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# A MUSCLE RECEPTOR ORGAN IN *ELEDONE CIRRHOSA*

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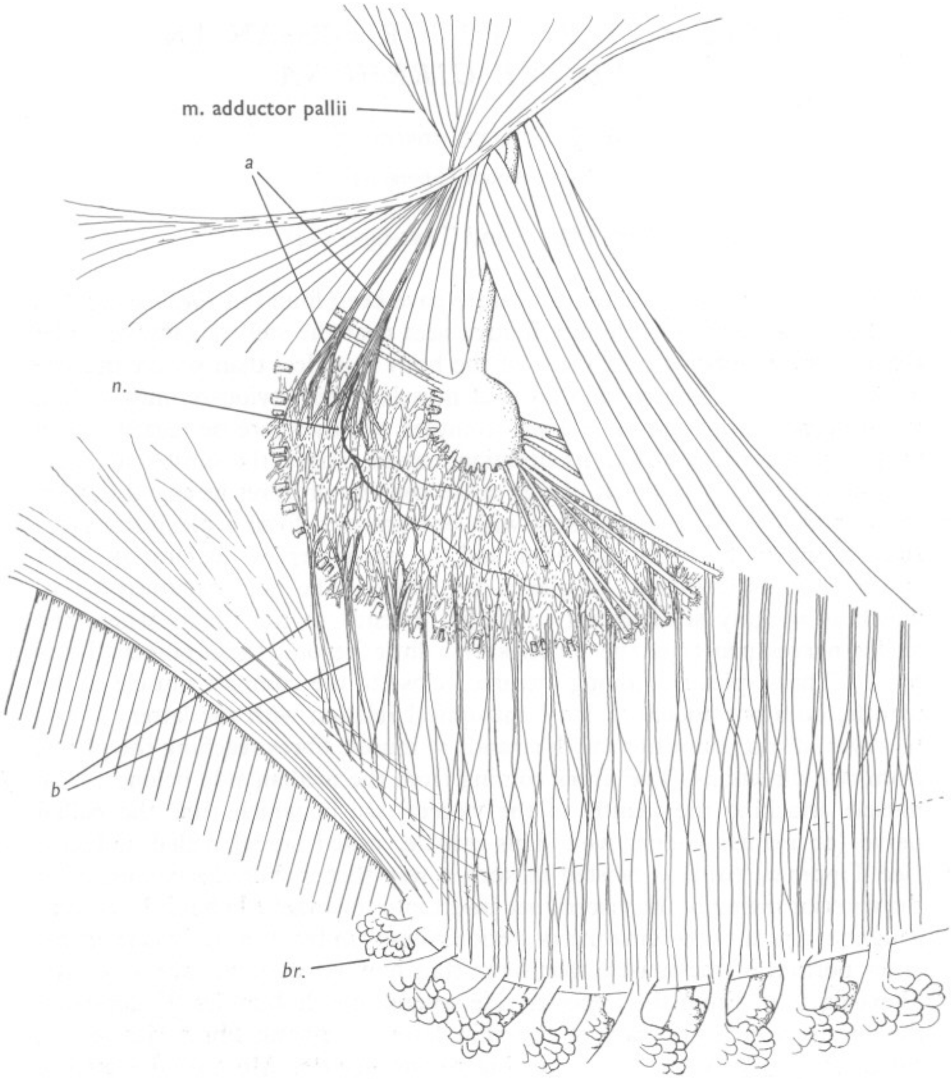
(With Plate I and Text-figs. 1–4)

Nerve cells evidently of a sensory nature have been found in *Eledone cirrhosa* on the inside of the mantle in a limited area near the stellate ganglion. The cells, whose number on each side of the body is no less than 50, are in close association with a special thin layer of muscles, and obviously must have a proprioceptive function. The whole complex can therefore be regarded as a muscle receptor which from its situation may be termed the substellar organ.

