Myelin-like sheaths in copepod axons

Copepods, the small planktonic crustaceans that are the most abundant metazoans in the oceans, are so successful partly because they have an escape response that accelerates them to 200 body lengths per second within milliseconds[1–3]. We find that nerve fibres of many copepods seem to be designed for rapid signalling. They have well-developed myelin-like sheaths, like those that give a tenfold boost to the conduction speed of nerve impulses in vertebrates[4]. By reducing a copepod's reaction time to predatory attack, these sheaths may be crucial to the survival of the large copepod populations that inhabit dangerous oceanic ecosystems.

Using transmission electron microscopy, we investigated the morphological substrates of this exceptionally quick reaction in copepods of the order Calanoida, which dominates planktonic communities and provides key links in marine food webs[5]. Cross-sections through the first antenna of 11 calanoid species revealed major contrasts in the way nerve fibres, or axons, are enveloped. Simple sheaths envelop axons in seven of the species, whereas multilayered sheaths resembling vertebrate myelin surround axons in the remaining four (Fig. 1a).

Species lacking the myelin-like sheaths belong to two superfamilies, the Arietelloidea and Centropagoidea. Although abundant, they are restricted in their distribution: the Arietelloidea are deep-sea forms, and the Centropagoidea occur primarily in freshwater and coastal marine habitats[6]. Species with myelinated sheaths belong to the Megacalanoidea and Clausocalanoidea, which are more widely distributed. These dominate open-ocean planktonic communities and also have representatives in coastal and deep-sea habitats.

In copepods possessing the myelin-like sheaths, nearly all axons of both sensory and motor nerves of the first antenna are ensheathed. Myelination of sensory axons is common among vertebrates but has not been reported previously among invertebrates[7]. Copepod myelin is characterized by concentrically arranged layers of membrane around the axon (Fig. 1b). The number of layers in a sheath varies for each axon, ranging from just one to more than fifty.

The highly organized laminae are tightly wrapped around microtubule-filled axonal cores. Bounding the core is a typical trilaminar unit membrane, or axolemma. The laminae consist of electron-dense layers of uniform thickness alternating with less dense layers of more variable thickness. The dark layers appear to represent a fusion of the apposed intracellular surfaces of sheath-cell membranes, without any intervening cytoplasm, whereas sheaths in other invertebrates have a thin ribbon of cytoplasm between the membranous layers[7]. Sheaths in copepods have extensive radial attachment zones where the space between membranes is less than 1 nm (Fig. 1b).

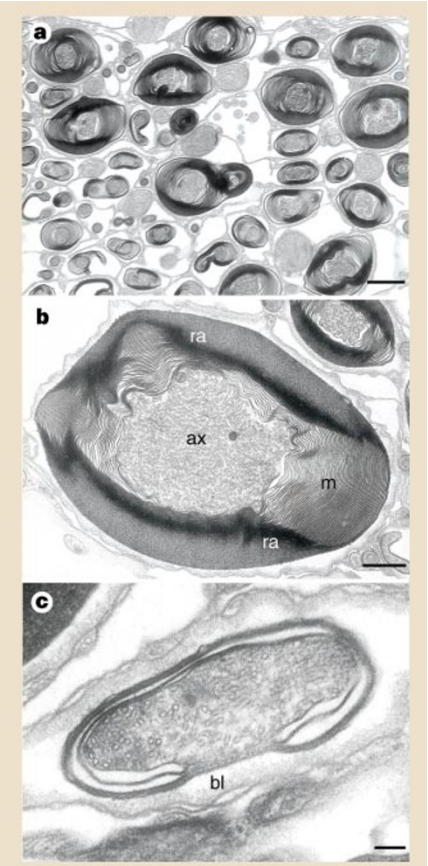

Figure 1 Transmission electron micrographs of cryofixed nerve in the first antenna of *Euchaeta rimana* (superfamily Clausocalanoidea). **a,** Cross-section through sensory axons. All axons have myelin-like sheaths. Scale bar, 1 μm. **b,** Section of large motor axon, with many axonal microtubules, ensheathed by closely spaced myelin-like lamellae; ax, axon core; m, myelin-like laminae; ra, radial attachment zones. Scale bar, 0.5 μm. **c**, Focal node. Sheath laminae end against the axonal membrane, leaving the naked axon exposed to the basal lamina (bl). Scale bar, 0.1 μm.

In vertebrates, the myelin sheath is interrupted by circumferential regions called nodes of Ranvier, spaced along an axon to allow the flow of ionic current[4]. The myelin sheaths in copepods have discontinuities that resemble invertebrate patch or focal nodes[7] (Fig. 1c), but none extends completely around the axon. The sheath laminae terminate at the axolemma in an orderly, stepwise fashion, with the innermost layers terminating first, allowing each layer to end in contact with the axolemma.

Considering its potential advantages, it is surprising that myelination is so rare in invertebrates[7]. Some do use myelin-like sheaths to increase the speed at which nerve impulses are conducted; indeed, speeds of 200 m s^{-1} in myelinated axons of penaeid shrimp are the highest in the animal kingdom[8]. The value of using neural specializations to decrease reaction times in small animals has been questioned because all parts of the animal are in very rapid communication anyway. But the existence of conduction-enhancing adaptations in small species, such as *Drosophila*[9] and copepods[10], and now including myelination in copepods, suggests a substantial value.

A preliminary comparison of copepod escape responses has shown significant differences in reaction times among species. *Undinula vulgaris*, which has myelinated axons, takes just 2 ms to initiate escape behaviour[3]; *Pleuromamma xiphias*, which has only unmyelinated axons, takes 6 ms (unpublished data). In an animal with 2 mm of axon 5 μm in diameter between the antennal sensors and the central nervous system, and an estimated minimum of 1 mm more to the muscles, the conduction time for impulses travelling at 1.5 m s^{-1} in typical unmyelinated nerve[11] would be about 2 ms. For a tenfold increase in conduction speed due to myelination[4], the same pathway would be 1.8 ms faster, explaining the faster reaction time of *U. vulgaris*. This improved performance may help calanoids with myelinated axons to dominate open-ocean communities.

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