THE STRUCTURE AND CONDUCTION VELOCITY OF THE MEDULLATED NERVE FIBRES OF PRAWNS

BY W. HOLMES, R. J. PUMPHREY[1] AND J. Z. YOUNG

From the Department of Zoology and Comparative Anatomy, University Museum, Oxford

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(With One Text-figure)

INTRODUCTION

THE observation that the nervous system of prawns contains fibres surrounded by a sheath which blackens on treatment with osmium tetroxide was first made in studies of *Palaemon squilla* by Retzius (1888, 1890) and Friedländer (1889). The descriptions which they gave of these remarkable fibres seem to have attracted little attention since their time, and the only more recent investigation on the subject is that of Nageotte (1916).

THE STRUCTURE OF THE MYELIN SHEATH

In the nervous system of the prawn *Leander serratus* upon which the present investigation[2] was made, almost all fibres have a sheath which blackens after osmium tetroxide treatment.

The relations of the myelin sheath with other parts of the fibre are essentially as described by Retzius in his later paper (1890) and by Nageotte (1916). The osmiophil layer does not lie directly upon the axon as in vertebrates, for the two are separated by a thin nucleated sheath. Nageotte described the nuclei of this sheath as being the nuclei of the myelin sheath, and he compared them with the Schwann nuclei of vertebrates, which he considered to be similarly the nuclei of the myelin layer. However, until we have further information as to the derivation and behaviour during development of the inner sheath and its nuclei, this homology with the Schwann sheath elements of vertebrates remains entirely speculative. Further light can be cast on the question of the nature of the inner sheath by consideration of the nerves of other invertebrates. Recent studies of the nerve fibres of crabs and other decapod crustacea have shown that even in forms in which the nerves are usually considered to be non-myelinated there is a layer of orientated fatty molecules in a position round the axon corresponding with that of the myelin sheath of the prawn (Schmitt & Bear, 1939). In some fibres of crabs this layer is sufficiently thick or dense to be visible as a thin black line after osmium treatment (Young, 1936, fig. 15). Thus the fibres of prawns differ from those of other Decapods only in that the sheath layer containing orientated lipoids is thicker,

[1] Beit Memorial Research Fellow, Department of Zoology, Cambridge.

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and probably contains a higher proportion of fatty to protein elements. Indeed, all fibres of crustacea and molluscs which have been carefully studied show this same arrangement of the sheaths, so different from that in vertebrates, and the prawn is peculiar among invertebrates only in the great development of the fatty layer.

SHEATH THICKNESS AND FIBRE DIAMETER

The problem of the relationship between the diameter of the nerve axon and the thickness of its myelin sheath has been studied in vertebrates by Arnell (1936), Schmitt & Bear (1936–7), and Gasser & Grundfest (1939); and in earthworms by Taylor (1940). Both in vertebrates and in earthworms the thinner axons have

