

THE PROPERTIES AND CONNECTIONS OF  
SUPERNUMERARY SENSORY AND MOTOR NERVE CELLS  
IN THE CENTRAL NERVOUS SYSTEM OF  
AN ABNORMAL LEECH

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SUMMARY

The characteristic features of individual neurons in leech ganglia are highly consistent from animal to animal. By chance a leech was discovered that had more cells to be seen than usual in many of its ganglia.

In some segmental ganglia of the abnormal animal there were four or even five sensory cells responding independently to touch (T cells) instead of the usual complement of three on each side. Ganglia also contained three or four pressure sensitive cells (P cells) and three or four nociceptive cells (N cells) instead of two of each. The membrane properties, as well as the shapes, sizes, and positions, of all these cells were normal. Their axons reached the skin by the appropriate nerve bundles.

Two sensory neurons of one modality, often independently innervated, overlay regions of skin that normally would be supplied by one cell. On the other hand, the areas innervated by some supernumerary cells were abnormal in their shape and position.

In some ganglia instead of one motor neuron that raised the skin into bumps (the annulus erector, or AE cell) there were two, each of which could independently erect annuli. The regions innervated by the extra AE cells appeared normal and overlapped extensively.

Normal synaptic interactions were found between supernumerary sensory cells and motor cells.

The results with this animal indicate that two or more nerve cells can form effective connections with other neurons and with skin that normally would be innervated by a single cell.

INTRODUCTION

The sensory innervation of the skin of a leech resembles a patchwork quilt, where each sensory cell innervates a well-defined area that overlaps with neighboring fields near its boundaries only. For each modality the

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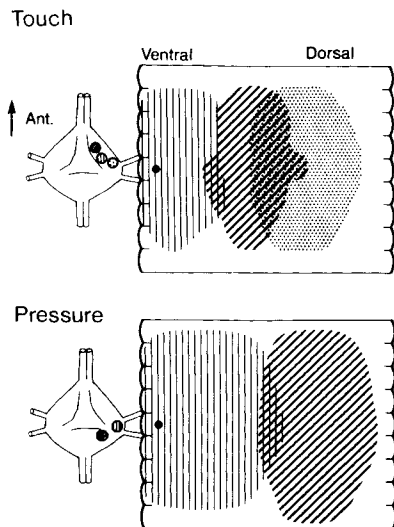


Fig. 1. Normal receptive fields of cells driven by touch (T) and by pressure (P), superimposed upon a representation of skin, and the positions within the segmental ganglion of the sensory cell bodies. The distribution of receptive fields for cells driven by noxious stimuli (N) is similar to that of P cells. The positions of the annuli are indicated by markings on opposite scalloped edges; each annulus's width is approximately 1 mm. The central annulus is that in which the sensilla appears as a small, solid circle. The ganglion, which is attached to the skin through the roots, and is viewed from its ventral aspect, is not drawn to scale. (From Figs. 11 and 13 of Nicholls and Baylor, 1968).

arrangement of the receptive fields is orderly and consistent, from segment to segment and from animal to animal. In a ganglion of a normal leech there are three touch cells (T), two pressure sensitive cells (P), and two nociceptive cells (N), each of which responds to appropriate stimulation of a particular region of skin (Nicholls and Baylor, 1968). The three T cells divide the skin up into three roughly equal areas, situated dorsally, laterally, and ventrally. The paired P cells and N cells divide the same territory into two halves. These fields are shown diagrammatically in Figure 1, which also indicates the circumferential annuli that provide convenient landmarks. The degree of specificity is further emphasized by the arrangement of endings within a single receptive field. The different branches of a single cell each innervate a small, well-defined subdivision of the whole field, with almost no overlap.

This stereotyped regular and detailed pattern of skin innervation poses a number of problems. For example, it is not clear why a particular sensory cell should supply only a restricted area of skin (cf. Jacobson and Baker, 1969). One possibility is that the presence of innervation precludes further innervation, as in vertebrate skeletal muscle, where an innervated fiber will not normally accept additional nerves (Jansen, Lømo, Nicolaysen, and Westgaard, 1973). And yet the situation in leech

skin is complex; for example, although two pressure cells encroach only marginally on each other's territory, the same area of skin does receive innervation from touch and nociceptive cells.

In theory, this type of problem could be approached by attempting, through genetics, to produce leeches whose nervous system contained an abnormal complement of sensory nerve cells, too few or too many. Unfortunately, the leech develops so slowly—up to nine months—that this appears impracticable. However, in the course of other experiments, we happened to notice an animal with an abnormal nervous system. Its swimming and walking behavior and reflexes appeared normal, and it had the usual number of segmental ganglia. Upon inspection of its ganglia with the dissecting microscope it was obvious that they contained an abnormally large number of distinctive nerve cells. From their shapes, sizes, and positions some of these appeared to be supernumerary T, P, and N sensory cells. Also conspicuous were additional Retzius cells, which induce mucus secretion (Lent, 1973), and annulus erector motor neurons (AE cells) that raise the skin into bumps (Stuart, 1970). This unique animal, therefore, provided a favorable specimen for examining how receptive fields would be laid out in the periphery with more cells than usual in the CNS. For example, with three pressure cells instead of two, would they now divide the skin of the segment into three receptive fields? A closely related problem concerns the distribution of an additional motor neuron's endings on the muscle fibers in the periphery.

