DISCONTINUITY IN THE NERVOUS SYSTEM OF COELENTERATES

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INTRODUCTION

THE occurrence of nerve nets in such places as the skin, the tunica media of the blood vessels and the enteric plexuses in vertebrates is frequently unquestioned by reason of the prevalent notion that the simplest invertebrates possess a nervous system in which there is syncytial continuity between the nerve elements. Recent unpublished investigations in mammals have thrown doubt upon the existence of such nerve nets. It therefore seemed advisable to restudy the primitive nervous system in coelenterates.

The extensive literature relating to the nervous system of coelenterates has been summarized by Bozler (1927) and Heider (1927). The histology of the coelenterate nervous system was first investigated by the Hertwigs (1878, 1879, 1880) and by Schäfer (1878), following up the experimental work of Romanes (1876, 1877). The former worked on Medusae and Actiniae and were non-committal with regard to continuity, but Schäfer, who worked on the common jelly-fish, *Aurelia aurita*, was definite that the nerve fibres were discontinuous. The succeeding papers dealing with this problem were consistently in favour of the continuity of the nerve fibres and therefore of the existence of a true nerve net. However, Bozler (1927), describing the nervous system of the large jelly-fish *Rhizostoma*, concurred with the views of Schäfer, and mentioned that few investigators appear to have appreciated the important work of the latter. Heider (1927), working on ctenophores, and McConnell (1932), working on *Hydra*, are the most recent investigators who claim evidence for the idea of continuity.

OBSERVATIONS

Material. The forms studied included the sea-anemones *Tealia felina* and *Actinia equina*, and the jelly-fishes *Cyanea lamarcki* and *Chrysaora isosceles*.

Methods. Whole animals or fragments from the subumbrellar ectoderm of the jelly-fishes were placed for ½–2 hr. in 0·1–0·05 %.methylene blue in sea water. The tentacles of the sea-anemones were studied similarly, as well as by the gold chloride-formic acid method. The jelly-fish material was studied in the living, since like other workers we found the preservation of these animals very unsatisfactory.

Findings. Nerve cells are scattered all through the plexuses and as many as five or six may be present in a 1/12th oil-immersion field. They are mainly bipolar; a few are multipolar. In the bipolar type the nerve processes start from opposite ends of the ovoid cell body. The cell body is small, and its small size seems out of proportion to the size and length of the processes. The nucleus is small and compact. It often shows the characteristic nucleolus of the mammalian nerve cell. With methylene blue staining, granules are demonstrable in the cytoplasm of the cell and also in the basal part of the processes. Groselj (1909) thought that these granules might represent tigroid substance. In none of the regions studied are the nerve cells gathered together in ganglionic masses.

The fibres show no structural differentiation. Myelin sheath and neurilemma are both absent, and there is nothing to suggest any structural difference indicating conduction to or from the cell. Either process (or, where there are several, any or all of them) may subdivide. Some fibres are thick and others thin. On tracing individual fibres it can be seen that the same fibre may begin as a thick one, but as it extends it grows thinner, eventually becoming so thin as to pass beyond the powers of resolution of the microscope. At their origin from the cells the fibres are all of about the same thickness. The diameter, therefore, would seem rather a function of the distance travelled by the fibre than a distinction in form and an indication of different physiological properties.

Many of the processes have a varicose appearance; irregular swellings occur at varying intervals. When portions of tissue are immersed for several hours in the methylene blue, the swellings become very large. It is tentatively concluded that the prolonged action of the methylene blue leads to a loss of viability of the tissues and thus to a pathological increase in size of the varicosities. Small irregular thickenings are demonstrated by gold chloride impregnation (Pl. I, fig. 3), and can be seen in methylene blue staining before viability is appreciably altered.

The direction pursued by the fibres appears at first sight quite irregular, but on further observation many are seen to run towards the muscular layer (Pl. I, figs. 1, 2). Round pigment cells are scattered singly or clustered in groups. The nerve cells are seen as small ovoid swellings interposed in the course of the fibres (figs. 2, 3). Single fibres can be traced for relatively long distances. They may take a straight or a sinuous course. Some do not branch, while others soon subdivide. As they approach the muscle many of the nerve fibres become somewhat thinner. Upon reaching the muscle fibres they undergo subdivision into a number of very small branches which end upon the surface of the muscle cells by means of small expansions. This pericellular investment appears to be similar to the nerve endings that occur in non-striated muscle in mammals.

