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Las células nerviosas intermusculares de la lombríz terrestre.

1. En la lombríz terrestre existen células nerviosas diseminadas, que probablemente representan vestigios de la red nerviosa primitiva de los invertebrados inferiores. 2. Existen por lo menos cuatro tipos celulares, que difieren por su morfología, en ciertas regiones intermusculares, a saber: En los anillos nerviosos circulares colocados entre las capas musculares longitudinal y circular, y en los nervios periféricos situados dentro de la capa de músculos circulares. 3. De los cuatro tipos celulares, tres de ellos, las celulas bipolares fusiformes, las semilunares bipolares y las triangulares tripolares, son considerados por el autor como asociados con la porción efectora del sistema nervioso, representando células externas que, en el desarrollo filogenético del sistema nervioso central, no se han incorporado al cordón ventral. 4. El cuarto tipo, formado por células largas, delgadas, piramidales o fusiformes, está contenido casi exclusivamente dentro de la capa muscular circular, pero tambien envía finos procesos a la epidermis. En su estructura, propiedades colorantes y en su relacion con el cordón ventral se asemejan a las células de los órganos sensoriales epidérmicos, habiéndose interpretado como células sensoriales colocadas profundamente.

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THE INTERMUSCULAR NERVE CELLS OF THE EARTHWORM

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SEVEN FIGURES

INTRODUCTION

The so-called intermuscular nerve-cells of the earthworm have been referred to, usually incidentally, in several papers on the central and peripheral nervous systems of this animal, but in no paper has a complete description of the size, form, distribution, and relations of these cells been attempted. In view of the more or less general acceptance of the annelid theory of the origin of the vertebrates and since several annelids, viz., Sigalion, Nereis and Allolobophora, have been pointed out as exemplifying progressive stages in the transformation of the diffuse peripheral nervous system of the lower invertebrates into the centralized deep-lying system of the higher invertebrates and vertebrates (Parker, '19, pp. 204–5), the writer has thought it worth while to place on record the following observations, based upon a study of a large amount of earthworm material which had been prepared according to well-accredited neurological methods.

In order to eliminate needless description and comment, both in the review of literature and in the presentation of the results of this investigation, it seems advisable at this time to outline briefly some of the main features of the structure of the earthworm nervous system and to explain the descriptive terms which will be used here. From each body somite three pairs of lateral nerve trunks arise, one pair from the sides of the ventral nerve-cord just behind the anterior septum and two pairs, more posterior and close together, from the ganglionic mass itself. These lateral nerve trunks pass ventrolaterally across the body cavity to the layer of longitudinal muscle fibers, and in this position each gives rise to dorsal and ventral rami. The dorsal rami run between the two muscle layers of the body wall as far as the middorsal line, forming the dorsolateral portions of the so-called nerve ring. From each dorsal portion there is given off first of all branches to the intersetal tract and along the rest of its course dorsally many small peripheral branches pass vertically or obliquely toward the epidermis.

The ventral rami run ventrally in the same relative position as the dorsal ones, extend to the midventral line, and give rise along their course to numerous peripheral branches. In this way three main nerve rings, an anterior, middle, and posterior, are established for each body segment.

In referring to the nerve cells, their locations will be designated in the terms of the preceding description and the direction of their processes will be indicated by the phrases proximal, distal dorsally, distal ventrally, and peripheral, according as the processes extend toward the ventral chain, toward the middorsal line in the dorsal portion of a nerve ring, toward the midventral line in the ventral portion of a nerve ring, and toward the epidermis in a peripheral nerve.

REVIEW OF LITERATURE

Hesse ('94) dsecribed groups of ganglion cells in the course of the nerves of the prostomium of the earthworm, but in the nerve rings of the body segments he observed only one nerve cell. It was bipolar. The brief statement by Hesse regarding ganglion cells caused Langdon ('95) to reexamine the material she had studied. As a result of the reexamination she discovered that a series of alum-carmine preparations showed a number of ganglion-cells in the nerve rings and gave in a foot-note the following record for the first thirteen metameres: first metamere, none; second metamere, one on its median nerve ring; third metamere, one on its anterior ring and four on its posterior ring. In metameres three to thirteen, two to eight ganglion cells were found on every nerve ring. All the cells noted were of the bipolar type.

