

ORGANIZATION OF THE SPINAL CORD

**PROGRESS
IN BRAIN RESEARCH**

Volume 11

PROGRESS IN BRAIN RESEARCH
VOLUME 11

ORGANIZATION OF THE SPINAL CORD

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Preface

This volume includes contributions from almost all of the leading neuroanatomists who have in recent years devoted their attention to the spinal cord. Neurophysiologists like myself realize how much we are indebted to the careful systematic studies that have formed the basis upon which we design experiments and interpret our results. Yet the traffic in ideas is in both directions, for physiological discoveries such as Renshaw cells and γ -motoneurons give rise to anatomical problems of recognition that are discussed by several contributors.

It is remarkable that these anatomical investigations yielding such important data for neurophysiologists have been carried out by light microscopy together with the new developments in staining of degenerating fibres and synaptic knobs and of chromatolizing neurons and not by electron microscopy. It is clearly demonstrated that light microscopy has still much to yield that is of the greatest value in the joint efforts of anatomists and physiologists to understand the nervous system.

Besides this fine collection of classical neuroanatomical papers, there are also in this volume fascinating accounts of the spinal cord in the various orders of vertebrates. Clearly there is a rich field here that is just being opened up.

In a sense, anatomical investigations have a descriptive and qualitative bias — necessarily so at the pioneering level of investigation. The possibilities of a more quantitative attack are illustrated in the final two papers, which give new insights into problems of design and the quantitative relationships of the neuronal elements.

Besides these primary contributions there is much of value in the discussions which aroused much interest and helped to open up new problems for investigation.

It is good to know that by means of this volume the value of this conference will be shared by a much wider audience.

J. C. ECCLES

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Comparative Anatomy of the Spinal Cord

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(1) *Introduction*

It is the intention of this paper to present a survey of the evolutionary development of the spinal cord, by way of introduction to this meeting which will be devoted almost entirely to the structure and function of the mammalian cord. Comparative neurology is an old discipline and this implies that a review has to start far back in the past. My initial plan was to focus on the results of the earlier generations of comparative neuro-anatomists, and more specifically on the great advances made during the last decade of the 19th century, because it is truly amazing what men like Cajal, Retzius, Von Lenhossék and Van Gehuchten, to mention only a few names, achieved, especially during these so-called gay nineties. However, in confining myself entirely to paying homage to the old masters in our field, I would, perhaps, create the impression that the comparative approach has now only historical significance, and that is precisely what I wish to deny. Particularly in recent times a number of important contributions to the comparative anatomy of the spinal cord have been made, and therefore I feel that I have to speak not only about the gay nineties, but that it is also my task to herald in the gay sixties we have and we are going to have in the realm of comparative neurology.

The spinal cord is generally considered as the lowest level and the most simply organized part of the central nervous system. Yet, to give a survey of the structure and progressive development of this organ within the time here permitted is a task which can be accomplished only if a great number of limitations and schematizations are accepted. I apologize beforehand for a vast amount of important data which I will leave unmentioned.

(2) *General relations*

Of all the parts of the central nervous system the spinal cord or medulla spinalis preserves the early embryonic tube-like shape most clearly and although secondary form changes occur in some groups it may be said that this organ is generally of a cylindric appearance. The length of the spinal cord varies considerably. In most groups (the various classes of fish, the tailed amphibians, the reptiles and birds) the cord extends throughout the whole vertebral canal (Fig. 1a), but in some (tailless amphibians, mammals) it appears to occupy only a part of this space. In most mam-