In the experiments reported here intracellular recordings were made from as many sensory and motor cells as possible. For sensory cells we established (1) the characteristics of the impulse, (2) the modality, (3) the position and shape of the receptive field, and (4) the branching pattern of the axons running toward the skin. Similar experiments were made with motor AE cells. Finally, the synaptic connections of sensory and motor cells within the ganglia were examined.

#### METHODS

The abnormality in the CNS of the leech was discovered only after three ganglia had already been removed. Thereafter, one or two ganglia were dissected at a time, together with a portion of skin and body wall of the segment on one side. This preparation was studied as fully as possible, usually for 8 hr or more, while the rest of the animal was kept in a beaker of Ringer's fluid in the refrigerator. In many other experiments we have seen that for several days the ganglia and reflexes remain normal and receptive fields are unchanged when leeches that have had ganglia and some skin removed are kept in this way. The experiments on the abnormal leech were carried out over a period of five consecutive days with no detectable signs of deterioration, except in the investigators.

The procedures for recording from and stimulating leech neurons with intracellular and extracellular electrodes have been described fully elsewhere (see Nicholls and Baylor, 1968; Nicholls and Purves, 1970). In brief, microelectrodes filled with 4 *M* potassium acetate and having resistances of 50–100 M $\Omega$ , were inserted into the cell bodies and the recorded potentials were displayed on an oscilloscope. Receptive fields

were mapped for T cells by stroking the skin lightly with a fine stylus. For P and N cells the skin was pressed harder, but in most experiments a more convenient method of activating the sensory endings was to stimulate the skin through a suction electrode, using pulses of 3 msec duration and less than 8 V. The results obtained by both methods were identical (see Nicholls and Baylor, 1968). The presence or absence of a response was marked on a grid representing the area of skin. For the AE motor cell the field was mapped by examining the raised ridges of the skin under the microscope when the single cell was stimulated intracellularly. The boundaries are sharp and readily determined in this way.

Sensory and motor fields spread longitudinally beyond the edges of a segment and extend over seven annuli rather than five. Since only one or two segments were removed from this animal at a time, it was usually not possible to map the full longitudinal extent of each field. Accordingly, many of the figures show fields covering only six annuli instead of seven, some of the skin having been removed earlier as part of the previous preparation.

The normal Ringer's fluid in which the skin, muscle, and ganglion were bathed contained (mM): NaCl, 115; KCl, 4; CaCl<sub>2</sub>, 1.8; Tris-maleate buffered to pH 7.4 with NaOH, 10; glucose, 13. In some experiments 20 mM MgCl<sub>2</sub> was added (substituting for NaCl) in order to block chemical synaptic transmission.

### RESULTS

Ganglia along the length of the abnormal animal varied considerably in appearance from each other and from those seen in ordinary leeches. Plainly, there were more large distinctive cells than usual. Figure 2 shows a tracing of an abnormal ganglion. In this ganglion one could see

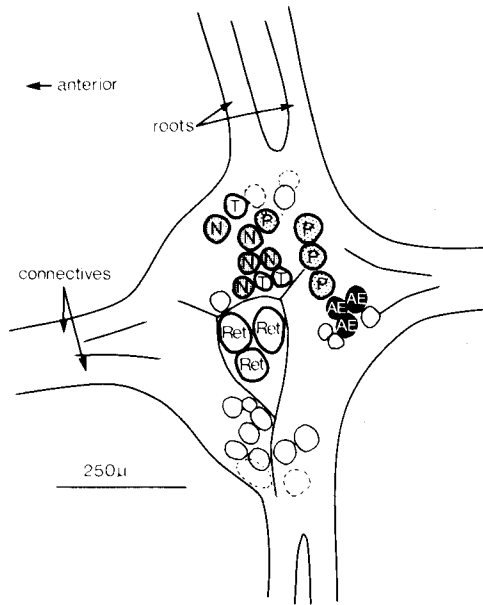


Fig. 2. Tracing of the ventral aspect of segmental ganglion 16, including some identified supernumerary cell bodies (P, N, Retzius, and AE). The paired connectives run to adjacent ganglia, the roots to the body wall (compare with Fig. 3 of Nicholls and Baylor, 1968).