Dechant ('06), by means of intravitam methylene blue, succeeded in demonstrating ganglion cells in the nerve rings of the earthworm, but, unfortunately, owing to the fact that he was working with animals which were densely pigmented dorsally, his studies were confined to cells found in the more ventral portions of the earthworm body. For the anterior and posterior nerve rings he found the ganglion cells regularly arranged, usually in groups of three, in the region of the dorsal pair of setae. In the median nerve ring, however, only a single cell was occasionally observed in the vicinity of a setal follicle. The cells were of two types, either spindle-shaped and bipolar or triangular and tripolar. In the tripolar cells two processes lay in the nerve ring, while a third much shorter process passed vertically through the circular muscles toward the epidermis.

More recently tripolar cells have been described by Kowalski ('09) who used Boule's ('07, '09) modification of the silver-nitrate method of Ramón y Cajal for neurofibrillae. Kowalski describes specifically and figures (figs. 60, 61) two tripolar cells which he refers to as 'cellules sensitives profondes tripolaires.' Figure 60 represents a cell in the nerve ring, with two processes lying within the ring itself, while from the outer pole a bundle (faisceau) of neurofibrils passes vertically to the epidermis. In figure 61 the tripolar cell lies at the bifurcation of a lateral nerve trunk. One of its processes extends proximally in the lateral trunk while the two others pass distally, one in the dorsal and the other in the ventral portion of the nerve ring.

Boule ('13), in the course of a detailed discussion regarding the evidence in the earthworm of a correlation between the structure of the nerve cells and the direction of conduction of the impulse, refers incidentally to both bipolar and tripolar cells in the lateral nerve trunks and nerve rings. The tripolar cell (fig. 21) corresponds, in its position and in the extension of its processes, with the one figured by Kowalski ('09, fig. 61).

In the following year von Szuts ('14), in an extended account of the finer structure of the central nervous system of the earthworm, failed to make any mention of the tripolar cells observed by Dechant ('06), Kowalski ('09), and Boule ('13). He describes, however, two types of bipolar cells which are distinguished from one another by the differences in their size and in the arrangement of their neurofibrils. The smaller cells were referred to merely as 'die Nervenzellen' and contained neurofibrils which, although often highly branched, transversed the cell bodies without anastomosing. The large bipolar cells, on the other hand, showed the intracellular fibrils anastomosing to form complex networks and were given the descriptive title, 'die intermuskulären sensorischen Ganglienzellen.' The small cells were observed on the inner side of the nerve ring close to the longitudinal muscles and in the margin of the ventral nerve cord at the point of exit of a lateral trunk. Boule ('13) also shows small bipolar cells in the latter position (fig. 13). Of the large bipolar cells, some were situated in the nerve ring, while others lay entirely within the circular muscle layer.

MATERIAL AND METHODS

Helodrilus caliginosus and Allolobophora (Eisenia) foetida, readily obtained in any market garden, were utilized in this work. All the material studied was taken from the midbody region, somewhat posterior to the clitellum. Very satisfactory preparations were obtained with intravitam methylene-blue staining and Boule's modification of the Ramón y Cajal technique for neurofibrils. Intravitam methylene-blue staining was secured by means of two methods. Some animals were injected intracoelomically with a 1 per cent solution of methylene blue in normal saline. Others were partially immersed in the solution and allowed to remain in the fluid till they became colored a deep blue. In both cases the color was fixed with Bethe's invertebrate fluid and the tissue imbedded in paraffin and cut in serial sections 20 μ thick.