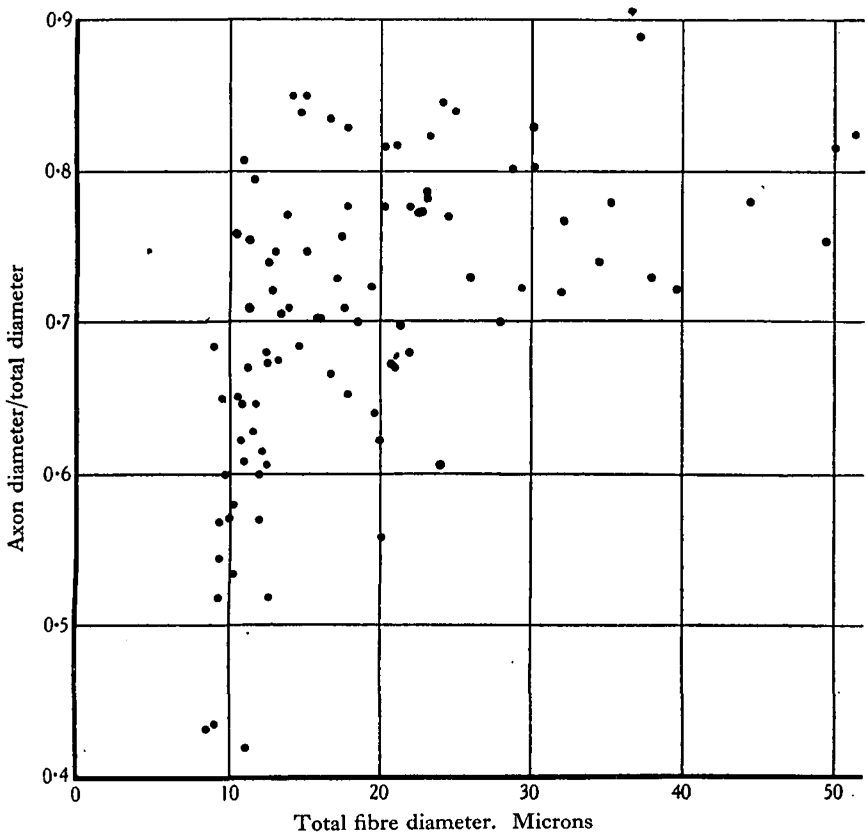

Fig. 1. Plot to show the relative thickness of the myelin sheath in fibres of the central nervous system of *Leander serratus*. The measurements given were made on transverse sections of two separate nerve cords.

relatively thicker sheaths. The ratio axon diameter/total diameter (g) at first increases with fibre diameter and then becomes constant. For vertebrate fibres the plateau of the curve is reached at total fibre diameter of from 6 to 8μ; for earthworm fibres at 40μ.

The accompanying graph (Fig. 1) shows the result of a series of measurements made on the fibres in the prawn central nervous system. Enlarged microphotographs were made of transverse sections of the ventral nerve cord fixed in 0·5 % osmium tetroxide solutions, and the measurements were carried out by means of a travelling micrometer microscope stage which carried a glass slide marked with fixed points over the surface of the photograph. This method of course suffers from several disabilities, particularly that fixation and staining may alter the thickness of the myelin sheath from that existing in the living fibre. The measurements show a considerable variability of the axon/sheath ratio for fibres of the same size, yet the general relations resemble those in earthworms and vertebrates. The myelin is relatively thicker on the smaller fibres. The ratio averages at 0·53 for fibres of 10μ and less; at 0·69 for fibres between 10 and 20μ diameter. For the large fibre group of total diameter from 20 to 50μ the trend is still further marked, and the ratio averages at 0·77. This shows a smaller relative thickness of the myelin than is found in any vertebrate fibres, corresponding with the unusually large total diameters of the fibres. In the largest earthworm fibres, of diameter greater than 40μ, Taylor found a ratio as high as 0·9.

THE NODES

Both Retzius and Nageotte, when describing the prawn fibres, drew attention to the fact that the myelin sheath is interrupted at intervals by structures closely resembling the nodes of Ranvier in vertebrate nerves. We find that in the nerves we have examined only the larger myelinated fibres have nodes, for we found none in fibres of a total diameter of less than about 13μ. The median giant fibres of the central nervous system, although they are connected with several cell bodies and are thus unlike simple neurons (Holmes, unpublished), also have segmental constrictions which may function as nodes although they are structurally unlike those on the smaller fibres.

Retzius (1890) stated that at the node the myelin sheath is completely interrupted, but Nageotte (1916) believed that the myelin, although much thinner at the node, was continuous over it. Recent investigations of the ultrastructure of nerves (Schmitt & Bear, 1939) have shown that no clear line of distinction can be drawn between medullated and non-medullated fibres. For a myelin layer may be present round a nerve although not sufficient in thickness or in density of fatty elements to blacken visibly on osmium treatment. Thus only the search for such a metatropic sheath at the node could determine whether the myelin is actually absent or merely thinned. We can, however, state that the myelin layer decreases in thickness at the node so much that it is no longer made visible by osmium treatment. The probability that it is actually completely interrupted is increased by the fact that in some preparations a distinct edge to the myelin sheath can be seen running transverse to the axon on either side of the thinnest region of the node.

We have not found in the prawn any such correlation between internodal distance and fibre size as was described by Kubo & Yuge (1938) in vertebrates. The internodes vary very greatly in length even along a single fibre. In one case, for instance, four successive internodes along a fibre were 0·13, 0·22, 0·29 and 0·60 mm. in length. Although in this case the internodes are shorter than those usually found in vertebrates, we have also found in prawns nodes spaced as far apart as 3 mm., without any corresponding change in fibre diameter.