Table 1

Ganglion Number from Brain <sup>a</sup>	Supernumerary Cells Studied	Fields Mapped	Axons Traced by Stimulation and Cutting Roots	Synaptic Con- nections Traced
8	left: 3P, 4N, 2AE; 3 Retzius total	P, N		
9	left: 4P, 4T	P, T		
11	left: 3N                      right: 3P			x
12	left: 3P			x
13	left: 3P, 4T                      right: 3P			x
14	left: 2AE	AE		
15	left: 4P, 5T, 3N, 2AE; only 1 Retzius	P, T, AE	x	
16	left: 4P, 5N, 2AE; 3 Retzius total		x	
17	left: 3P		x	
18	left: 3P		x	

<sup>a</sup> Normal ganglion: Each side = 3T, 2N, 2P, 1AE, 1 Retzius (2 total).

cells that are not normally apparent. For example, an extra Retzius cell was obvious in addition to supernumerary sensory and motor cells, and the extra P cells were particularly clear. Supernumerary cells were usually more abundant on the left side of the animal but they were also observed on the right; for technical reasons, in only two ganglia were they studied on that side.

Generally it was possible to identify the type of cell, as usual, by its shape, size, and position. The diagnosis was then confirmed unambiguously by recording from the cell body with an intracellular micro-electrode, since T, P, N, AE, and Retzius cells all give quite distinctive action potentials (see Fig. 3 in Nicholls and Baylor, 1968; also Fig. 7). However, it was not possible to say which of the cells of a given type were the "extra" ones and which the normal representatives. Thus, when there were four P cells instead of two, the impulse configuration and the electrical properties of all four were indistinguishable from each other and from P cells in normal ganglia.

In several instances the modality of the sensory cells was next tested by applying various stimuli to the skin. All the cells classified as T, P or N by morphological and physiological criteria responded characteristically to the appropriate stimulus, touch, pressure or noxious (see Nicholls and Baylor, 1968). Similarly, motor cells classified as AE caused annuli in the skin to be erected and produced no other muscular contraction (Stuart, 1970).

Table 1 presents a summary of the cells that were studied in ten ganglia. We have numbered the ganglia from anterior to posterior along the ventral nerve cord. Number 1 lies directly behind the head ganglion (or "brain") and number 21 is the last one before the large tail ganglion. Only cells that were actually recorded from are included in Table 1, therefore the supernumerary cells are underestimated (particularly on the

right side). We did see additional cells that appeared on inspection to be sensory or motor, including cells on the dorsal surface, but these have not been included in Table 1, either because the penetration was not attempted or because it damaged the cell.

#### *Shapes, sizes, and positions of sensory receptive fields*

Some of the receptive fields of supernumerary cells appeared normal in shape and area, while others had quite unusual contours. An example obtained with P cells is shown in Figure 3. The three P cells each have fields of approximately the type one would expect to find in a normal animal.  $P_1$ , situated most laterally in the ganglion, was driven by pressing on ventral skin, while the fields of  $P_2$  and  $P_3$  were located more dorsally, with some overlap occurring in the lateral region. As in normal leeches, the density of sensitive spots was highest in the center of the field.

The striking feature of these fields is that there were two cells,  $P_2$  and  $P_3$ , instead of a single one supplying the territory. By pressing on an appropriate restricted area, either  $P_2$  or  $P_3$  could be activated on its own. This suggests that the innervated areas are not rigidly linked and the overlap, therefore, is not complete. Further evidence to support this will be presented later.

In marked contrast to these relatively normal fields were those of the four P cells shown in Figure 4. Here, once again, a single cell  $P_1$  innervated a ventral field of the usual size in the usual position. But cells  $P_2$  and  $P_3$ , while having receptive fields with their centers situated more or less correctly, did not overlap with  $P_1$ ; and the field of  $P_4$  was situated laterally instead of dorsally and was far smaller than we have ever encountered in normal leeches. Here, then, three cells covered the area normally dealt with by one on its own, and individual fields were shrunk in size and displaced. Similar distortions of the dorsal fields were obtained with another set of P cells, the four of ganglion number 15. As in Figure 4, the ventral field of  $P_1$  was normal but  $P_2$ ,  $P_3$ , and  $P_4$  had abnormal fields that overlapped extensively.

The receptive fields of supernumerary touch cells in two ganglia also showed both normal and abnormal configurations. In one ganglion four touch cells were identified instead of the usual three. They responded with characteristic, rapidly adapting discharges to a light touch, insufficient to activate P or N cells. Their fields are shown in Figure 5 and the appearance is not far from normal. The principal difference is that there are two cells innervating lateral skin instead of one. In addition the areas covered by  $T_3$  and  $T_4$  were smaller than normal, but it is likely that the ganglion contained extra T cells that were not detected.

In the ganglion of another segment five touch cells were identified and their fields mapped. The two T cells innervating ventral skin,  $T_1$  and  $T_2$ , had overlapping fields that appeared normal (Fig. 6). Similarly,  $T_3$  and  $T_4$  occupied the expected positions on the lateral skin. A single cell,