For silver impregnation, portions of worms, 5 to 10 mm. long, were fixed in one of Boule's mixtures, usually formula B (formalin, 25 cc.; glacial acetic acid, 5 cc.; ammonia, 0.5 cc.; distilled water, 100 cc.), for from twenty-four to forty-eight hours, impregnated six days in a $1\frac{1}{2}$ per cent silver-nitrate solution at 38°C.

and reduced in a 1 per cent solution of hydroquinone for twenty-four hours. Following routine procedure, the tissue was sectioned and mounted in balsam, with cover-glasses. Preparations left uncovered were found to deteriorate very rapidly. The pyridine-silver method of Ranson, and Ramón y Cajal's technique unmodified were also tried, but did not yield so uniform and excellent results as the method just outlined.

Both the methylene-blue stain and Ramón y Cajal's modified silver-nitrate impregnation left the intermuscular cells clearly outlined, although the pictures presented differed greatly. The silver method showed only neurofibrils and left the cell body and nucleus practically colorless, while successful methylene-blue stains colored the entire cell. Since the silver-nitrate method was known to be uniform in its action, it was chiefly relied upon in the determination of the number of nerve cells present in the different regions. Methylene blue, while capricious and discouraging to work with, proved very useful in the tracing of cell processes and in the determination of their relations to other cells and tissues.

THE INTERMUSCULAR NERVE CELLS

All preparations showed both bipolar and tripolar cells, but the number of bipolar cells was greatly in excess of the number of tripolar, the proportion being approximately 5 to 1. The cells did not exhibit any very definite or regular arrangement, but were usually scattered irregularly along the nerve rings. There was, however, in many cases a marked tendency toward grouping in the intersetal tracts.

The number of cells found in the three nerve rings varied considerably. The largest numbers were invariably found in the posterior rings, and the highest record for this location was fifteen, eleven bipolar and four tripolar cells. Next in order came the anterior nerve ring with an average of six cells, while the middle ring usually contained very few cells, five being the maximum observed.

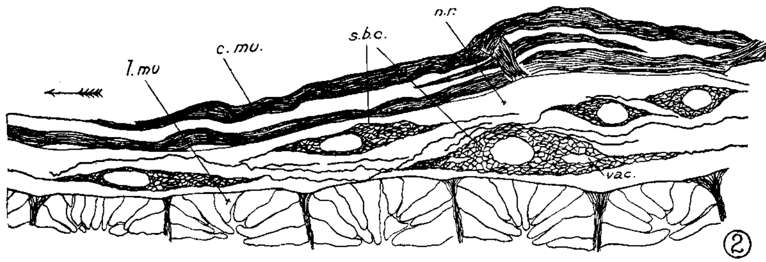
a. Tripolar cells

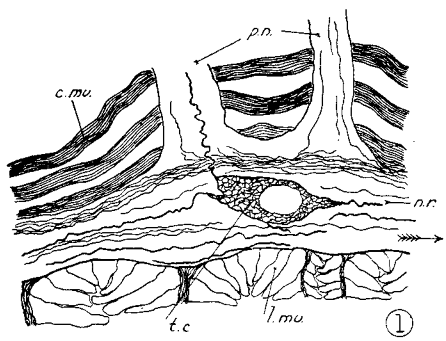
The tripolar cells are found in locations where branchings of the larger nerve trunks occur; that is, at the bifurcation of the lateral nerve trunks to give rise to the dorsal and ventral rami of the nerve rings and along the nerve rings at the points of origin of the many peripheral nerves; but they are not found uniformly in these positions. This is especially true along the nerve ring, since four or five tripolar cells is usually the maximum number found on any one ring.

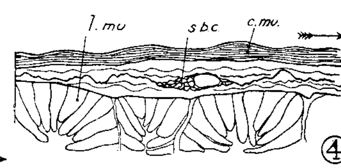
The cells approximate a triangular outline. Their nuclei are spherical and in all methylene-blue preparations a well-defined nucleolus and a delicate chromatin network can be distinguished. Silver preparations leave the nuclei unstained, but show a dense network of neurofibrils occupying the bodies of the cells (fig. 1). In most of the tripolar cells the nuclei occupy central positions. When eccentrically placed, however, they are invariably found nearest that pole from which a proximal process arises.