The muscular component of this organ consists of fibres arranged in very flat bundles which, anastomosing with one another, form a plexiform layer situated under the stellate ganglion and the stellar nerves. It may be called substellar muscle plexus (ss-plexus for short). The area occupied by it, which is roughly semicircular in shape, extends to the points where the stellar nerves penetrate the muscles or a little beyond these points (Text-fig. 1). The ss-plexus, although situated close to the compact muscle of the mantle, does not appear to have anatomical relation with the latter; it has, however, direct connexions with strands of muscle fibres reaching the plexus from two directions. The fibres coming from the median side belong to the muscle attaching the mantle to the visceral sac in which runs the pallial nerve (or mantle connective). This muscle, called lateral pallial adductor (see Tippmar, 1913) is twisted in such a way that its bundles coming from the anterior region of the visceral sac insert into the mantle behind the stellate ganglion, and those originating posteriorly insert in front of it. It is from the latter portion of the muscle that some thin bundles pass into the ss-plexus (Text-fig. 1 *a*). From the opposite side several muscle bundles (*b*) approach the plexus which are part of the thin layer of muscle fibres situated in the membrane attaching the branchia to the mantle. Most of the muscle fibres of this membrane run in the same direction towards the line of insertion of the pallial adductor and the area of the ss-plexus; near the free border of the branchial membrane they form a somewhat thicker band running parallel to this border.

It should be emphasized that a part only of the ss-plexus is connected with the muscle fibres of the pallial adductor and of the branchial membrane. Its other fibres spread in the connective-tissue sheet lining the mantle and terminate in this tissue independently of the neighbouring muscles. On the




Text-fig. 1. *Eledone cirrhosa*. Inside view of portion of the mantle showing the situation of substellar muscle plexus of the right side. Most of the stellar nerves have been cut out to show the plexus connecting with (*a*) the fibres of m. adductor pallii, and (*b*) the fibres of the muscle of the branchial membrane. *n*, nerve to the substellar muscle plexus; *br.*, branchia.

other hand, many fibres of the branchial membrane passing on to the area of the ss-plexus do not fuse with its bundles and insert into the connective tissue in the meshes of the plexus.

The muscle fibres of the plexus which are *ca.* $3\mu$ thick can branch and exchange anastomoses. The mode of their arrangement can be seen in Pl. I, fig. 1.

The ss-plexus is often very distinct in methylene-blue preparations. In order to facilitate its staining it is advisable to remove the epithelial layer lining the mantle cavity, to cut out the stellar nerves and to take away carefully the loose tissue beneath them. For better observation of the muscle and nerve elements the plexus can be separated from the mantle wall, but this should be done when the preparations after staining, fixing, etc., have been transferred into xylol. One must proceed from the outside, taking piece by piece the mantle muscles from the plexus and not vice versa. Preparations shown in photographs (Pl. I) were made in that way. The muscle fibres stain with methylene blue readily but unevenly. Much better pictures of the plexus structure can be obtained with Bodian's method; in such preparations, however, it is much more difficult to remove the unwanted tissues from the plexus muscles.

*Nerves*

The nerve supplying the plexus muscles arises from the mantle connective. It is covered at its point of origin and in its initial course by that portion of the pallial adductor which passes in front of the stellate ganglion. After giving off to this muscle several branches the nerve emerges near one of the bundles fusing with the plexus and runs across the latter in a wavy line obliquely backwards distributing branches to the muscles. In addition to this system of nerves which are doubtless of motor character there is on the plexus a second system connecting with some of the stellar nerves by thin nerves. The greatest number of the latter was four in one preparation, but how many they actually are remains uncertain. They are difficult to find for they join thinner stellar nerves situated deeper under the thick ones, and as the space between the stellar nerves is filled by loose tissue which must be removed one can never be sure whether in this operation some tiny nerves have not be torn away. On the other hand, there are here thin arteries which can easily be mistaken for nerves.

It seems very probable, as will be shown below, that this system of nerve fibres is formed by the axons of receptor neurons.

*Nerve cells*

Nerve cells are scattered over the ss-plexus at a distance from one another; sometimes two or, more rarely, three can be seen lying close together. They are all multipolar and can have a variety of shapes depending on the disposition of their processes (Pl. I, figs 3–5). Owing to this feature their dimensions can only be generally defined as being in the range between 40 and 100 $\mu$. How many nerve cells there are in all on the plexus could not be exactly determined because they are difficult to stain: sometimes they do not show at all, in other instances only a few can be spotted. The greatest number seen in one preparation was 25 in an area approximately equal to half of the plexus. Hence it may be deduced that their total number is not less than 50, but it can be higher than that. Because of their poor staining properties it has not been possible to gain a precise knowledge of their distribution. Such pictures as in Pl. I, fig. 2, showing several cells not far from one another, are not often seen, and there is no certainty whether the cells are spaced in the same way on the whole plexus. It is true that groupings with similarly or even more densely arranged cells have been observed at various points near the central region of the plexus as well as towards its periphery, but there is still not sufficient evidence whether the cells are distributed so closely everywhere or merely at certain points.