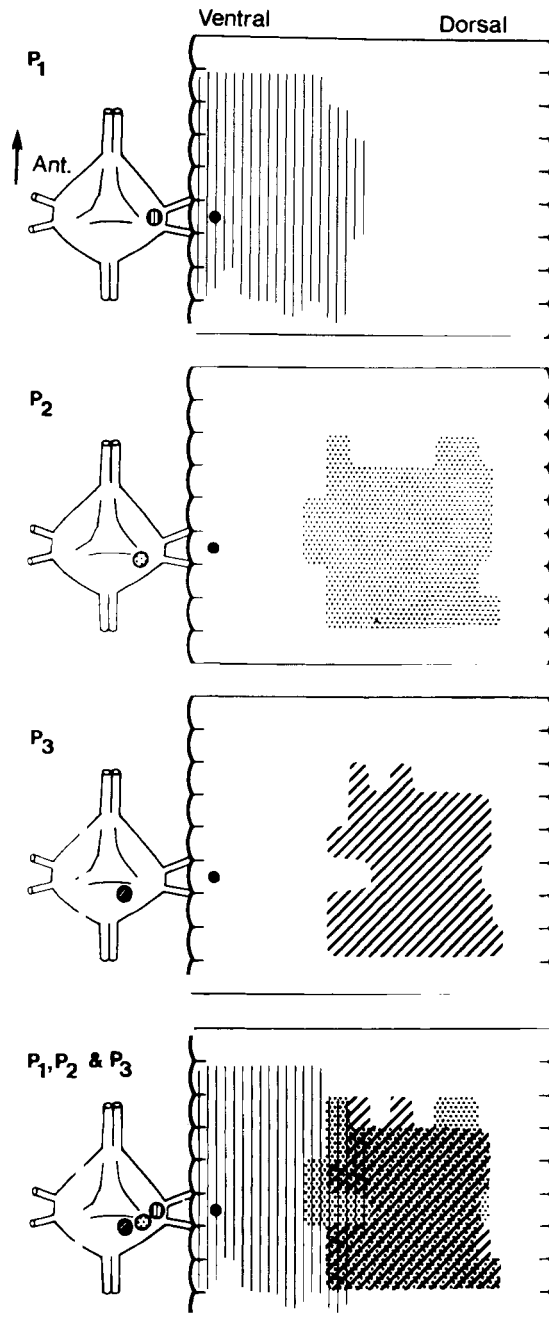


Fig. 3. Receptive fields and positions in ganglion 8 of pressure sensitive (P) cells. The receptive fields are shown individually and then superimposed as they appeared within the segment. Cells P<sub>2</sub> and P<sub>3</sub>, which are duplicates, overlap extensively but function independently and appear normal.

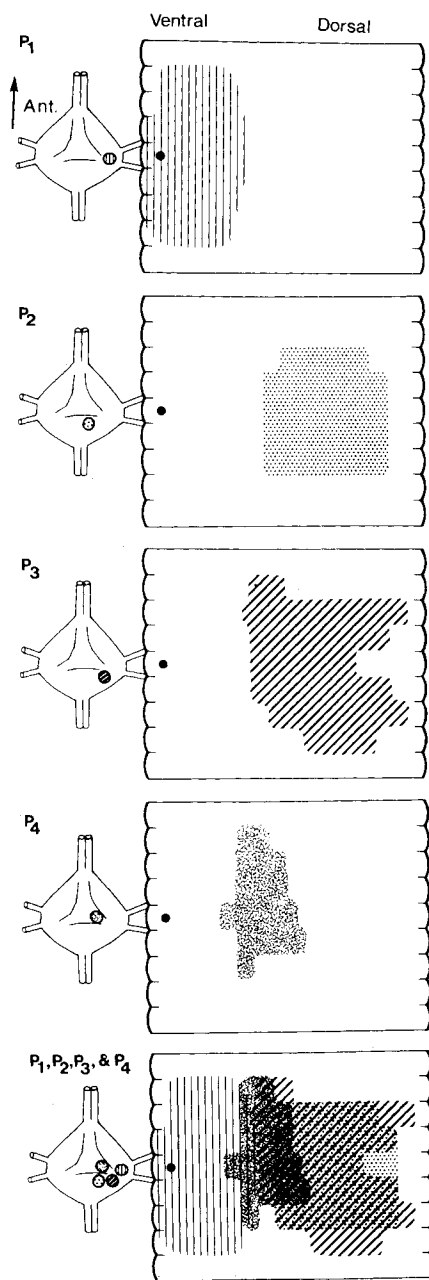


Fig. 4. The receptive fields and positions in ganglion 9 of pressure cells (P), shown individually and then superimposed as they appeared within the segment. There are four instead of two P cells;  $P_4$  covers the region normally overlapped by dorsal and ventral fields, which here are slightly shrunken and displaced.



