SYMPOSIUM ON COMPARATIVE NEUROLOGY¹

1. THE PHYLOGENETIC ORIGIN OF THE NERVOUS SYSTEM

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The highly differentiated nervous system, such as is found in the vertebrates and other higher metazoans, is described as composed for the most part of many inter-related reflex arcs. Each of these arcs involves at least three parts: a sense organ or receptor which receives the external stimulus and originates the nervous impulse; a central nervous organ or adjustor in which the impulse may be variously modified and directed; and a muscle, gland, or other effector by which the animal responds to the external stimulus. Nerve fibers connect, of course, the receptor with the central apparatus and the latter with the effector. At least two classes of neurones are concerned in this mechanism, one afferent or sensory and the other efferent and usually motor. The sensory neurone is modified at its peripheral end to form the receptor and its nerve fiber extends as a rule to the central organ in which it ramifies; its cell-body may occupy a peripheral position even forming an essential part of a sense organ as in many invertebrates and in the olfactory organ of vertebrates, or it may be nearly central in location as in the spinal ganglia of the vertebrates. The motor neurone has its cell-body within the central organ and its fiber as an efferent fiber extends to a muscle where it terminates. Besides these two classes of neurones, afferent and efferent, the central organs usually contain a vast congregation of correlation neurones which in one way or another intervene between those already mentioned.

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Such a nervous system as the one just described is found in the vertebrates, mollusks, anthropods, worms, and other higher metazoans, but is only feebly represented, if in fact it can be said to be represented at all, in the echinoderms, ctenophores, and coelenterates. The part that is least developed in these lower animals is the central organ, and, though this part cannot always be said to be absolutely unrepresented, it is so deficient, especially in the coelenterates, as to have led to the designation of their nervous apparatus as diffuse rather than centralized. The so-called diffuse nervous system of these animals is the simplest nervous system with which we are acquainted, for, notwithstanding repeated efforts, no true nervous structure has ever been demonstrated in those metazoans which, like the sponges, are more primitive than the coelenterates. If, therefore, the beginnings of the nervous system are to be sought for, attention must be directed to the coelenterates.

The coelenterate body is composed chiefly of two specialized epithelial layers, ectoderm and entoderm, each of which contains both nervous and muscular elements. The nervous elements are epithelial sense-cells whose receptive ends are at the periphery of the layer in which they are contained and whose nervous ends form a system of extremely fine interlacing branches many of which are probably directly connected with the deep-seated muscle-cells. The fine branches from many neighboring sense-cells establish what is probably a true nervous net by which transmission is accomplished not only to the subjacent muscle-cells but to those some distance away. Here and there this net contains conspicuous, multipolar cells which contribute fibrils to it and which for this reason are believed to be nervous. It is with the origin of this relatively simple neuromuscular mechanism that we are concerned.

In 1872 Kleinenberg announced the discovery in the fresh-water hydra of what he designated as the neuromuscular cell. The peripheral end of this cell was situated on the exposed surface of the epithelium of which it was a part and was believed to act as a nervous receptor; the deep end was drawn out into a muscular process and served as an effector to which transmission was supposed to be accomplished through the body of the cell. Each such cell was

regarded as a complete and independent neuromuscular mechanism, and the movements of an animal provided with these cells were believed to depend upon the simultaneous stimulation of many such elements. It was Kleinenberg's opinion that these neuromuscular cells divided and thus gave rise to the nerve-cells and muscle-cells of the higher animals. In fact he declared that the nervous and muscular systems of these animals were thus to be traced back to the single type of cell, the neuromuscular cell, which morphologically and physiologically represented the beginnings of both.

Some years later, in 1878, the Hertwigs published an account of the minute structure of the coelenterate nervous system and showed that Kleinenberg's so-called neuromuscular cells were probably merely muscle-cells in process of differentiation. They consequently proposed for these cells the more appropriate name of epithelio-muscle cell. They also claimed that in the evolution of the neuromuscular mechanism in coelenterates the three types of cells that they had identified, the sense-cells, ganglion-cells, and muscle-cells, were simultaneously differentiated from ordinary epithelial cells. Thus these three elements, though regarded as derived from a common layer, were, according to the Hertwigs, not the descendents of any single type of cell such as the neuromuscular cell.