The number of processes arising from cell bodies is variable. Five or six of them are usually met with, but their true number can be greater since in addition to the thick processes some tiny ones can be frequently noticed, but they do not stain well. The processes which must be classified as dendrites project in all directions giving off branches spreading on the muscles. The thicker of them cross the muscle bundles at various angles, whilst the thin ones take their course alongside the muscle fibres. Very thin branches can arise directly from the stout cell processes, sometimes several of them close to each other. No special end-organs could be seen, and whether the nerves terminate on the muscle fibres or on the connective tissue between them I am unable to say.

The cell processes can be followed in favourable conditions for about 250 $\mu$ from the cell body, but appear not to end there, at least not all of them. Their tracing in methylene-blue preparations is uncertain because of the difficulty in distinguishing the nerves from the muscle fibres that stain readily and give off fine branches frequently looking like nerve filaments. There are, moreover, on the same muscles, motor fibres coming from the nerve mentioned above. Besides, methylene-blue preparations are often indecipherable because of deformations of fibres produced by longer immersion of tissues (8–10 h, sometimes up to 20 h) in methylene-blue solution in sea water

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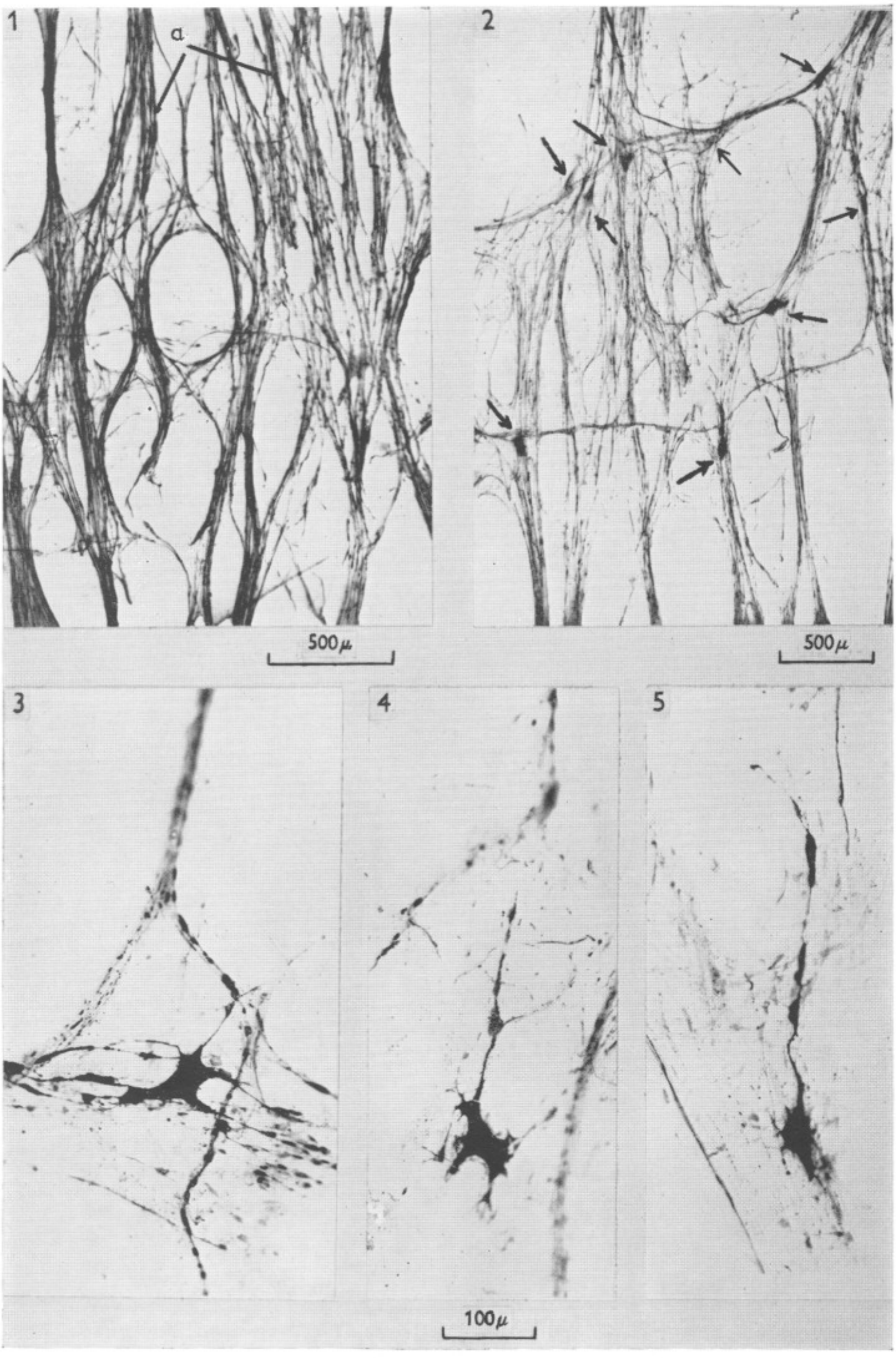
EXPLANATION OF PLATE I