The tripolar cells which are found at the bifurcation of the lateral nerve trunk do not always bear the same relations to the nerve system. In some cells, one process extends proximally in the nerve trunk, while the other two processes extend distally and ventrally, and distally and dorsally, respectively, in the nerve ring. In other cells, one process extends proximally, one distally and ventrally and one peripherally. Again in others practically the same relations are maintained as in the second case except that one process, instead of passing ventrally, passes dorsally in the nerve ring. From the tripolar cells, situated at the points of origin of the peripheral nerves, whether in the dorsal or ventral portion of the nerve ring, one process always passes peripherally toward the epidermis while one of the two others passes proximally toward the ventral nerve cord and the other distally toward either the middorsal or midventral line, as the case may be.

The processes passing peripherally were traced readily in many cases to the bases of the epidermal cells, but were lost in the basiepithelial network (Dechant, '06), so that positive evi-







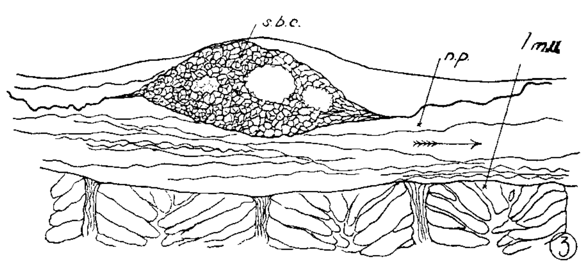


Fig. 1 Tripolar cell in the dorsal portion of a nerve ring at the point of origin of a peripheral nerve. *c.mu.*, circular muscles; *l.mu.*, longitudinal muscles; *n.r.*, nerve ring; *p.n.*, peripheral nerve; *t.c.*, tripolar cell. Ramón y Cajal method modified. × 540. In all figures the arrow points proximally.

Fig. 2 A group of spindle-shaped bipolar cells in the intersetal region of a nerve ring. *c.mu.*, circular muscles; *l.mu.*, longitudinal muscles; *n.r.*, nerve ring; *s.b.c.*, spindle-shaped bipolar cells; *vac.*, vacuole. Ramón y Cajal method modified. × 540.

Fig. 3 Large spindle-shaped bipolar cell in the ventral portion of a nerve ring. *l.mu.*, longitudinal muscles; *n.r.*, nerve ring; *s.b.c.*, spindle-shaped bipolar cell. Ramón y Cajal method modified. × 540.

Fig. 4 Small spindle-shaped bipolar cell in the ventral portion of a nerve ring. *c.mu.*, circular muscles; *l.mu.*, longitudinal muscles; *s.b.c.*, spindle-shaped bipolar cell. Ramón y Cajal method modified. × 540.

dence concerning their possible continuity with intra-epidermal fibers is lacking. In no case, however, was there any evidence of a peripheral bundle of fibers (Kowalski, '09) being given off by a tripolar cell. In many instances numerous fibers were observed running parallel with a peripheral process of a tripolar cell, but they were not connected with the cell itself, and, furthermore, a process of a tripolar cell could usually be easily distinguished from the majority of the fibers in a peripheral nerve by its coarseness and the kinked, irregular course it pursued (fig. 1).

b. Spindle-shaped bipolar cells

Spindle-shaped bipolar cells, unlike the tripolar cells, are not restricted in their distribution. In a body segment they may be found anywhere along the course of the three pairs of segmental nerves, i.e., at the margin of the cord itself, along the lateral nerve trunk, at the point of bifurcation of this trunk, along the dorsal and ventral portions of the nerve rings running between the two muscular layers, and in the peripheral nerves passing through the layer of circular muscles. Near the dorsal and ventral midbody region the bipolar cells are more often found in the peripheral branches. This of course would be expected since the nerve rings in this region are greatly reduced. Nearer the setae, however, the number of cells found in the nerve ring gradually increases and in the so-called intersetal tract small groups of cells, three, four, and five, are commonly found (fig. 2).