THE CONDUCTION VELOCITY OF THE MEDIAN GIANT FIBRES

For a preliminary study of the conduction velocity of these invertebrate myelinated fibres the median giant fibres of the central nervous system were used (Johnson, 1924). These fibres are convenient for experimental purposes as they pass without synaptic interruption along the ventral nerve cord from the brain to the telson, but they are unlike other fibres in the prawn in that they possess no Ranvier nodes. However, as has already been suggested, it may be that the segmental constrictions of the axon in each ganglion have a function similar to that of more typical nodes. The diameter of the fibres studied varies considerably along the length of the nerve cord, fluctuating between a maximum total diameter of about 50μ and a minimal diameter of 25μ. The average total diameter of the fibres used in these determinations may be taken as 35μ, with a myelin sheath thickness of $4{\cdot}5\mu$.

To determine the velocity of impulse conduction in these fibres the whole central nervous system of the prawn was dissected out in sea water, and then lifted from this on the platinized platinum wire electrodes into a layer of paraffin oil. The stimulating and recording system was essentially similar to that used by Pumphrey *et al.* (1940). The stimulating electrodes were placed on one of the circumoesophageal connectives, and the recording electrodes on the posterior abdominal region of the cord. A conduction distance of about 30 mm. was thus obtained. Conduction velocities were obtained by measuring on the face of the cathode ray tube the distance between the stimulus artefact and the base of the spike for which the giant fibre was responsible. No difficulty was experienced in distinguishing this spike, as it was quite separate from those produced by impulses travelling along the other more slowly conducting pathways.

From determinations made in this way we found the median giant fibre to have a conduction velocity varying between 18·4 and 23·0 m. per sec. at temperatures close to 17° C.

DISCUSSION

The method used for determining the conduction velocity suffers from the errors inherent in any derivation of conduction velocity from measurement of the shock-spike interval; and the fact that the measurements were made in oil means that the recorded conduction velocity is probably somewhat less than the normal value (Hodgkin, 1939). However, neither factor is large enough to affect the conclusion that the nerve fibres of prawns conduct very much faster than do those of any crustacean yet examined. A crab fibre of diameter 30μ conducts at a maximum velocity of 5·5 m. per sec. (Hodgkin, 1939), and the greatest conduction velocity hitherto recorded in a crustacean is one of 9 m. per sec. in *Homarus* (Monnier & Dubuisson, 1931). We have found that in *Munida* a fibre of 50μ diameter conducts at 6·4 m. per sec., and one of 56μ at 6·9 m. per sec.; and the fibres of this animal resemble those of *Maia* and *Carcinus* in having a fatty sheath which just blackens with osmium tetroxide. The fact that such a high conduction velocity is found in the prawns, whose fibres differ from those of other crustacea only in the greater development of the fatty layer gives great weight to the view that the value of a myelin sheath lies in the increased speed of impulse propagation which it makes possible. The only other invertebrate fibres which conduct at comparable rates are those of the earthworm, which are heavily myelinated (Eccles *et al.* 1932; and see Taylor, 1940), and those of the squid which are of very much greater diameter (Pumphrey & Young, 1938).

The largest prawn fibres are somewhat smaller than the largest fibres of the earthworm; both have sheaths of the same order of thickness, and their conduction velocities are similar. However, further details are needed before an exact comparison can be made. Although the prawn fibres conduct faster than those of other crustacea, they conduct more slowly than do those of a cold-blooded vertebrate such as the frog, although the latter are of lesser diameter. This fact may be attributed to any of the several differences which exist between the prawn and vertebrate fibres.

SUMMARY

1. The structure of the myelinated fibres of prawns is described, and the homologies of the nucleated sheath which lies between the axon and the fatty layer discussed.

2. The relative thickness of the myelin sheath increases with decrease in total diameter of the fibre along a curve similar in shape to that found in vertebrates and earthworms.

3. Nodes of Ranvier are found in the sheaths of most fibres of a diameter greater than about 13μ.

4. The nodes are similar to those in vertebrate nerves in that the myelin sheath is interrupted at the node.

5. The conduction velocity of fibres in the central nervous system of axon diameter 26μ and total diameter 35μ is between 18 and 23 m. per sec., a rate faster than is found in the "unmyelinated" fibres of similar size in other crustacea.

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