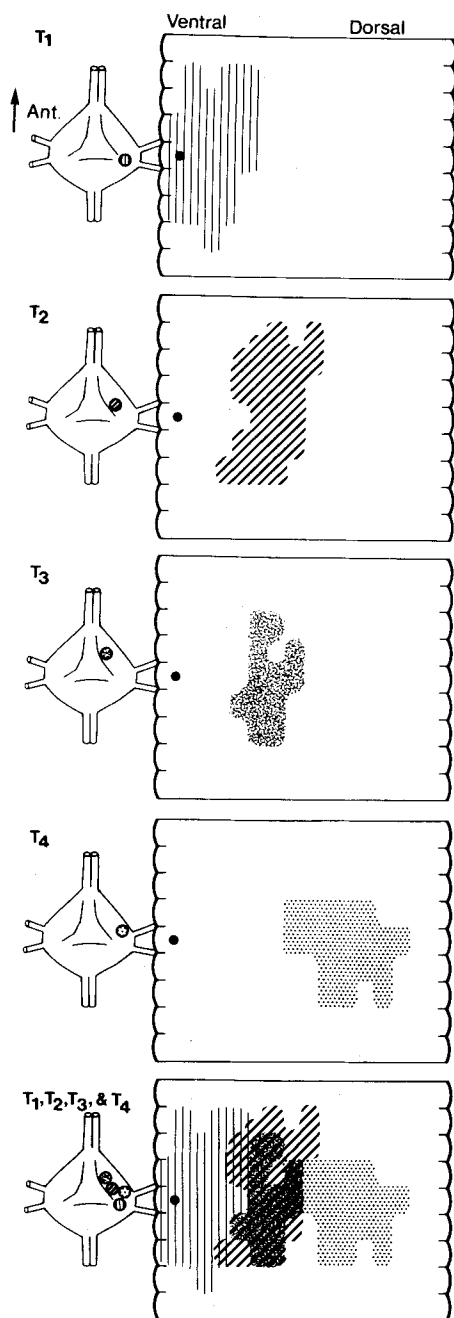


Fig. 5. Receptive fields and positions in ganglion 9 of supernumerary touch (T) cells, shown first individually and then superimposed. Two cells instead of one innervate the lateral skin. Light touch in the dorsal region not occupied by  $T_4$  caused, in normal Ringer's, synaptic activation of  $T_4$  indicating the presence of another, unimpaired T cell.

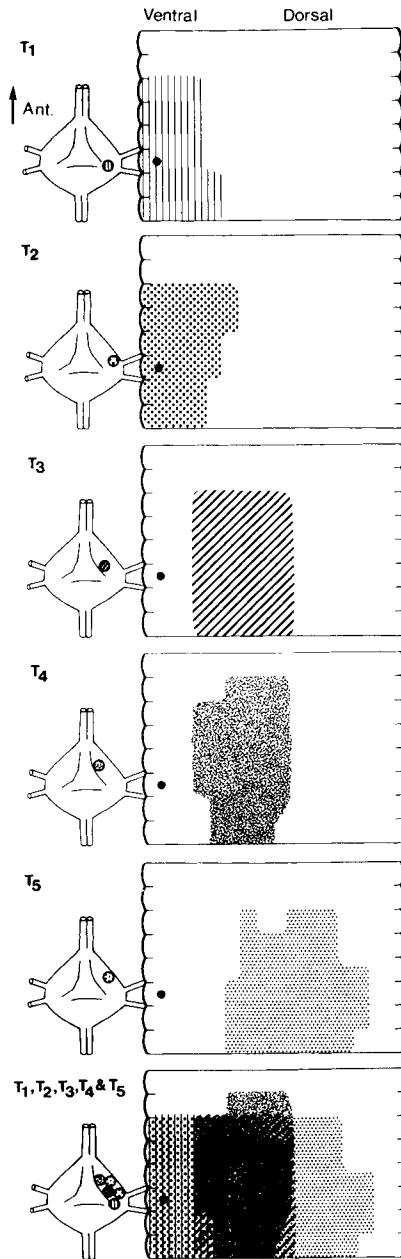


Fig. 6. Receptive fields and positions in ganglion 15 of supernumerary touch (T) cells, shown first individually and then superimposed. Duplicate cells  $T_1$  and  $T_2$  and cells  $T_3$  and  $T_4$  have overlapping but nearly normal fields, while the field of  $T_5$  is unusually large. Although all five cells did not overlap, some regions were innervated by as many as three or even four cells.

T<sub>5</sub>, was driven by touching dorsal skin. Its field was unusually large, extending to the exact boundaries of T<sub>1</sub> and T<sub>2</sub> but not encroaching upon them. A remarkable feature of the pattern in Fig. 6 is that some areas of the skin were innervated by a single T cell, some by two and some by three or even four from the same ganglion. In some cases the presence of a T cell could be inferred without actually recording from its cell body by observing *epsp*'s produced by it in another, identified T cell (see below and Baylor and Nicholls, 1969).

Fields were also mapped for two N cells in a ganglion that contained four (instead of two). The two that were picked for study both innervated ventral skin, as we had predicted from their positions in the ganglion. Their fields overlapped, but were smaller than usual. In general it is harder to stimulate the nociceptive cells and to map their fields, because stronger stimuli have to be used. Since only a limited time was available for investigating each ganglion, no other N cell fields were mapped in this animal.

#### *Independent activity of individual sensory cells*

Experiments were made to determine whether supernumerary sensory cells were driven directly from the skin or whether they were indirectly activated by other cells. This was particularly important for the touch cells which are interconnected by excitatory synapses (Baylor and Nicholls, 1969). To test this the ganglion and skin were bathed in Ringer's fluid containing 20 mM Mg<sup>++</sup>, which is known to block chemical synapses in the leech (Nicholls and Purves, 1970). The receptive fields plotted for T, P, and N cells in this fluid were identical to those of the same cells in normal Ringer's fluid. However, in high Mg<sup>++</sup> fluid one could no longer see synaptic potentials in one touch cell when a neighboring field was stroked.