The spindle-shaped bipolar cells also exhibit some striking variations in size (figs. 3, 4). As already noted, von Szuts ('14) mentioned this as one of the characteristics by which he distinguished two types of cells, 'intermuskulären Nervenzellen' and 'intermuskulären sensorischen Ganglienzellen.' However, it does not seem possible to use this as a basis of classification, since a careful comparison of a large number of cells by means of camera lucida measurements shows that between the two extremes (figs. 3, 4) there is a nicely graded series of cells. Von Szuts ('14) also described a difference in the arrangement of the neurofibrils within the cells. He found that in the small cells, although the neurofibrils might branch frequently, they never anastomose, while in each large cell a definite, dense network is conspicuous. In my preparations (silver nitrate), on the other hand, the difference in the arrangement of the neurofibrils, like the difference in size, does not appear to be at all important. Within all cells a definite network could be distinguished. (In studying the neurofibrillar arrangement within the cells a binocular mon-objective microscope, equipped with a substage condenser and an 1.8 fluorite immersion objective, was used.)

Moreover, the density of the network in different regions of individual cells was also found to vary. These differences in density seemed to be due to two factors: the presence of large 'vacuoles,' and the position of the nucleus. The significance of the 'vacuoles' is still a matter of conjecture (Kowalski, '09; Boule, '13), but in the region of a 'vacuole' (fig. 3) the network was usually sparse. The nuclei are spherical or ellipsoidal and with rare exceptions are eccentric in position, being nearer the proximal pole of the cell (figs. 2, 3, 4). The neurofibrillar network in the distal pole of the cell appears coarse and dense, but toward the proximal pole, in the vicinity of the nucleus, the density of the net is decreased and, as the cell narrows to give off its proximal process, the meshes of the net become elongated in the direction of the long axis of the cell (fig. 3).

The eccentric nuclei of the spindle-shaped bipolar cells give to these nerve elements a well-defined morphological polarity. Just what relation there is between the structure of these cells and the direction of conduction of impulses cannot be decided until some conclusion is reached regarding the nature of these cells; i.e., whether they are connected with the receptor or the effector portion of the nervous system. Kowalski ('09) points out that in the earthworm the neurofibrils which form an efferent ('cellulifuge') process are not united into a net, but converge without branching and fuse, giving rise to the single fiber; while on the other hand, the afferent ('cellulipete') process on entering the body of the cell is broken up into a number of branching and anastomosing neurofibrils. Boule ('13) criticises this view of Kowalski and figures the intermuscular nerve cells with anastomosing neurofibrils in both poles.

c. Crescent-shaped bipolar cells

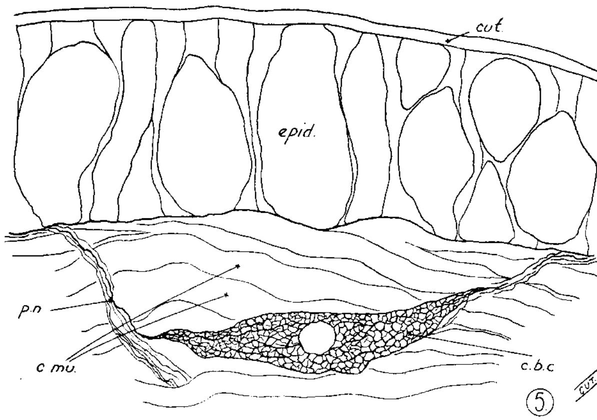
Relatively few crescent-shaped bipolar cells were observed in the earthworm, but they were distinctly shown by both the methylene-blue and the silver-nitrate methods. All the cells observed were remarkably uniform in size and form. Their distribution, too, was decidedly limited, as all the examples noted were situated between the dorsal and ventral members of the several pairs of setae.