Although Kleinenberg's theory and the theory of the Hertwigs differ in certain important details, they agree in declaring for the simultaneous and interrelated evolution of nerve and muscle. As contrasted with this view is the hypothesis that was first advocated by Claus and later by Chun that the two types of tissue arose independently and became secondarily united. In 1880 Chun called attention to the fact that in vertebrates the motor nerve-fibers grow out of the medullary tube and become connected with the muscles secondarily and he regarded this as evidence that nerve and muscle had arisen in phylogeny independently and had become secondarily united. But the majority of investigators have sided with the opinion expressed by Samassa (1892) that a nervous system purely receptive in function and without effectors of any kind is practically inconceivable. Hence the hypothesis of Claus and Chun has been generally regarded as untenable.

The current opinion among investigators as to the evolution of the nervous system of primitive metazoans remains essentially that of the Hertwigs, namely that nerve and muscle have been differentiated simultaneously and in close physiological interrelation but from cells which were separate members of an epithelium. To this view I wish to offer certain opposing facts obtained from a study of sponges. It has already been stated that no nervous structures have been definitely identified in the sponge, nor is there, so far as I am aware, any physiological reason to suppose that such exist. Nevertheless these animals are capable of some movements and their movements are so related to changes in the environment as to be classed as normal reactions. Under this head may be placed the closing and opening of the oscula and of the pores, and certain general movements of the whole body of the sponge. The closing of the oscula and of the pores is carried out by sphincters composed of spindle-shaped cells which in many respects resemble smooth muscle-fibers. These cells are unprovided with nerves and are brought into action, so far as I have been able to ascertain, by direct stimulation. I therefore believe them to be independent effectors and that the sponge is an example of an animal that possesses muscle but no nerve. If, as seems probable, muscle without nerve exists in these primitive metazoans, it follows that we are no longer justified in concluding that nerve and muscle have differentiated simultaneously, but it must be admitted that muscle is phylogenetically the older. I therefore believe that the beginning of the neuromuscular mechanism is to be found in the appearance of independent effectors such as muscles and that sponges probably represent this initial stage in the evolution of the mechanism concerned. Some physiologists may be inclined to question the actual occurrence of normally independent effectors, but the heart of *Salpa*, and that of the chick embryo before it becomes invaded by nervous tissue are examples of this kind, and it is now well known that though the sphincter pupillae of the vertebrate eye is under the control of nerves, it also responds directly to light. These instances seem to me a sufficient warrant for a belief in the existence of independent effectors.

Although the sphincters of sponges are effectors without nerves,

they are good examples of the kind of centers around which nervous tissue probably first arose. This development can be conceived to have occurred in the epithelial cells in the immediate proximity to such a center, in that these cells gradually assumed a special receptive function whereby they could stimulate the adjacent muscle more efficiently than it could be stimulated directly and thus an ordinary epithelial cell would gradually be converted into a receptive or sense-cell. From this standpoint the original function of the sense-cell was merely that of a delicate trigger by which the muscle would be more certainly and efficiently brought into action than through its own receptive capacity and many sense-cells in the lower metazoans probably still retain this as their sole function. Such cells occur abundantly in the coelenterates and hence I regard the sense-cell as the first type of nervous tissue to be differentiated. Since sense-cells and muscle-cells make up the chief part of the neuromuscular apparatus of coelenterates, I have designated this apparatus as a receptor-effector system.

But coelenterates usually show more than a simple receptor-effector system, for the fine branches from their sense-cells not only reach their muscle-cells but also anastomose with one another and form a nervous net. Such a net is the first step toward the formation of a central nervous organ or adjustor and its origin in relation to the sense-cells and the muscle-cells is probably so strictly local that it practically realizes Hensen's view as to the histogenetic relations of nerve and muscle, namely that these elements are not developed separately and brought into connection secondarily, but that their connections are original and give evidence of the incompleteness of cell division in the course of ontogeny. Such nets serve as more or less diffuse transmitters and are supplemented by the fibrils from certain contained cells, the so-called ganglion cells, which have migrated into the net and which probably mark the first step in the growth of those accumulations of cell-bodies that characterize the central nervous organs of the higher animals.