Where continuity has been described in the coelenterate nervous system, this has been represented as an end-to-end fusion between the fibres. That such a simple arrangement does not occur is seen in Pl. I, figs. 1, 2. Although at low magnifications it seems possible that fusion between the nerve fibres occurs where these cross one another, this doubt can be dispelled by the use of high-power objectives (Pl. I, fig. 3). At such points of crossing one of the fibres sometimes shows a thickening. No fusion, however, occurs.

The fibres frequently present a characteristic relation to one another, that of intertwining. The fibres may wind round one another once (figs. 1, 2 and 4) or several times (fig. 1). At these intertwinings no fusion occurs, each fibre retaining its individuality. Schäfer was also impressed with the frequency with which fibres intertwined and suggested that such an arrangement presented the opportunity for "induction" to occur. Fibres have also been observed to lie in close contact with the surface of nerve cells. Sometimes a structure that possibly represents a "bouton" can be observed.

Many neuro-sensory cells have been seen, especially in the methylene blue material. They correspond in every detail with the careful descriptions of such cells that have been given by Groselj. These neuro-sensory cells give off a process from their deep aspect, but this conducting process we were unable to trace far.

COMMENT

It is permissible here to refer to the recent physiological investigations of Pantin (1935) on various coelenterates. In addition to other observations, Pantin showed that the nervous system of sea-anemones possesses some degree of polarization and facilitation. The reactions are diffuse and the frequency of "after-discharge" complicates considerably the interpretation of what Pantin believed from the literature to be a nerve net. It appears to us that a nervous system such as our observations lead us to believe occurs in the coelenterate would account more satisfactorily both for the diffuseness of response and for the other properties, viz. facilitation, polarization and "after-discharge" described by Pantin.

Certain histologists (Boeke, 1935; Stöhr, 1928; Rieser, 1933; etc.) believe that in vertebrates neural syncytia (variously described as the sympathetic ground plexus, the periterminal network, and the terminal reticulum) occur throughout the body. Such a conception, however, cannot be supported by any appeal to more primitive types of nervous systems. Their existence and their significance must be proved by investigations upon the animals in which they are said to occur.

The existence of a neurencytium amidst an otherwise synaptic system in higher animals would be surprising in the light of the occurrence of discontinuous neurones in primitive forms.

SUMMARY

1. The histology of the nervous system in the sea-anemones *Tealia felina* and *Actinia equina*, and the jelly-fishes *Cyanea lamarcki* and *Chrysaora isosceles*, studied by the methods of methylene blue and gold chloride, is described.

2. It is concluded that the nervous system in these coelenterates consists of nerve cells the processes of which are discontinuous.
3. The nerve fibres frequently intertwine but never fuse.
4. Nerve fibres terminate on muscle cells by small expansions.

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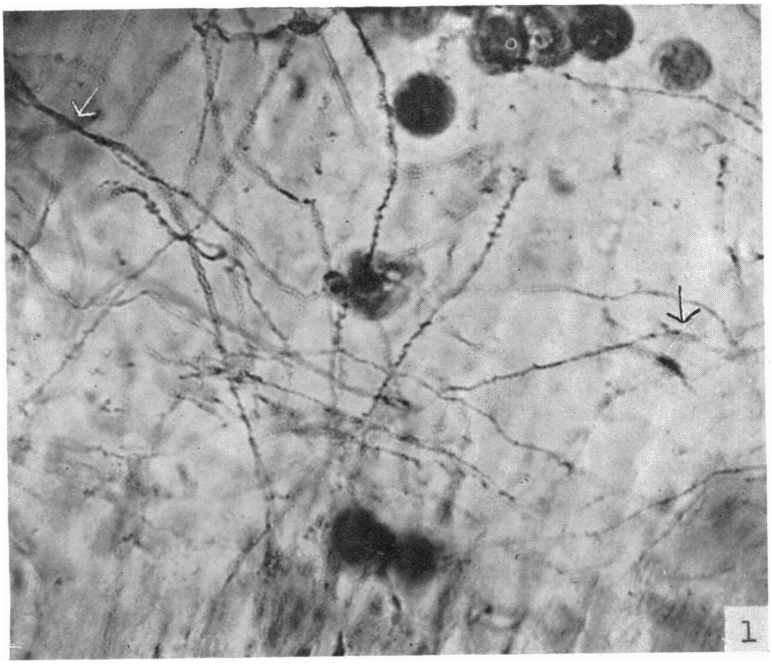
EXPLANATION OF PLATE I