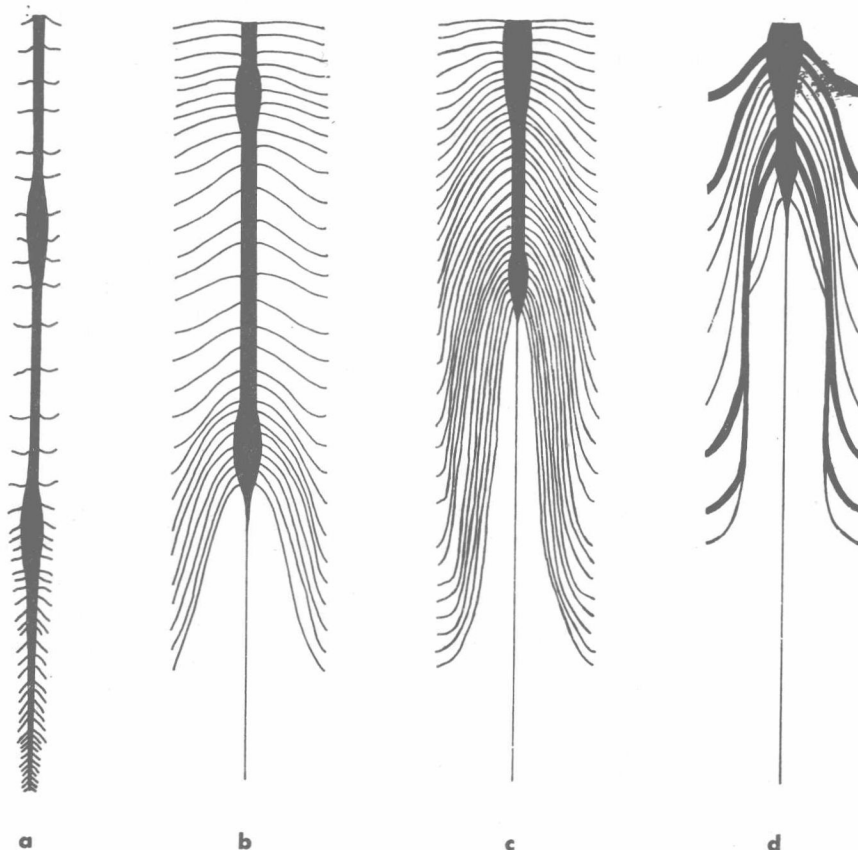


Fig. 1. A diagrammatic representation of the spinal cord and its nerves of (a) turtle (after Bojanus), (b) man, (c) seal, and (d) South American toad (after Tensen). In the turtle the spinal cord extends throughout the vertebral canal, but the other 3 forms show different degrees of shortening of the cord ('ascensus medullae spinalis'). In order to give a correct impression of the relative differences in length of the cord, the 4 figures have been standardized at the same vertebral column length.

mals the end of the spinal cord is found in the lumbar region of the vertebral column (Fig. 1b), but in a few species of this class (*Echidna*, *Phoca*, Fig. 1c) the conus terminalis is situated as high as the thoracic level. The most shortened spinal cords are, however, not found among the mammals, but among the lower vertebrates. In the South American toad *Pipa* the spinal cord terminates already at the level of the third vertebra (Tensen, 1927; Fig. 1d), and in *Mola*, a highly specialized teleost with a very short trunk, the cord does not even extend beyond the limits of the skull. In this species the vertebral canal is filled only with a bundle of nerve roots, the so-called cauda equina (Haller, 1891; Burr, 1928).

It is convenient to consider the spinal cord as consisting of a series of segments. Each segment gives off a dorsal and a ventral root on each side, which unite in all vertebrates, except the Petromyzontes, to form a pair of spinal nerves. The number of these spinal nerves varies widely, ranging from 10 pairs in the tailless amphibians to more than 500 pairs in certain snakes.

After these introductory notes on the gross anatomical relations we pass on to a discussion of the microstructure of the spinal cord. The nerve cells in the spinal medulla retain their primary position bordering the central canal, thus forming a column of central gray matter. This gray column is surrounded by a thick mantle consisting of nerve fibres. The spinal gray can be divided into 2 principal regions: a dorsal, chiefly sensory, and a ventral, predominantly motor area. Sensory impulses reach the dorsal area of the cord by way of the dorsal roots. From here, some of the incoming stimuli are directly relayed to the motor area of the same segment, others are propagated to more rostral and caudal spinal levels, and still others reach the brain along the so-called sensory pathways. The motor region of the cord does not merely receive stimuli from the spinal sensory region; its activity is also regulated by various supraspinal centres, which discharge their impulses along the descending fibre-systems of the cord. The axons of the cells which constitute the spinal motor area emerge from the cord through the ventral roots and reach the various effector organs.

The special aim of the present report is to review how the pattern just outlined has been realized in the various classes of vertebrates. The magnitude of this subject makes some limitations necessary. I shall confine myself, therefore, mainly to the lower forms, only briefly comment upon the reptiles and birds, and leave discussion of the mammalian spinal cord almost entirely to other participants of this conference, who are much more qualified to deal with this matter than I am.

The following account opens with some general remarks on the embryonic cord. Then the main groups of vertebrates will pass in review. A brief survey of certain major trends in the evolution of the spinal cord concludes this paper.