All photographs were made from preparations of *Eledone cirrhosa* stained with methylene blue, fixed in ammonium molybdate and mounted in xylol-dammar.

Fig. 1. Substellar muscle plexus. *a*, bundles of fibres coming from m. adductor pallii.

Fig. 2. Receptor cells (indicated by arrows) on the substellar muscle plexus.

Figs. 3–5. Receptor cells of various shapes.

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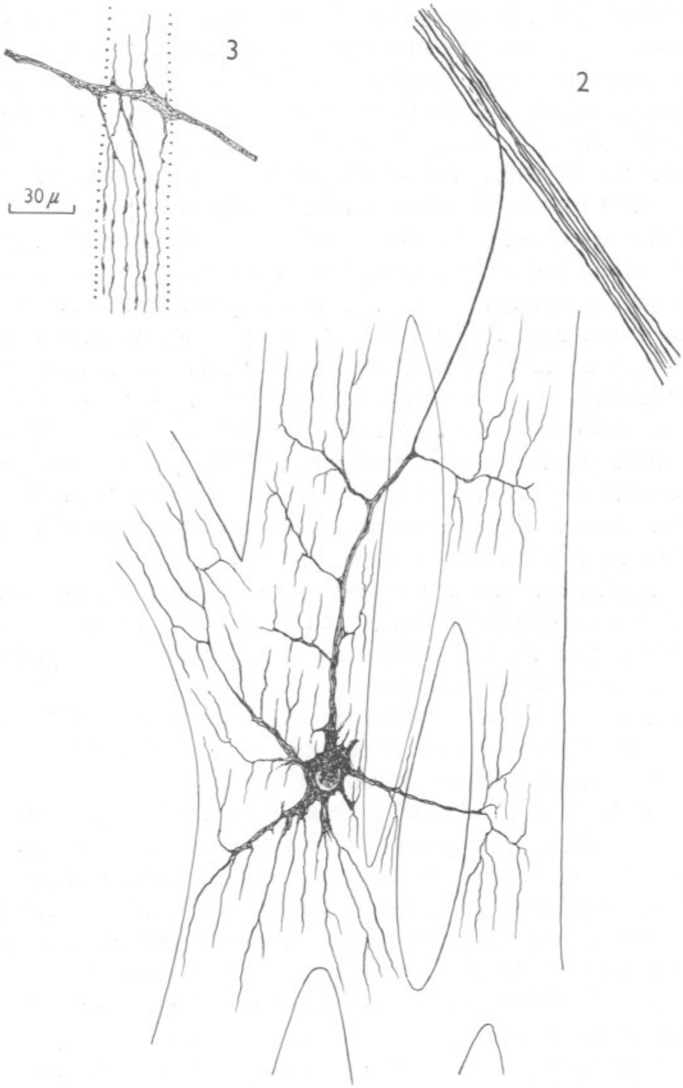
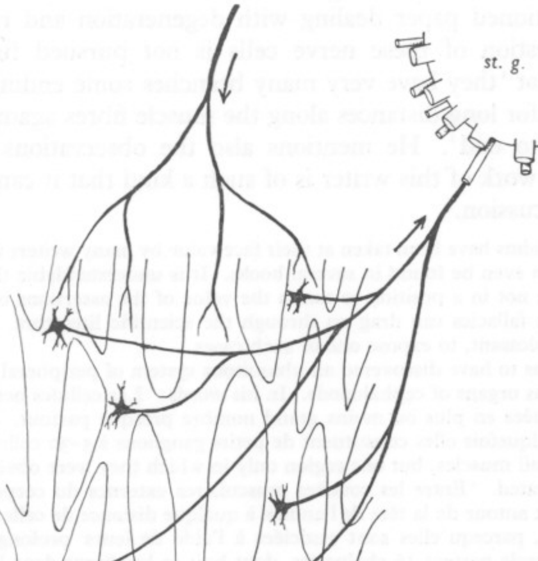