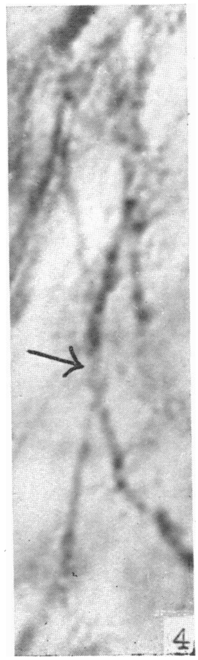
Fig. 1. Photomicrograph showing the nerve plexus in a tentacle of *Actinia equina.* The two arrows indicate intertwinements between fibres. In the lower part of the figure some of the nerve fibres are seen to enter the muscle layer. Gold chloride. ×900.

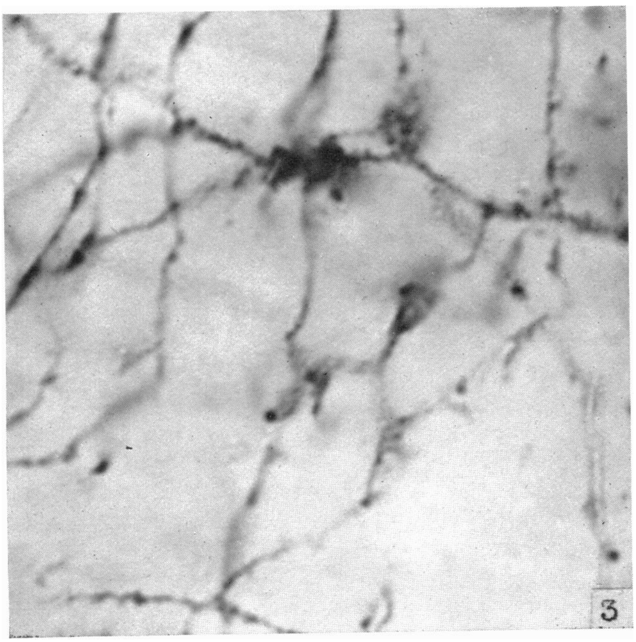
Fig. 2. Photomicrograph showing the nerve plexus in a tentacle of *Actinia equina.* In the upper part of the figure nerve fibres are seen to course in among the muscle fibres. In the centre of the picture a group of nerve cells is seen. In the lower part of the figure an arrow points to an intertwinement between fibres. Gold chloride. ×900.

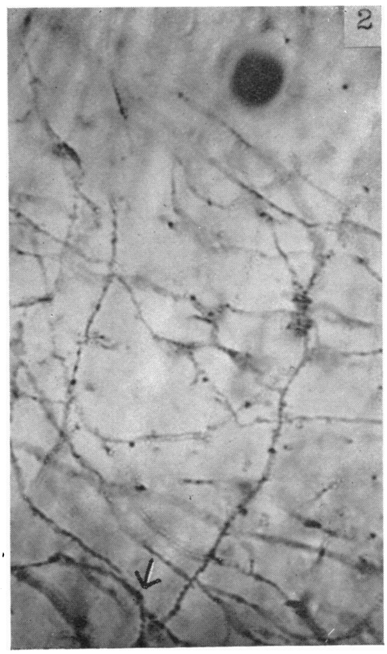
Fig. 3. A portion of the plexus illustrated in fig. 2 at a higher magnification, showing nerve cells and the varicose appearance of the fibres, which cross each other but do not fuse. ×2200.

Fig. 4. Photomicrograph showing an intertwining between nerve fibres in a tentacle of *Tealia elina.* An arrow points to the position of intertwinement. Gold chloride. ×1550.









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