If this view as to the mode of origin of the central nervous organs is correct, it follows that these organs must be controlled in their incipency by the sense organs. In such coelenterates as sea anemones where the sensory specialization is slight, there is scarcely

any evidence of centralization in the nervous net, but in jelly fishes where the sense organs are specialized and in groups, each group has associated with it a region of special development, an incipient central organ in the nervous net. In bilateral animals such as the annelids and the crustaceans, the chief portion of the central nervous system, the so-called brain, is also associated with a group of sense organs and these organs, essential to the anterior end of any animal that moves forward, determine, in my opinion, the position of the brain rather than the reverse. Even in the vertebrates where the brain arises to a dignity not attained by any other nervous organ, its anterior position has been determined, I believe, by the location of the sense organs rather than that the sense organs are at the anterior end because the brain is there.

But although the central nervous organs have probably developed from a nervous net under the influence of the sense organs, they have taken in their later evolution a course more or less their own. Even the nervous net, which, in my opinion, unquestionably exists in the lower metazoans, has been denied in the central nervous organs of the higher animals. But it is not impossible that in these more specialized forms a nervous net may have a local existence. Evidence that nervous nets do not exist in certain parts of the vertebrate nervous system does not prove that they may not occur in other parts of this system. In the myenteric plexus of the vertebrate intestine the relations of nerve and muscle are such as to recall most strikingly the conditions already portrayed in the nervous net and muscles of the coelenterates and it is possible that nervous transmission in these animals follows the same rules that it does in the vertebrate intestine. In the vertebrate retina, too, the histological evidence is strongly in favor of a nervous net and the fact that the cells of the retina are members of the same epithelial layer and may therefore always have retained primary connections, suggests a fundamental similarity with the conditions in the coelenterates. Thus there are localities in the nervous systems of even the most highly differentiated animals where these most primitive of central structures, the nervous nets, very probably occur. But to claim on the basis of these instances that the whole central nervous system of the vertebrate is con-

structed on the plan of a nervous net would be going far beyond the facts.

It is well established that in the histogenesis of the central nervous organs of the higher animals, many cells that are ultimately in most intimate physiological relations, are in their early stages of development far asunder and that they attain to their final close relations by throwing out processes that grow toward one another. It is probable that these processes never really unite into continuous transmitting tracts but retain at least a certain physiological separateness, for in such parts of the central organ where these relations occur, transmission is not diffuse, as in the nervous net, but is limited to a single direction. Central nervous systems having these peculiarities have been called synaptic because the contact points between their cells, the synapses, are believed to be the parts that in some way govern the direction of transmission. This synaptic system has in the higher animals replaced to a considerable extent the more primitive nervous net and though this nervous net may still exist in some parts of the central nervous apparatus of such animals as the vertebrates, it is not the structure that gives to these organs their distinguishing characteristic. In these organs the fully differentiated nerve-cell or neurone with its synaptic connections is the characteristic structural unit of the system. Combinations of such units make up large parts of the central nervous organs of the higher animals and possess apparently physiological possibilities of a vastly higher order than can be found in the more primitive nervous nets; they have thus afforded the structural basis for the nervous activities of all the higher animals. Although the nervous net with its capacity for diffuse transmission was the structure in which the central nervous system took its origin, I nevertheless believe that this system early underwent fundamental changes whereby synaptic neurones with transmission in restricted directions replaced in large part the more primitive system of diffuse nervous nets.

The facts briefly stated in the preceding paragraphs justify the conclusion, I believe, that muscular tissue and nervous tissue have not arisen at the same time phylogenetically, but that muscle in the form of independent effectors preceded nerve in its develop-

ment and that nervous tissue differentiated in close proximity to muscle tissue as groups of sense-cells or receptors. Still later central nervous organs developed between the receptors and the effectors, first as clusters of nerve or ganglion cells which added to the nervous nets and later as aggregates of synaptic neurones from which were formed the more complex nervous organs of the higher animals. Thus the three parts of the differentiated neuromuscular system of the higher animals have, in my opinion, developed in sequence: first, the muscle or effector; next, the sense-organ or receptor; and last, the central organ or adjustor.