Text-fig. 2. Receptor cell of the substellar organ. Drawing compiled from several preparations.
Text-fig. 3. Fine branches of a receptor cell dendrite given off to a small strip of plexus muscle (outlined by dots). From preparation stained with Bodian's method.

(1:30,000). The dendritic processes proved to be particularly susceptible to this treatment and disintegrated readily. More reliable pictures have been obtained with Bodian's method which proved to be helpful in determining (on whole mounted preparations) the course of the cell processes and their finer branches. The representation of the receptor neuron shown in Text-fig. 2 is based on pictures obtained with both staining methods. It may be that the expansions of some dendrites reach farther than seen in this drawing, and it must be realized that the fine terminal branches are much more numerous than is shown. How dense they in fact are can be judged on the evidence of preparations in which the impregnation of some branches was more complete. In Text-fig. 3 is shown a muscle strip only $32\mu$ wide crossed by a cell process which sends to this muscle several branches running parallel with each other and obviously destined exclusively to this muscle strip. Although such pictures, because of uneven impregnation of nerve elements, are not of common occurrence, there is every reason to believe that in the dendritic field of each neuron the nerves fibres are in similar relations with the muscles. Furthermore, considering the length of the cell processes and the distribution of the nerve cells, it may be assumed that in those regions where the nerve cells are situated not far from one another all muscle bundles are covered by their processes. Should the cells be equally densely spaced over the whole ss-plexus then the latter would be everywhere pervaded by the ramifications of their dendrites.

The axon at its root and in its initial course is not easily discernible since it gives off branches looking exactly like those of the dendrites. Occasionally it stains better than the other processes and then can be recognized at first sight (Pl. I, fig. 5). When the processes stain equally well it can sometimes be distinguished by its greater thickness, but this is not a reliable characteristic. Thus, the identification of the axon can only be certain when it is possible to trace it for a longer distance. It can be then seen that its outlines are somewhat uneven up to the point at which branches cease to spring from it. When the last of these branches is given off (this point can be at a distance of about $500\mu$ from the cell body), the axon changes in appearance and proceeds farther as a smooth fibre which finally joins one of the nerves running on the plexus. Sometimes three or four axons associate and run together before entering a thicker bundle of fibres. In a few cases when such a nerve carrying the axons could be followed in its proximal course it was found to join one of the thinner stellar nerves. This observation revealed the existence of connexions, already alluded to, between the nerves of the plexus and the stellate ganglion and provided indicative evidence as to the course taken by the axons of the receptor cells. Whether they all behave in the same way is difficult to ascertain because the nerves on the ss-plexus run in all directions anastomosing occasionally with each other, and the tracing of fibres of different origin is possible in exceptional cases only. Anyhow, in view of the evidence available it seems more probable that the centripetal paths of these receptor cells are directed towards the stellate ganglion. According to this assumption the basic pattern of nerve elements in the substellar organ would be as diagrammatically represented in Text-fig. 4.

In *Octopus vulgaris* the structure of the ss-plexus was found to be essentially the same as described above, and the presence of nerve cells in it could be ascertained. Therefore the substellar organ in this species appears to be quite similar to that in *Eledone*, but, as I examined one specimen only and more material was not available, the present account had to be restricted to a single species of the Octopoda.




Text-fig. 4. Simplified diagram of the arrangement of nerve elements in a part of the substellar organ. *st.g.*, stellate ganglion.