(3) *Notes on the embryonic cord*

A discussion of the ontogenetic development of the spinal cord falls outside the scope of the present survey. Some features of the organization of the cord in larval stages of the lower vertebrates, which are of basic importance for our understanding of the structure of the adult organ, will, however, briefly be pointed out. Attention is directed first to some results of the classic studies of Coghill (1913, 1914, 1929) and of Herrick and Coghill (1915) on the nervous mechanisms underlying the early behaviour of the amphibian *Ambystoma*. These authors found that at the time of the earliest somatic movements in response to external stimuli most cells in the nervous system of *Ambystoma* are still in the neuroblast stage (Fig. 1), but that the comparatively few elements which have differentiated, constitute a definite neuronal circuit, consisting of three types of nerve cells (Fig. 2).

In the dorsolateral region of the cord large elements were found, the offshoots of which show a remarkably wide distribution. The dendrites of these cells leave the spinal cord, reach the skin and ramify here as free nerve endings. These dendrites have, however, in addition branches which enter the dorsal tip of the myotomes. The axons of the large dorsal cells are directed cephalad and constitute a laterally situated tract in the cord. It may be stated that the cells under discussion are sensory in function and the distribution of their peripheral offshoots suggests that they receive both

exteroceptive impulses from the skin and proprioceptive impulses from the developing muscle segments. In the cord these stimuli are conveyed rostrally along the neurites of the dorsal cells, which thus form a primitive sensory pathway. At the level of the junction of the spinal cord and the medulla oblongata commissural cells are present, which transmit the impulses from the sensory to a primitive motor system.

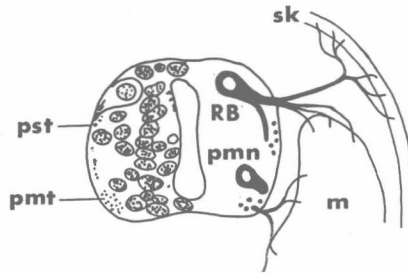


Fig. 2. Cross section through the cord and some adjacent structures of a larval *Ambystoma*, at the time of the first somatic movements. Combined from figures of Coghill. See for abbreviations Fig. 3.

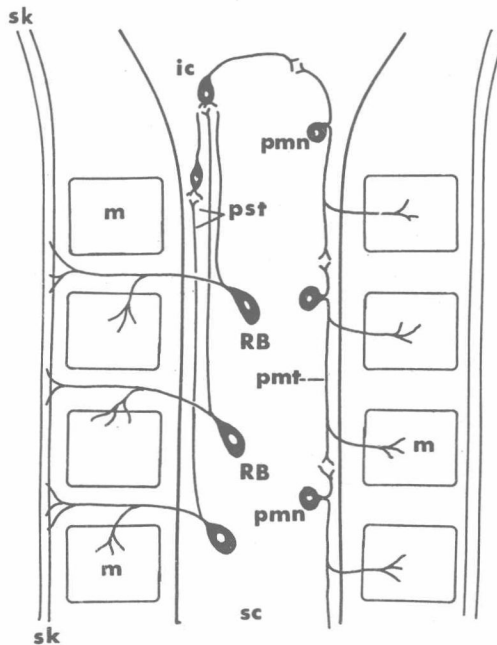


Fig. 3. Diagram of a dorsal view of the upper end of the spinal cord of larval *Ambystoma*, at the same stage as in Fig. 2. Adapted from Herrick and Coghill. ic, internuncial cell; m, myotome; pmn, primitive motor neuron; pmt, primitive motor tract; pst, primitive sensory tract; RB, Rohon-Beard or giant sensory cell; sc, spinal cord; sk, skin.

The axons of these internuncial elements cross to the opposite side in the ventral commissure.

The spinal motor system in the early larval *Ambystoma* consists, according to Coghill (1913), of a chain of neurons situated in the ventrolateral part of the cord.

The longitudinally conducting axons of these neurons are intrinsic to the cord and constitute a polysynaptic, primitive motor path which conducts impulses from the head tailward (Fig. 3). The stem fibres of the primitive motor neurons give rise to collaterals which issue through the ventral roots and reach the myotomes, thus completing the long reflex arc of the early motile stage of *Ambystoma*.