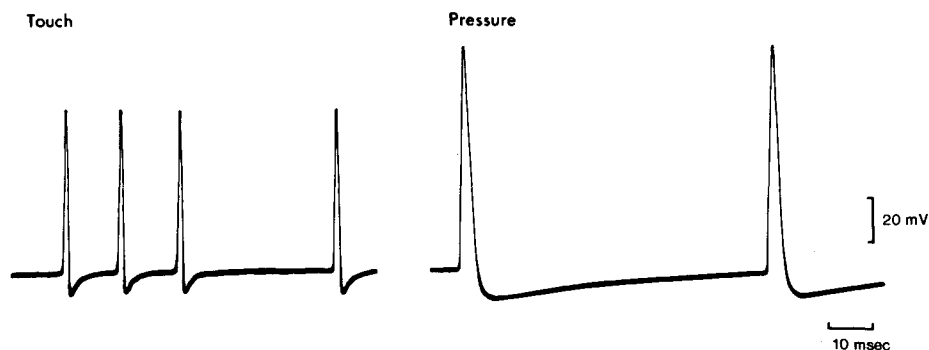


Fig. 7. Lightly touching the receptive field of a T cell or pressing on the receptive field of a P cell sets up impulses which are recorded intracellularly from the cell body. The impulses rise steeply with no step preceding the impulse, indicating that the cell was being activated directly.

Further evidence of independent action was provided by stimulating at the borders of receptive fields where there was no overlap. Here it was possible to stimulate a single T or P cell without activating its duplicate. Besides, it was apparent from the rising phase of the impulse, which rose steeply with no "step" or notch, that the cell was being activated directly. Examples are shown in Figure 7.

Supernumerary sensory cells were not tightly coupled by electrical synapses. No systematic studies, however, of coupling between sensory cells were made in abnormal ganglia, except to ascertain that one P cell could fire independently of another without evoking any measurable coupling potentials. Normally some current spread occurs between cells of a given modality (Baylor and Nicholls, 1969), but is too weak to produce impulses.

#### *Pathways and arborization of supernumerary sensory cells*

In normal ganglia each individual sensory cell sends its axons to the skin through certain specific nerve roots but not others. The question therefore arises of what pathways are followed by supernumerary axons and whether they take the normal routes to the periphery.

The branching pattern for normal T, P, and N cells is shown in Figure 8, taken from Nicholls and Baylor (1968). The axons of three sensory cells innervating dorsal skin,  $T_3$ ,  $P_2$ , and  $N_2$ , leave the ganglion by way of the posterior root and then run through the dorsal nerve. In normal ganglia one can almost always identify these cells from their positions in the ganglion (Fig. 8). The axons of the other T, P, and N cells all leave through both the anterior and the posterior roots but do not enter the dorsal nerve.

To examine the arborization of sensory cells in abnormal ganglia, the roots and the dorsal nerve were stimulated with external electrodes while intracellular recordings were made from the cell body to see if impulses were evoked. All the experiments were made in Ringer's fluid containing

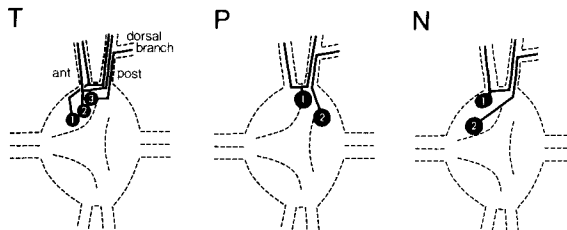


Fig. 8. Positions of T, P, and N cells and their branching patterns at the roots, on one side of a segmental ganglion, shown schematically. One cell of each type ( $T_3$ ,  $P_2$ , and  $N_2$ ) sends its axon solely down the dorsal nerve branch by way of the posterior root. The pathways of axons may be determined by stimulating electrically and by observing the effects on receptive fields of cutting various roots and branches. (Adapted from Nicholls and Baylor, 1968).

20 mM  $Mg^{++}$ . The pattern of responses and failures of P and N cells to stimulation of the three nerves was similar to those of cells in normal animals. For example, in ganglion number 16 two centrally located supernumerary P cells both gave impulses only when the dorsal branch of the posterior root was stimulated. In contrast, stimulation of the anterior root or the distal part of the posterior root was ineffective. This is what one would predict for a P cell in this position in the ganglion, which normally innervates dorsal skin.

In the same preparation three N cells situated at the edge of the ganglion, corresponding to  $N_1$ , were all activated by stimulating the anterior root, but not the dorsal nerve. This was to be expected for a normal N cell in this position, innervating ventral skin. Similar results were obtained in two other ganglia.