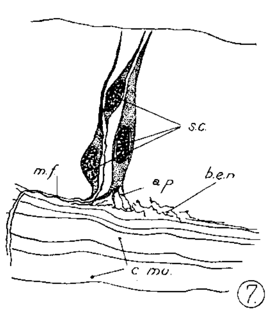
The cells lie in spaces in the outer portion of the circular muscle layer quite close to the epidermis (fig. 5). The poles of the cells (horns of the crescent) were directed outward and the processes leaving both poles also passed outward, becoming lost eventually in the basiepithelial network described by Dechant ('06) and others. I have been unable to find any mention of a cell of this type in the literature. Its significance will be discussed later.

d. Long, slender, pyramidal, or spindle-shaped cells

These cells are quite different from any already described and were successfully demonstrated by means of the methylene-blue-immersion method. The cells appeared only in preparations in which the sense organs of the epidermis were selectively stained, and in the use of methylene blue in this work it was generally found that if the cells of the ventral chain and the intermuscular tripolar and bipolar cells were brightly stained, the epidermal sense cells were very faintly stained, and vice versa. Long, slender pyramidal cells were never observed in silver-nitrate preparations. In this connection it should be added that the writer was unable, with the modification of Ramón y Cajal's method, to secure satisfactory impregnations of the epidermal sense organs. Kowalski ('09, figs. 47 to 50), however, following a similar procedure, did not apparently encounter this difficulty.

The staining characteristics noted above suggested at once that these deeper-lying cells might be similar in nature to the epidermal sensory cells, and both their position and the relation of their fibers to other tissues strengthen this idea. All the examples (eight) of the slender cells were found on the ventral side





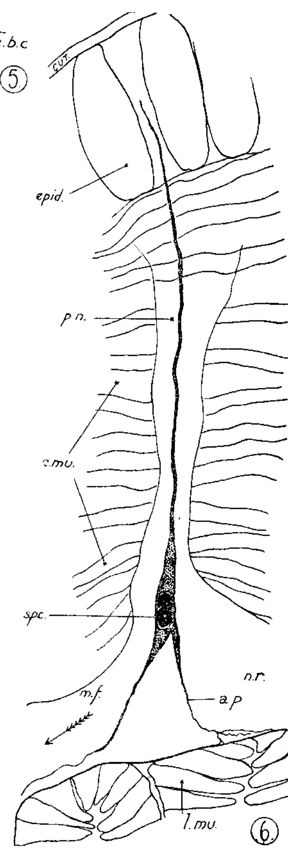


Fig. 5 Crescent-shaped bipolar cell lying within the layer of circular muscles and between the ventral pair of setae. *c.b.c.*, crescent-shaped bipolar cell; *c.mu.*, circular muscles; *cut.*, cuticula; *epid.*, epidermis; *p.n.*, peripheral nerve. Ramón y Cajal method modified. × 540.

Fig. 6 Deep lying sensory cell on the ventral surface of the earthworm. *a.p.*, accessory process; *c.mu.*, circular muscles; *cut.*, cuticula; *epid.*, epidermis; *l.mu.*, longitudinal muscles; *m.f.*, main fiber; *n.r.*, nerve ring; *p.n.*, peripheral nerve; *s.p.c.*, pyramidal sensory cell. Immersion methylene-blue method. × 540.

Fig. 7 A group of three cells from an epidermal sense organ. *a.p.*, accessory process; *b.e.n.*, basiepithelial net; *c.mu.*, circular muscles; *m.f.*, main fiber; *s.c.*, sense cells. Immersion methylene-blue method. × 540.

of the earthworm. It is difficult to decide whether this is the normal distribution or whether only the cells in this position were stained, since the preparations were not obtained by intracoelomic injections, but by partially immersing the live animal in the staining solution. The dorsal portion of the animal accordingly was not in direct contact with the stain.