The large dorsal cells are in the literature often named after Rohon and Beard: two of the earlier authors who described these elements. Rohon (1884) observed the cells in alevins of the trout and Beard (1889, 1892, 1896) found them in larvae of various ichthyopsids (*Raia*, *Mustelus*, *Pristiurus*, *Lepisosteus*, *Salmo* and *Trinon*). Both authors pointed out that the cells under discussion are the first elements in the cord that exhibit a clear neuron appearance. During the last decade of the 19th century numerous papers appeared, in which large nerve cells, situated in the dorsal region of the cord of larval as well as adult lower forms were described, and in which different opinions regarding the nature, fate and homology of these elements were expressed.

Beard (1889) who observed initially only the offshoots directed toward the myotomes considered the large dorsal cells as constituting a primitive motor apparatus, and a similar opinion was expressed by Studnička (1895). Later, Beard (1896) noticed also the branches to the skin and regarded the dorsal cells now as 'largely if not entirely sensory in nature' (1896, p. 387), a view which was later considerably corroborated by Coghill (1914).

Concerning the fate of the large dorsal cells during further development Rohon and Beard did not agree. Whereas Rohon (1884) held that these elements persist throughout life and become the large neurons of the dorsal horn, Beard was of the opinion that the dorsal giant cells disappear at the end of larval life and are replaced by spinal ganglion cells. The dorsal cells constitute according to the latter author 'a transient nervous apparatus', and he presented in his 1892 and 1896 papers a detailed analysis of the involution of these elements in *Raia*. Studnička (1895) observed that in the tailless amphibians the dorsal giant cells degenerate at the approach of metamorphosis, but he believed that in *Lampetra*, *Triturus* and *Protopterus* the elements persist throughout life. As far as the two latter forms are concerned he referred to the work of Burckhardt (1889, 1892) who observed in adult stages of these species large cells, situated in the dorsolateral part of the cord, provided with an offshoot in the direction of the dorsal root. Herrick and Coghill (1915) held, however, that in *Ambystoma* the dorsal giant cells are gradually entirely superseded by spinal ganglion cells. Hughes (1957), finally, studied the development of the spinal sensory apparatus in *Xenopus*. He found no definite degeneration of the Rohon-Beard cells and suggested that these elements gradually decrease in size and thus become inconspicuous.

I shall defer consideration of the question whether Rohon-Beard cells occur in adult forms until the separate discussion of the spinal cord of the various vertebrate groups. However, it may be mentioned here that Rohon (1884) regarded 'his' cells as homologous with large elements, seen by Reissner (1860) in the cord of the adult lamprey. Rohon called the large dorsal cells of the larval trout accordingly: 'Reissner'sche Zellen'.

From the survey presented above it seems to appear that Rohon-Beard cells can be found in larval stages of all Ichthyopsida. Part of the studies mentioned were carried out on material stained with routine methods and furnish consequently insufficient information on the distribution of the offshoots of the cells. Work, partly of more recent date, in which specific techniques were employed, has confirmed, however, that true Rohon-Beard cells — *i.e.* large elements, situated in the dorsal or dorso-lateral part of the larval cord, provided with 1 or 2 long offshoots, running longitudinally and with another one, leaving the cord through a dorsal root — occur in most groups of lower vertebrates. Elements answering to the standards just mentioned have been described by Whiting (1948: *Lampetra*), Van Gehuchten (1895a, b: trout), Johnston (1900: the teleosts *Coregonus* and *Catostomus*), Coghill (1914: *Ambystoma*) and Hughes (1957: *Xenopus*).

There are data available which indicate that the total number of Rohon-Beard cells, present in a larva, is comparatively small. Coghill (1914) counted about 200 of these elements on one side of the cord, and Harris and Whiting (1954) established that in a trout embryo, at the early motile stage, there are only one or two Rohon-Beard cells per somite.

Various authors have pointed out that the dorsal giant, or Rohon-Beard cells as regards the distribution of their offshoots closely correspond to the spinal ganglion cells of adult vertebrates, and some (Van Gehuchten, 1895a; Johnston, 1900) advanced the idea that there exists a genetic relationship between these two categories. Such an homology was, on the other hand, vigorously denied by Beard (1896): '... any morphological relationship with spinal ganglion cells is out of the question' (p. 382). Scharf (1958), too, denied that the dorsal giant cells are homologous with spinal ganglion cells. This author stated that these categories of cells constitute two different generations of the peripheral sensory nervous system.