A further study of the branching pattern was made by mapping the receptive fields of P and T cells before and after cutting the dorsal nerve. With one exception, to be mentioned later, the fields of supernumerary cells were changed according to prediction. For example, the field was plotted for cell  $T_5$  in Figure 6 and was found to be situated dorsally. After the dorsal nerve had been cut, the cell was reimpaired successfully but it could no longer be driven by mechanical stimulation of the skin. The fields of the remaining four touch cells which innervated ventral or lateral skin were unchanged, indicating that their axons did not run in the dorsal nerve. When subsequently the anterior root was cut, the fields of two touch cells innervating lateral skin ( $T_3$  and  $T_4$ ) were partially denervated. As in normal animals, these duplicate T cells supplied the anterior annuli of the segment by way of the anterior root.

The fields of pressure cells were also examined in the same preparation before and after cutting the dorsal nerve. The duplicate cells  $P_3$  and  $P_4$  (Fig. 9) innervated dorsal skin. No responses from these cells could be elicited by stimulating skin mechanically or electrically after the dorsal nerve had been cut.

All these results indicate that duplicate cells innervate skin by way of the usual pathways. There was, however, one interesting exception—the pressure cell  $P_2$  that also innervated dorsal skin. Its field extended farther ventrally than those of  $P_3$  and  $P_4$  (Fig. 9). Section of the dorsal nerve curtailed but did not eliminate the area from which responses could be initiated. Pressing on or electrically stimulating a small lateral area of skin continued to evoke impulses in the cell body. They were not the result of synaptic action, since they rose sharply with no inflection and occurred in fluid containing 20 mM  $Mg^{++}$ . In this case it appears that the pressure cell had an axon running to the skin by way of one of the roots in addition to the dorsal nerve.

A more direct way of tracing axons of sensory cells was attempted by injecting Procion yellow into reduplicated P cells in two ganglia. The positions of the cells and electrical stimulation of the roots indicated that they sent their axons through the dorsal nerve and not the distal portion

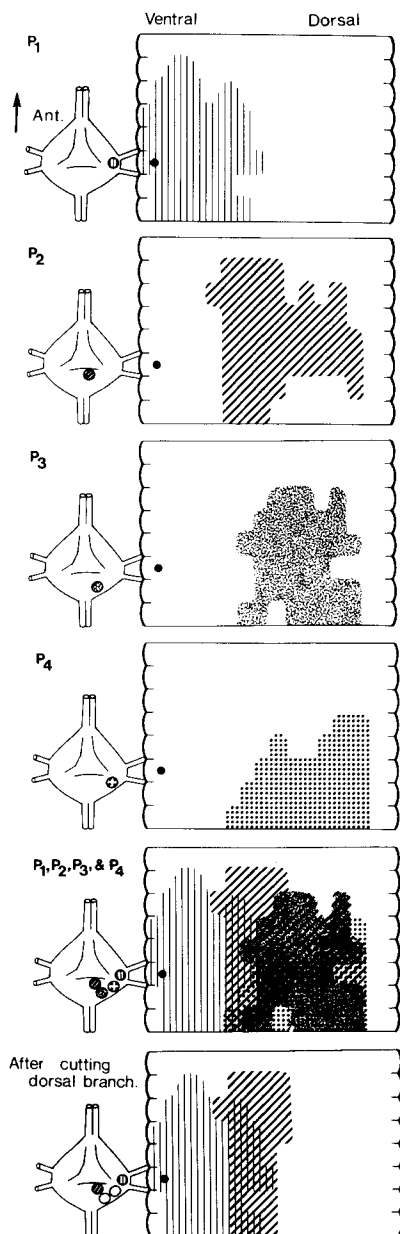


Fig. 9. Receptive fields and positions in ganglion 15 of supernumerary pressure (P) cells, shown first individually and then superimposed before and after cutting the dorsal branch of the posterior nerve.  $P_3$  and  $P_4$  did not respond to stimulation of the skin after cutting the nerve, but  $P_2$ , which had a more ventrally extending receptive field, could be stimulated directly, indicating that it had an axon running to the skin via one of the remaining roots.

of the posterior root as in normal animals. After injection the axons could be seen to enter the posterior but not the anterior root. Unfortunately, they could not be followed as far as the dorsal nerve.

### *Supernumerary motor cells*

In several ganglia an extra annulus erector motorneuron could be identified. In normal animals there are two such cells, one on each side at the posterior end of the ganglion. The impulses are characteristically different from those of other cells in the vicinity (Stuart, 1970). Firing causes the skin annuli to be raised into ridges over the whole of a segment on one side, and slightly beyond into adjacent segments. Duplicate AE cells had similar properties. Their fields were similar and overlapped extensively (Fig. 10). There were, however, areas at the edges where only one cell could cause annulus erection. Since normal AE cells are weakly coupled by electrical synapses, tests were made on supernumerary AE cells to determine whether each could act independently of the others. Although some of the current injected into one AE cell spread to the other two in both directions, impulses in the three cells were not synchronized. Finally, to demonstrate that both cells on one side were ca-