## DISCUSSION

It is evident that the nerve cells in the substellar organ are of a sort differing markedly from all known types of cells in other organs of cephalopods. On account of their position in a muscle layer a comparison might be made with the ganglion cells of the nerve plexus in the digestive tract and those in the auricles. However, the former are unipolar or bipolar and only rarely tripolar, and evidently it is not their dendrites, but their axons, which are spreading over the muscle fibres. The cells in the auricles are unipolar and are doubtless of a different sort (Alexandrowicz, 1928, 1960). As regards the mantle muscles there is only one reliable record of the presence of multipolar cells in them, viz. in the paper of Sereni & Young (1932), in which a photograph is reproduced showing a section through the mantle muscles with such nerve cells stained after Cajal. If these sections were made, as seems very probable, from the region of the mantle under the stellar nerves, the cells found in them would be doubtless the same as described in the present paper, for, as Young states, they were situated 'in the thin coats of muscle cells which lie outside the main mass of muscles' which might well be the substellar muscle plexus. In the above-mentioned paper dealing with degeneration and regeneration of nerves the question of these nerve cells is not pursued further. Young briefly states that 'they have very many branches some ending near the cell others running for long distances along the muscle fibres against which some of them seem to end'. He mentions also the observations of Mikhailoff (1921), but the work of this writer is of such a kind that it can be ignored in the present discussion.[1]

[1] Mikhailoff's claims have been taken at their face value by many writers and reproductions of his drawings can even be found in several books. It is understandable that the authors of synoptic works are not in a position to assess the value of the assertions of each writer and consequently some fallacies can drag on through the scientific literature. I consider it my duty, however unpleasant, to expose one of such cases.

Mikhailoff affirms to have discovered an ubiquitous system of peripheral nerve cells in the muscles and various organs of cephalopods. In his words: 'Les cellules nerveuses périphériques sont disséminées en plus ou moins grand nombre presque partout. Quelquefois elles sont solitaires, quelquefois elles constituent de petits ganglions à 5–30 cellules.' He assumes that they occur in all muscles, but one region only in which they were observed is somewhat more exactly indicated. 'Entre les couches musculaires externes du corps ces cellules nerveuses se localisent autour de la tête de l'animal à quelque distance de celle-ci, en constituant le véritable collier, parcequ'elles sont associées à l'aide de leurs prolongements nerveux. De ce collier ou cercle partent 16 chaînettes, dont huit se localisent dans la musculature du corps et les huit autres—dans les bras, par une chaînette à chaque bras.' In order to verify what this intriguing system might be, I tried to stain it with methylene blue in *Sepia* and could easily find the 'chaînettes' in the arms. They are nothing else but the components of the complicated innervation of the arms described by Guérin (1908). There are in fact several such peripheral nerve trunks in each arm called by Guérin (not quoted by Mikhailoff) cordons (or chaînes) nerveux intramusculaires. Mikhailoff's 'collier ou cercle' was most probably the ring formed by commissures between the arm nerves known already to Cuvier and represented in all the works dealing with nervous system in cephalopods. The other eight nerves connecting with the 'collier' could have been the main arm nerves which Mikhailoff did not follow to their origin in the brachial ganglia and assumed that they pass on to the muscles of the body. If therefore, as it is evident, his belief to be a discoverer of new nerve elements in the muscles and his ideas about their structure were chiefly, or perhaps entirely, based on the observation of the peripheral trunks in the arms, they resulted from the basic ignorance of the anatomy of the animals investigated. What structures he saw in other muscles and considered them to be nerve cells is difficult to say. His statement that the size of these 'cells' was $4–9\,\mu$ makes the supposition probable that they were swellings produced on fibres during staining since the nerve cells in cephalopods are as a rule much larger and even the smallest of them measure more than $10\,\mu$.

As regards other organs mentioned by Mikhailoff his remarks about the presence of nerve cells in the heart and 'certain glands' are very vague and hardly trustworthy. What, however, he saw in the intestine were true nerve cells, but, first, their presence in this organ was already known and, secondly, his description was inadequate.

No importance whatsoever can be attributed to Mikhailoff's classification of nerve cells (motor, sensory, trophic), based on structural differences of their processes as he saw them.

The first question which arose when the nerve cells on the ss-plexus were noticed was that of their nature and this was really puzzling as long as it was not evident how the cell processes that ended on the muscles and seemed to be all of the same kind should be classified. After it had been ascertained that each cell possesses one long projection joining a nerve trunk it became clear that the others are dendrites and that the basic structure of these neurons is that of typical units of the nervous system. Nevertheless they are remarkable in many respects.

The fact itself that such sensory cells with their dendrites terminating on muscles are present in cephalopods is interesting because elements of a similar sort have been found in a small number of animals, and in those in which their presence is known, as in crustaceans and insects, they occur in a very limited number and only in particular regions of the body.