The larval motor neurons have not been the subject of as many studies as the Rohon-Beard cells. From the literature it appears, however, that a primitive motor apparatus, essentially similar to that of *Ambystoma* (Fig. 3), occurs also in larvae of the lamprey and of the trout (Whiting, 1948, 1955). As to the fate of the primitive motor cells Herrick and Coghill (1915) supposed that, during further development, these elements are transformed to typical ventral horn neurons. So far investigations which confirm this hypothesis have not been reported.

The number of primitive motor neurons in a larval cord seems to be restricted, just like that of the Rohon-Beard cells. Harris and Whiting (1954) reported that in the early motile trout embryo there are about 4 motor neurons per somite.

The third element in the early embryonic cord of *Ambystoma* — the commissural cell — bridges, as we have seen, the gap between sensory system of the one side and the motor apparatus of the other. Cells of this type have been observed in larvae of various vertebrates but there seems to be some variation with regard to the time of their appearance. In *Ambystoma* the commissural cells mature after the sensory and motor parts of the reflex arc have developed (Herrick and Coghill, 1915; Fig. 3). In the dogfish Harris and Whiting (1954) found, however, another order of development. Here the commissural cells develop first, later followed by respectively the

Rohon-Beard and the motor neurons. Still another order of development occurs in the lamprey embryo. According to Whiting (1955) the first intrinsic neurons of the cord develop in this form almost synchronously with each other, in a cephalo caudal order.

Notwithstanding the variations just mentioned, the data reviewed in the preceding pages strongly suggest that most if not all groups of lower vertebrates pass through a stage in which the spinal cord is simply organized, containing as functioning elements: a sensory column of typical Rohon-Beard cells, a chain of primitive motor neurons, and a number of internuncial cells, which connect these two systems. This pattern seems to be, indeed, of basic importance and the supposition may be raised that it approximates to a considerable degree the organization of the cord of the central ancestor of the backboned animals. Other, more direct information on the structure of the earliest vertebrates may be provided by *Amphioxus*, a highly primitive survivor of a group probably directly ancestral to the vertebrates. It is well, therefore, to focus our attention now to the structure of the cord of this form.

(4) *The spinal cord of Amphioxus (Branchiostoma)*

Amphioxus, the lancelet, is a small, translucent animal that, although fish-like in appearance, is organized much more primitively than any fish. There is no true head or brain, and no special sense organs, except for some photo-receptor cells. Its body axis is formed by a well-developed notochord, which extends to the tip of the rostrum. The musculature of *Amphioxus* consists of a segmental series of some 60 muscle blocks on each side of the notochord. The animal responds to external stimuli always with sinuous movements of the whole body; localized reflexes are entirely lacking (Ten Cate, 1938). In this respect *Amphioxus* resembles, according to Ten Cate, the vertebrate embryo (*cf.* Hooker, 1952).

The central nervous system consists of a hollow, dorsally situated nerve cord. The central canal is slit-like, but anteriorly it widens as to form a ventricular cavity. There is no unanimity as regards the nature of the thin walled, rostral part of the nervous system, which surrounds this ventricle. Some consider this 'brain vesicle' as the homologue of the deuterocephalon of vertebrates (Delsman, 1913), but others (Rohon, 1882; Ariëns Kappers, 1929) hold that it represents, in primordial form, the entire vertebrate brain. Although the head end of the nerve cord of *Amphioxus* contains a few types of cells not found further back in the cord (Bone, 1959, 1960b) it may be confidently stated that a true brain in the sense of a superimposed integrative centre, is entirely lacking. *Amphioxus* is in essence a spinal animal.

The nerve cord is connected with the periphery by bilateral series of dorsal and ventral nerve roots. The dorsal and ventral root of one segment do not emerge at the same level, but alternate: the ventral roots lying opposite the myotomes to which they carry motor fibres; the dorsal roots running out in the intermuscular septa to the skin. Since, in addition, the left half of the body is shifted somewhat rostrally with respect to the right half (Rohde, 1888b) it may occur that the dorsal roots of the one side lie at the same level as the ventral roots of the other side (Fig. 7).

The microstructure of the nervous system of *Amphioxus* has been the subject of

numerous investigations. Most important among these are the contributions of Rohde (1888a, b), Retzius (1891a) and Bone (1959, 1960a, b). Particularly the studies of the last mentioned author, carried out on both larval and adult material, have greatly extended our knowledge of the neuro-histology of *Amphioxus*, and the following synopsis is largely based on his work.