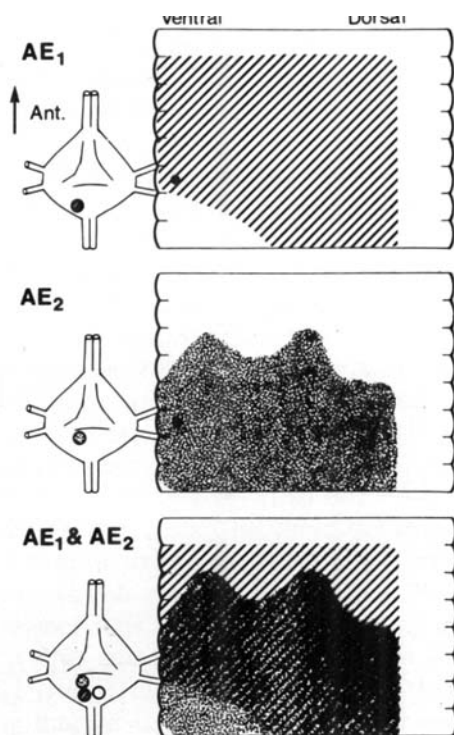


Fig. 10. Innervation of the body wall by duplicate annulus erector (AE) motor neurons, shown individually and then superimposed. The position of the third AE cell, innervating contralateral body wall, is also indicated.

pable of raising ridges on their own, one was stimulated while the other was prevented from firing by hyperpolarizing it with current. Both cells appeared to be equally effective.

#### *Synaptic connections in abnormal ganglia*

What synaptic connections do supernumerary cells make in an abnormal ganglion? One possibility would be that an extra cell might fail to connect with its postsynaptic target. That this was not so was shown by experiments that were made on three ganglia containing extra P and N cells. Normally the two P and N cells of a ganglion give rise to monosynaptic excitatory synaptic potentials on the AE motor neuron of the same side (Muller and Nicholls, 1974). In abnormal ganglia we saw that three P and three N cells also evoked synaptic potentials in the AE cell. Furthermore, as in normal animals, impulses in one T cell gave rise to excitatory synaptic potentials in all the other T cells, even when there were two supernumerary cells (see Baylor and Nicholls, 1969).

#### DISCUSSION

Since only a single animal was available for this study, many obvious questions could not be answered. For example, we do not know if the abnormality of the nervous system was caused by a mutation or by some developmental defect (cf. Hotta and Benzer, 1972). In addition, numerous straightforward experiments were omitted because there was no time.

Nevertheless, certain clear conclusions could be drawn. The supernumerary cells resembled those in normal ganglia with respect to their sizes, positions, electrical properties, modality, and the branching pattern of their axons in the various nerve bundles. As with twins, no distinction can be drawn between the "true" cell and the "extra" one.

The question arises whether supernumerary cells are also present but unobserved in normal ganglia. They might perhaps be small and therefore escape notice. This seems unlikely for a number of reasons. First, in normal animals, while recording with external electrodes from touch cell axons running in the nerves, a single unitary action potential follows each stimulus applied to the skin (except at the boundary of a field). Second, in the abnormal animal, on occasion the fields of some of the supernumerary sensory cells innervating an area were small and displaced (see Figs. 4, 6, and 9). Third, in normal animals one cannot find any extra cell in the region of the AE that causes skin ridges to be raised. Neither does one find a third Retzius cell, a very conspicuous neuron with a number of distinct properties (Lent, 1973). It is worth noting that all the nerve cells are visible in normal ganglia and can be impaled and stimulated by microelectrode. For these reasons it appears that the CNS of the abnormal animal did indeed contain extra cells and not simply a few cells that were larger than usual. Even though no cell



counts were made, this conclusion was supported by visual inspection. The extra cells were often obvious on both sides. In this respect Table 1 conveys a false impression, since it lists only cells that were actually recorded from and greatly favors the right side of the animal.

One of the main conclusions to be drawn from the experiments is that neurons as well as skin can receive inputs over and above the normal quota. One example is provided by the ganglion that contained three Retzius cells instead of two, all three being electrically coupled. Another is the synaptic connections of extra P and N cells to the AE motor cell. It would be interesting to know where the extra endings were located on the postsynaptic cell.

The situation in the periphery with regard to connections is not clear. Thus, reduplicated AE motor cells might have innervated different muscle fibers. With overlapping sensory innervation the total number of sensory endings per unit of skin might be the same as normal. What is surprising is the large number of different cells of this correct type that could provide innervation for a small patch of skin. Normally, the adjacent fields of any two P cells overlap a little, but Figures 4 and 9 show that the fields of as many as four P cells can overlap at some places. Furthermore, there is presumably additional overlap from P cells in the adjacent segments.

All the results emphasize once again the specificity of the cell types in the leech. A P cell is not simply different from T, N, AE, Retzius or other cells. It is also a P cell of the type that innervates either dorsal or ventral skin, sending axons through the appropriate pathways to do so. It will be interesting to see if we can find other abnormal leeches, perhaps with too few cells, to see how they deal with the problem of innervating the periphery.

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