Compared with the muscle receptors in crustaceans the substellar organ in *Eledone* shows important differences in the way in which the muscular and nervous components are connected with each other. In the former the arborizations of the nerve cells end in a special region of the muscle in which the muscle tissue is replaced by connective tissue fibres, whereas in the substellar organ the branches of the dendrites spread over the wide areas of the muscles. Perhaps the enigmatic N-cells in thoracic muscles of some crustaceans show certain points of resemblance in the behaviour of cell processes since they have processes of considerable length running in various directions and terminating between the muscle fibres; however, the pattern of distribution of their terminal branches is different and their dendritic fields are limited to a small part of the muscle unit.

The presence of branches springing from the axon, but looking and behaving like the processes of the cell body, is a striking but not unknown feature. Similar processes from the axons have been found in sensory cells of insects (Zawarzin, 1912), in the cells of muscle receptor organs and N-cells of decapod crustaceans, and in certain sensory cells of stomatopods (Alexandrowicz, 1952, 1957).

A peculiar feature of the substellar organ which puts it into a special

He obviously exercised little criticism in interpretation of methylene-blue preparations and considered various artefacts to be distinctive features of nerve elements. Artefacts in Mikhailoff's preparations were presumably even more frequent than usual since he applied very hypotonic solutions (equivalent to 0·9 % NaCl), because, as he affirms, solutions of methylene blue in sea water or isotonic liquids are unobtainable. This is proof that not a single work of various writers who applied such solutions for staining the nervous system in marine invertebrates was known to him. There is indeed no reference to any work relating to the subject of his investigations. There is instead a list of the writer's own papers concerning the nervous system of vertebrates.

Thus, there can be no doubt that all Mikhailoff's claims were unfounded. At the best he can be credited for having given, although unintentionally, pictures of peripheral nerve trunks in cephalopod arms stained with methylene blue (his fig. 1 and evidently fig. 8), whereas their previous representation by Guérin was based on Golgi preparations.

category of muscle receptors is the multitude of neurons connected with its muscular component. In crustaceans a receptor consists as a rule of one cell and one muscle. In insects a similar basic pattern of structure of muscle receptors has been found (Finlayson & Lowenstein, 1955; Slifer & Finlayson, 1956). It is true that in some instances a fusion of receptor muscles can take place, as for example, in *Leander serratus* (Alexandrowicz, 1956) and *Praunus flexuosus* (unpublished observation of the writer), so that several nerve cells (up to 4) can end on one long muscle. The fact, therefore, that several cells are in relation with one muscle is not unique, but it is their number in the substellar organ that is striking. Considering the structure of this organ it does not seem probable that it could be functionally differentiated since to the best evidence the ss-plexus appears to be an anatomical unit. This would imply that the changes in condition of the plexus such as occur during contraction or stretching must affect all its muscle elements at the same time. Consequently, whichever of these changes is eliciting the response of the receptor cells the latter must be triggered simultaneously. It follows that when the receptor organs of the two sides of the body react together, as they probably do, the impulses to higher centres are transmitted by one hundred neurons at least.

The accumulation of so many nerve units in one organ may perhaps find its explanation in the fact that in cephalopods in general the number of neurons involved in innervation of any organ is comparatively much greater than in arthropods. I have already (1960) pointed out this 'uneconomical use of nervous substance' when discussing the abundance of nerve elements in the hearts of *Sepia*.

As regards the function of the substellar organ, the only conclusion which can be drawn from the histological evidence is that just mentioned, namely, that it responds to changes affecting the plexus muscles and, since the latter are connected with the pallial adductor and the muscle of the brachial membrane, the function of the receptor must also be related to the action of these muscles. It is, however, not obvious whether the receptor cells become stimulated by the contraction or by stretching of the plexus muscles. It is equally difficult to guess whether these organs are in action only during vigorous contraction of the mantle muscles such as occur when the animal swims backwards, or play some role in adjustment of respiratory movements varying in intensity.

The assumption that the axons of the receptor cells run towards the stellate ganglion harmonizes with the results of Young's experiments (Sereni & Young, 1932) on degeneration and regeneration of fibres in the stellar nerves and the mantle connective (in *Eledone* and *Octopus*). Young came to the conclusion that there are in these nerves 'afferent fibres whose cell bodies lie at the periphery'. He even mentions that this path of afferent fibres may include possibly a few proprioceptors.

