outward migration of the pigment, the chief change in the color differences of the lizard's skin is accomplished. The question that we have to consider is to what extent these changes are controlled by the central nervous organs.

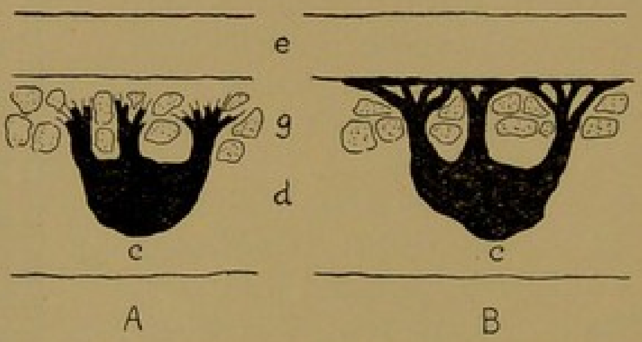

Fig. 2. Two Chromatophores from the Skin of a Lizard, showing the condition due to the dark (*A*) and to the light (*B*). *c*, chromatophore; *d*, derma; *e*, epidermis; *g*, irregular masses of ground color.

The inward and outward migration of the pigment of the chromatophores is well seen in the skin of the so-called Florida chameleon, *Anolis*. According to Carlton (1903), who has studied this animal with care, the passive state in its chromatophores is that in which their pigment is gathered together in the cell-bodies. This state is brought about when the lizard is removed from the stimulating effect of light, when the blood and nerve supply of a given region are cut off, when the animal is etherized, or when it dies. In fact any change that might be expected to interfere with nervous activity calls forth this condition. Since nicotine is a poison for the sympathetic nervous system, rendering it temporarily inactive, and since the inward migration of the chromatophoral pigment is immediately produced on injecting a very small amount of nicotine into the *Anolis*, it is probable that the reverse process, the outward migration, is dependent upon the normal action of these poisoned parts, the sympathetic nerves. For these reasons I believe that in *Anolis* the inward migration is a process which is ordinarily under the control of the chromatophore itself and that the outward migration, which takes place all over the animal when even only a small spot in the skin is illuminated (Parker and Starratt, 1905), is dependent upon the action of sympathetic nerves.

In the true *Chameleon,* as Brücke (1852) and many others have demonstrated, precisely the reverse is true; the outward migration is independent of nerves and the inward migration is produced by them. Moreover, judging from the results of experiments on the spinal cord, the nerves which in *Chameleon* are concerned with these changes are not sympathetic nerves, but spinal nerves.

These differences between *Anolis* and *Chameleon* I believe to be well founded. In my opinion both animals have descended from a stock in which the chromatophores were entirely independent of nervous control and in the process of descent the chromatophores of different lines became separately appropriated as effectors of the nervous system. In the ancestors of *Anolis* the sympathetic nervous system became related to the outward migration of pigment; and in those of the *Chameleon* the spinal system associated itself with the inward migration. The fact that *Chameleon* and *Anolis* belong not only to separate families, but to separate suborders of lizards, rather emphasizes this view than otherwise.

Such instances as the independent retinal chromatophores of *Palæmonetes* and the nervously dependent chromatophores of *Chameleon* and *Anolis* lead me to believe that chromatophores are effectors evolved independently of nervous control, but in some cases secondarily appropriated as nervous end-organs.

What has been said of chromatophores so far as their relation to nerves is concerned is probably also true of glands. The majority of glands are unquestionably independent of direct nervous control. In almost all instances a blood supply is essential to the action of a gland, and as this can be controlled by nerves there is thus an indirect influence of the nervous system on the action of the gland, but this nervous control over the blood supply is very different from a direct nervous control over secretion. I know of no good reason to assume that nerves have any direct influence on the secretions of the kidneys, the liver or even the pancreas. The pancreatic juice which appears with such precision on the arrival of food in the small intestine has been shown by Bayliss and Starling (1904) to be secreted not through the action of nerves on the gland, but through the action of a substance, secretin, produced by the food in the intestine and carried by the blood to the gland. If into the blood of a fasting animal whose nerves to the pancreas have been cut a small amount of secretin is injected, the pancreas will begin to produce its characteristic secretion.

Although most glands are not under direct nervous control, some are as completely under this control as the majority of muscles are. The best examples of this condition are the sweat glands and the salivary glands. The fact that when the nerves supplied to the salivary gland are stimulated, secretion may take place at a pressure higher than that of the blood supplied to the gland shows conclusively that the production of saliva is not a simple organic filtration process, but is dependent upon action called forth in the secretory cells by a nervous impulse. This view gains additional support from the fact that in the salivary glands nerve fibers have been found to end in connection with the secretory cells. There is therefore every reason to believe that the salivary glands, and the same may be said of the sweat glands, are organs whose secretions are directly controlled by nerves.