Reference to Fig. 4 shows that the spinal cord of *Amphioxus* is somewhat triangular in shape with the apex pointing dorsalward. The cellular elements are almost all situated in the immediate vicinity of the cleft-like central canal, and numerous nerve cells appear to be provided with one or more broad processes which terminate in the wall of this canal. In numerous cases the processes just mentioned, or even the cell bodies themselves are lying in the lumen of the ventricular space. According to Bone (1960b) these peculiar relations find their explanation in the fact that the fluid of the central canal is probably the only site where the neurons of the cord can exchange metabolites; blood vessels or glia elements specialized for neuron nutrition are entirely lacking in the central nervous system of *Amphioxus*.

The regions of the cord situated laterally to the narrow cellular area are largely occupied by longitudinally running fibres of highly varying diameters. Most conspicuous among these fibres are the coarse axons of Rohde (1888a, b), which constitute 5 distinct bundles in the cord (Fig. 4): 2 on each side; the 5th, consisting of 1 single fibre of really giant proportions, in the median plane, closely below the central canal. These Rohde fibres are often compared with the giant fibres of Annelids. Another feature reminiscent of the worms is the presence in the cord of segmentally arranged groups of simply organized eye spots; each consisting of a photoreceptor cell and a surrounding, cup-like pigment cell.

The dorsal roots of the cord of *Amphioxus* contain fibres of varying nature. Bone (1960a) distinguished a general cutaneous, a visceral sensory and a visceral motor component, a composition which, though on less firm grounds, was already mentioned by Johnston (1905). The somatosensory skin fibres end generally as free terminals in relation to the elements of the single-layered epidermis, though encapsulated nerve endings occur in certain regions. The visceral afferent fibres are the axons of peripheral neurons of the atrial nervous system and the visceromotor fibres are efferent to that system. Several authors (Rohde, 1888b; Hatschek, 1892; Johnston, 1905) have described spread or agglomerated cells along the dorsal roots or their branches, corresponding with the elements that constitute the spinal ganglia of vertebrates. However, the work of Retzius (1891a) and Bone (1960b) has sufficiently shown that spinal ganglia or even traces thereof are entirely absent in *Amphioxus*. The cells which constitute the somatosensory and the visceromotor systems are all situated within the spinal cord.

As regards the somato sensory system, Retzius (1891a) has already described the types of cells that contribute most of the peripheral fibres of this system. His observations were confirmed and extended by Bone (1960a, b).

The most common somatic sensory elements are bipolar in shape and constitute a continuous column along each side of the central canal near the dorsal surface of the cord (Figs. 4 and 5, ss1). The cells of this column are oriented longitudinally and

from their rostral and caudal poles there arise offshoots, which form a distinct somatic sensory bundle (Fig. 4). One of the fibres of each cell dichotomizes in the vicinity of a dorsal root, after which one branch passes out of the cord and the other continues in its longitudinal course.

There are in each segment a few cells which, although the distribution of their processes conforms to the pattern just sketched, must be considered a separate type (Bone, 1960b). These elements, indicated in the Figs. 4 and 5 as ss2, are larger than the common cells of the somatic sensory column and their perikarya possess a con-

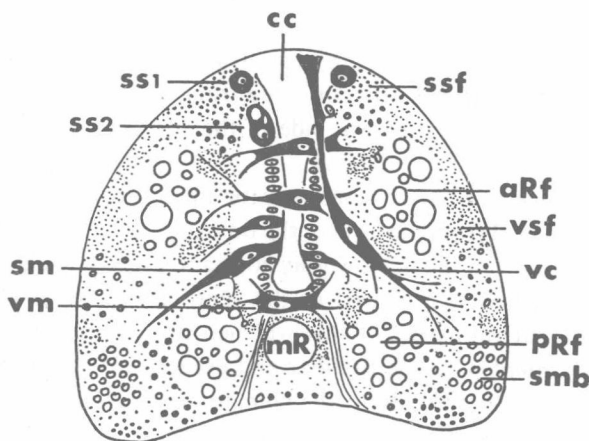


Fig. 4. A diagrammatic transverse section through the spinal cord of *Amphioxus*. Redrawn from Bone. See for abbreviations Fig. 5.