There is every reason for assuming that the axons of substellar receptors would behave like those in Young's experiments, but it is not evident whether the afferent path discovered by him consisted of these elements only. Young defines it as 'small' and referring to the afferent fibres in the stellar nerves says that 'they are very few in number compared with the motor fibres'. It is therefore possible that they could all come from the substellar organ; some other considerations, however, make this supposition questionable. My observations of the course of cell axons do not tally well with Young's results on one point. As stated in the foregoing description the axons of the receptor neurons appear to join the stellar nerves of thinner calibre, whereas the afferent fibres observed by Young were evidently running in the thick trunks, as he explicitly states: 'such fibres seem to be more numerous in the large posterior stellar nerves than in the lateral ones'. There are two possibilities: either some nerves carrying the receptor axons and joining the thick stellar nerves were not noticed by me—they could easily be torn away when removing the connective tissue between the nerves—or there is another system of fibres running into stellate ganglion from some yet unknown sensory cells. As these afferent fibres were apparently seen in many thick nerves the second alternative appears to be more probable. The conclusive evidence could possibly be provided if Young's experiments were repeated with the aim of estimating the number of afferent fibres in the stellar nerves. If it were found that this number in the stouter of these nerves surpassed their possible number from the substellar organ, there would only be the question where these other sensory cells sending their axons through the stellar nerves are situated. It would be also interesting to know where the axons of the receptor neurones of the substellar organ are ending. Young proved that there is a path of centripetal fibres in the mantle connective and concluded that the afferent fibres from the stellar nerves pass through the stellate ganglion. The question is whether or not some of them terminate in this ganglion. Here perhaps the comparison of the number of fibres entering the ganglion with the stellar nerves and leaving it with the mantle connective could provide some evidence.

Are there proprioceptors of a similar or of some different kind in other species of the Cephalopoda and in other regions of their body? Considering the high degree of development of the nervous system in these animals and the richness of nerve elements in all their organs it seems plausible that if in the neuromuscular mechanisms of vertebrates and arthropods the proprioceptors play an important role, the cephalopods should have them also.

In many attempts to solve this problem I examined various regions of the cephalopod body, paying special attention to those muscles which at certain movements of the animal become more forcibly stretched, on the supposition that in such muscles the proprioceptors are more likely to occur. This conjecture was based on the fact that the stretch receptors in crustaceans associated with the extensor muscles must become stimulated at the flexion of the abdomen. As one sort of these receptors (MRO 2) presumably responds to strong contractions of the flexor muscles, such as during the flipping of the abdomen in escape reaction, I ventured to suggest (1951) that its function may consist in inhibiting the giant fibres after each powerful contraction of the muscles produced by them. On this line of thought the occurrence of muscle receptor organs was rather to be expected in decapod Cephalopoda which have giant fibres, but the search for them in *Sepia* and *Loligo* has been as yet unsuccessful. This is not to say that they are in fact missing, and neither can it be maintained that in Octopoda they are present in that region only where they have been found. If their structure should be of a similar type as in the substellar organ this would add to the difficulties of research. A thin muscle unit with different pattern of innervation as in MRO of crustaceans can be often clearly distinguished amidst the ordinary muscle fibres even when the nerve cell does not show. If, however, the receptor organ should consist of nerve cells connected with muscles of common appearance, and these cells were refractory to staining, their discovery would depend on such a chance, as happened in the present case with *Eledone*, that a nerve cell was spotted and efforts could be concentrated on one region.

The conclusion to be made is that, since negative results have no value, the problem of the absence or presence of receptor organs in cephalopods cannot be solved until some infallible method of detecting nerve cells is found and with the aid of such a method the whole muscle system is submitted to systematic investigation.

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## SUMMARY

In *Eledone cirrhosa* a muscle receptor organ has been found situated under the nerves radiating from the stellate ganglion. This organ for which the term substellar organ is proposed consists of nerve cells scattered over a plexus of muscle fibres connected with the bundles of the pallial adductor muscle and of the muscle of the branchial membrane. The nerve cells whose number is no less than 50 on each side of the body are multipolar with long dendritic processes sending many thin branches alongside the muscle fibres. The axons of these receptor neurons join the stellar nerves and run in them towards the stellate ganglion. Whether all the axons of these neurons take the same course and where they end could not be ascertained.

The motor innervation for the muscular component of the substellar organ is supplied by a nerve arising from the mantle connective (pallial nerve).

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