As these several examples show, some glands are completely under the control of nerves and others are not. In my opinion the latter represent the primitive state of this form of effector and the former the condition after such organs have been appropriated by the developing nervous system.

Luminous or phosphorescent organs afford another class of effectors which have probably originated independently and fallen secondarily under the influence of the nervous system. These organs, however, have been studied so imperfectly that it is at present difficult if not impossible to get satisfactory evidence as to their exact condition. Some animals have been supposed to possess phosphorescent organs when in reality their luminosity was due entirely to reflection; others like certain earthworms were found to be phosphorescent because their slime contained photogenic bacteria. But aside from these spurious cases there is an abundant range of truly phosphorescent animals, examples of which occur from protozoans to vertebrates. One peculiarity in their distribution is that true phosphorescent animals are not found in fresh water; they are either marine or air-inhabiting.

In all cases where animal phosphorescence has been examined with care, it seems to be dependent upon the production of a special substance by the light-producing cells. This substance is not in the nature of a living, structurally organized material like muscle, for it can be crushed into a paste and still show light. Moreover, Bongardt (1903) dried the phosphorescent organ of a common firefly over calcium chloride and then kept it in a sealed tube from July 16, 1901, till August 3, 1902, a period of over a year. After this the tube was opened and the organ wet with distilled water; in twelve minutes it glowed so that it could be seen at a distance of two meters. Evidence of this kind supports the view that the phosphorescent substance is not living but rather formed material, such as a secretion, and resembles in this respect pepsin or trysin.

If phosphorescent organs produce a substance essentially a secretion to which their characteristic activity is due, they might without impropriety be classed as glands, but if they are thus classed, it must be remembered that the majority of them are so placed that they have no access to cavities or the exterior; hence they would be in the nature of ductless glands. In one respect, however, they differ even from ductless glands; the substance that they produce is not carried away from them even by the blood-stream but is used locally for the production of light. Hence though phosphorescent organs may be in many important respects like glands, they differ in certain ways from all ordinary glands.

Whether phosphorescent organs are under the control of nerves or not is a question of some uncertainty. The fact that many highly specialized phosphorescent organs have a rich innervation indicates that they are under nervous influence, but even this may be of the indirect kind such as has already been indicated for glands and not a direct control. In ctenophores Peters (1905) has shown that a few paddle-plates will glow on mechanical stimulation precisely as the rows of plates in the normal animals do. He has also shown that the primitive nervous system of these animals plays no direct part in this phosphorescence. This instance seems to me to be a perfectly clear case of phosphorescence not under the control of nerves, though in an animal with a nervous mechanism.

In the common firefly the relations are not so well understood. Thus Bongardt (1903), though he describes an intimate nervous plexus in the luminous organ of this animal, believes that its rhythmic photogenic activity is not under even indirect nervous control. He maintains, on what, however, is not really strong experimental evidence, that the firefly can not extinguish its light through nervous action and he believes that the phosphorescent rhythm is due to totally different factors. This case merely shows the fragmentary nature of our knowledge of this phenomenon even in so well-known an example as the firefly.

As a good instance of nervous control over phosphorescence the brittlestar, *Ophiopsila,* recently studied by Mangold (1907), may be quoted. On mechanical stimulation the ventral surfaces of the arms of this animal glow for a short time. The phosphorescence begins in the stimulated part and, if this be an arm, it may spread over this arm to the disk and thence to the other arms. The course that it follows is that of the radial and circular nerve-strands. If any of these are interrupted by being cut, the phosphorescence does not pass beyond the cut, thus showing that it is probably controlled by the nerve.

These instances, few and confessedly fragmentary as they are, indicate that phosphorescent organs, though in many important respects like glands, are in reality a separate class of effectors and that in some instances their action is independent of nervous control, while in others it is under this control. In my opinion the instances of independent action represent a primitive state; the others a condition brought about through the appropriation of these organs as end-organs by a developing nervous system.

If what has been stated in this article is correct, we must picture to ourselves as steps in the evolution of the nervous system not only the independent origin of muscle around which the nervous organs subsequently develop, but also the independent origin of other effectors such as chromatophores, glands and phosphorescent organs and the secondary appropriation of many of these by a developing nervous system. This principle of appropriation I believe to be as significant in elucidating the present condition of the nervous system and its appendages, as the principle of evolutionary sequence of parts, muscle, sense organ, and central nervous organ, as given in the first three articles.

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