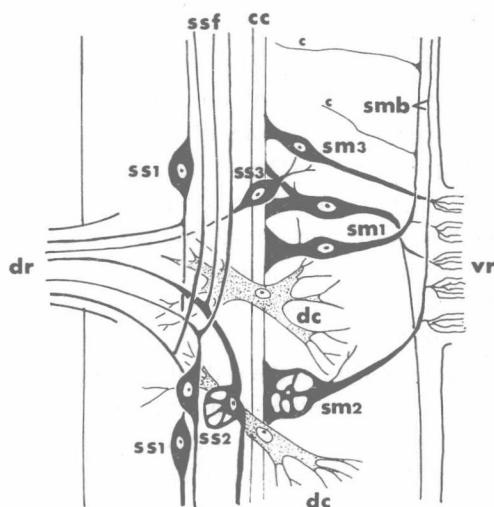


Fig. 5. Horizontal projection of a number of elements in the cord of *Amphioxus*. Combined from figures of Bone. aRf, anterior Rohde fibres; c, collateral; cc, central canal; dc, dorsal commissural cell; dr, dorsal root; mR, median Rohde fibre; PRf, Posterior Rohde fibres; smb, somatomotor bundle; sm 1, 2, 3, various types of somatomotor neurons; ssf, somatosensory fibres; ss 1,2,3, various types of somatosensory cells; vc, vertical cell; vm, visceromotor cell; vr, ventral root; vsf, viscerosensory fibres.

spicuous vacuole. Bone mentions in addition two other kinds of large cells that contribute fibres to the dorsal roots. These elements occur, often associated, segmentally and singly in each segment. Their central connections are imperfectly known.

Besides the elements termed here ss1 cells (Figs. 4 and 5) there is another common type of cell which sends a fibre out of the dorsal root (Fig. 5, ss3). The bipolar or tripolar cell bodies of these elements lie more or less transversely across the central canal; their central processes go contrary to those of the ss1 cells, to the side opposite to that of the dorsal root through which its peripheral fibre issues. Johnston (1905) was able to trace the central offshoots of a number of these cells. In most cases this fibre is only short and ramifies at once more or less profusely, in others it enters the dorsal bundle, sometimes dividing into rostral and caudal branches. Johnston observed in addition small bipolar cells, oriented transversely or obliquely, the central processes of which remain on the same side of the cord as the roots which the peripheral fibres enter.

The cells which give rise to the visceromotor fibres lie, contrary to the somatosensory cells, far removed from the level of the dorsal roots. These elements constitute, viz., the ventralmost part of the narrow gray zone and are located close to the bottom of the somewhat widened ventral part of the ventricle (Bone, 1960b). The somatic motor cells line the lateral aspect of this widened part of the ventricular cleft, and thus in the cord of *Amphioxus* the peculiar and exceptional condition exists that the visceromotor elements lie ventrally to the somatomotor system (Fig. 4).

The visceromotor column consists of large and small multipolar cells: the latter being the more numerous. The axons of these cells ascend to the dorsal roots and reach, by way of the ventral rami of the dorsal root nerve, the atrial region. Most of them innervate the pterygial muscle which forms the floor of the atrium. According to Bone it is likely that some of the dendrites of the visceromotor cells synapse directly with the visceral afferent fibres that enter the cord. The central course of these visceral afferents — as mentioned above the 3rd component of the dorsal roots — is not known with certainty; Bone presumes, however, that these fibres are assembled lateral to the dorsal bundle of Rohde axons (Fig. 4). In larval acraniates this author (Bone, 1959) found a bundle of visceral fibres which occupies a similar position.

Ventral to the somatosensory and dorsal to the somatomotor system, cells are found which, although widely varying in form and size, probably all are internuncial in function. A large proportion of these cells lies across the central canal, forming thus a protoplasmic commissure; others lie to one side of the ventricle but are provided with broad processes that terminate in the wall of the central canal (Fig. 4). The more dorsally situated elements of this intermediate cell group are clearly related to the somatic sensory system. Among them there are conspicuous dorsal commissural cells which extend their dendrites amongst the somatosensory columns of either side of the cord (Fig. 5). For a detailed description of the other cell types which occur in the intermediate grey of the cord of *Amphioxus* we may refer to Bone's paper. Here we mention only the remarkable vertical cells which he found segmentally in the cord, between the dorsal roots (Fig. 4). The dorsal part of these cells consists of a long process which terminates upon the roof of the cord; the ventral part is provided with