The bases of the cells were found to lie at the level of the nerve ring, while the long slender cell bodies extended outward through the muscle layer and pierced the epidermis (fig. 6). The intraepidermal portion, lying between the columnar cells, was represented only by a very fine process which in no case could be positively traced further than one-half the way to the cuticular surface. One main fiber and one or two accessory fibers usually arose from the bases of the cells. The main fiber in one case was traced through five successive sections, each 20 μ thick. It was found to enter the lateral nerve trunk, to pass into the ventral nerve cord, and, branching slightly, to terminate on its own side in a dorsal position. The accessory processes could rarely be traced among the fibers of the nerve ring, but in one cell a short process was seen to branch slightly and end at the surface of the longitudinal muscle layer (fig. 6).

In general appearance and structure the slender nerve cells differ in several respects from the other intermuscular cells as seen in methylene-blue preparations, but exhibit several features which are strikingly like those observed in epidermal sense cells (figs. 6, 7). Their nuclei are oval or ellipsoidal, contain no well-defined nucleolus, and stain densely. Their bodies stain less heavily, but take the color uniformly. The other intermuscular nerve cells and the cells of the ventral cord, on the other hand, have spherical nuclei, delicate chromatin networks, definite nucleoli, and well-defined neurofibrillar networks.

SIGNIFICANCE OF THE INTERMUSCULAR NERVE CELLS

The question of the significance of the intermuscular nerve cells is a difficult one to discuss. Schneider ('02, p. 392) suggested that these scattered cells were possibly sensory in nature, giving rise to some of the free terminations found within the epidermis. Kowalski ('09), in referring to the tripolar cells (he apparently did not observe those of the bipolar type), expressed his view as follows: "Ces cellules nerveuses profondes, origine peut-etre des terminaisions sensorielles libres intraepidermiques, permettent de rappocher le système nerveux des Oligochètes de celui des Polychètes, des Cestodes, et des Mollusques." Dechant ('06), although he recognized both tripolar and bipolar cells in the nerve rings, did not express any definite view as to their significance. In commenting, however, on the theory of the origin of the dorsal spinal ganglion of vertebrates from epidermal sensory elements which have retreated from their superficial position in invertebrates, he states:

> Es können demnach die Sinnesnervenzellen der Wirbellosen mit den Spinal-ganglienzellen der Wirbeltiere gar nicht vergleichen werden, sondern höchstens die Ursprungselemente der freien Nervenendigungen der Wirbellosen mit den Spinalganglienzellen der Wirbeltiere. Da aber jene noch nicht gefunden sind, so ist ein weiterer Ausbau dieses Vergleiches und der strenge Nachweis seiner Richtigkeit der Zeit noch nicht möglich. Unsere nächste Aufgabe wird in der Erforschung jener uns noch unbekannten Zellen gegeben sein.

Dechant's chief objection to the phylogenetic theory was based on his belief that the free nerve endings in the epidermis represent just as primitive a condition as sensory epidermal cells. Von Szuts ('14), on the other hand, who recognized only the two types of bipolar cells, accepts the evolutionary principle and homologizes the intermuscular ganglion cells of the earthworm with the ganglion cells of the dorsal spinal ganglion and ganglion cells of the retina.

In an attempt to interpret the function and significance of the four types of cells which have been described in this paper, it seems best, since there is little in the way of experimental work which bears directly on this subject, to approach the problem from the evolutionary view-point. In the primitive nervous system, as seen in the Coelenterata, there is usually a receptive epidermal cell which is intimately united by its branching processes with a deeper-lying cell, the ganglion cell or motor cell, which is in turn connected with the muscles or other effectors. In addition to this, the sensory cell and the motor cell may also be united with other ganglion cells of the nerve net, to provide for the diffusion of an impulse from any one point.

In the earthworm, although there is a well-defined central nervous system, there are still vestiges of the more primitive condition. It has been recognized for a long time that the epidermal sensory cells of this animal possess, beside their main fiber, several accessory processes (fig. 7) which extend into and apparently anastomose with the basiepithelial network. Extending from this network, according to Dechant ('06), there are many intercellular fibers which do not end freely in the epidermis at various levels as usually described, but which continue outward and end superficially just beneath the cuticula. They may even anastomose at this level. Definite pericellular nets have been described about the large unicellular glands and Dechant has also demonstrated a very complex nerve net in the region of the setae. In addition to these peripheral structures, there are the various nerve cells scattered through and between the muscular layers.

Both tripolar cells (Kowalski, '09) and bipolar cells (von Szuts, '14) have been interpreted as representing sensory cells retreating from a superficial position to give rise phylogenetically to the cells of the dorsal spinal ganglia of the vertebrates, and the intraepidermal fibers were believed to belong to these cells. However, in their structure and staining reactions, and in the appearance of their fibers (coarse and irregularly kinked), the tripolar and bipolar cells resemble very closely the motor and association neurones found within the ventral chain. Furthermore, the relation of the crescent-shaped bipolar cells between pairs of setae, with both processes extending into the basiepithelial net and with no fiber extending to the central system (fig. 5), argues strongly against any theory that these intermuscular cells are deep-lying sensory cells. From the evolutionary standpoint also it seems equally as logical to interpret them as scattered ganglion or motor cells of the primitive nerve net which have not yet been incorporated into the ventral nerve chain.

Indeed, the latter interpretation, for a number of reasons, appears the more probable. In the first place, there are the structural and staining resemblances between these cells and those of the ventral cord. In the second place, the position of the crescent-shaped, bipolar cells, the absence of any processes passing from them to the central system, and the relations of the cells to the basiepithelial nerve net are suggestive of a possible rôle in the correlation of the movements of pairs of setae. (The basiepithelial net is probably continuous with the net surrounding the setae, since the setae themselves have an epidermal origin.) A third reason, perhaps a stronger one than either of the foregoing, is that one finds spindle-shaped bipolar cells widely distributed along the nerve tracts from within the margin of the ventral chain to a position close to the epidermis. Finally, the varying positions of the tripolar cells and the varying relations of their processes to other parts of the metamere also suggest an associational rather than a receptor function.

The fourth type of cell described (fig. 6), however, appears to possess all the features characteristic of sensory cells, differing from the epidermal sensory cells mainly in their position and in the length of their peripheral processes (figs. 6, 7). In all other features, such as staining reactions, shape, nuclear structure, and the possession of both a main axone and one or more accessory fibers, the epidermal and deep-lying cells are essentially alike. Just what function these deep-lying sensory cells perform, it is difficult to surmise. Their position in the circular muscle layer and their possible restriction to the ventral region indicate a probable rôle in connection with the initiation or maintenance of the creeping movements of the worm.

If we accept the evidence in favor of regarding the bipolar and triangular tripolar cells as being concerned with a motor or associational function and not primarily part of the receptor system, we are necessarily required to attempt an explanation of the origin of the intraepidermal nerve fibers. They are too numerous to belong to the deep-lying sensory cells described, since each of these so far as observed sends but one fine process into the epidermis. However, in the midbody region, on which this study was made, the gland cells are predominant in the epidermis, and it does not appear necessary to regard the intraepidermal fibers as being part of the afferent system. They might, it seems with equal right, be regarded as part of the efferent system innervating the epidermal effectors, the unicellular slime glands.

SUMMARY

1. In the earthworm, scattered nerve cells, probably vestiges of the primitive nerve net of lower invertebrates, are found.

2. At least four morphologically distinct types of cells are present in certain intermuscular regions, i.e., in the circular nerve rings between the longitudinal and circular muscle layers, and in the peripheral nerves within the layer of circular muscles.

3. Of the four types of cells, three, the spindle-shaped and crescent-shaped bipolar cells and the triangular tripolar cells, are believed to be associated with the effector portion of the nervous system and to represent outlying cells which, in the phylogenetic development of the central nervous system, have not been incorporated in the ventral cord.

4. The fourth type, the long slender pyramidal or spindle-shaped cells, are contained almost entirely within the circular muscle layer, but also send fine processes into the epidermis. In structure, staining properties, and their relation to the ventral cord, they resemble the cells of the epidermal sense organs and have been interpreted as deep-lying sensory cells.

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