SYMPOSIUM

Cnidarian Nerve Nets and Neuromuscular Efficiency

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Synopsis Cnidarians are considered "nerve net animals" even though their nervous systems include various forms of condensation and centralization. Yet, their broad, two-dimensional muscle sheets are innervated by diffuse nerve nets. Do the motor nerve nets represent a primitive organization of multicellular nervous systems, do they represent a consequence of radial symmetry, or do they offer an efficient way to innervate a broad, two-dimensional muscle sheet, in which excitation of the muscle sheet can come from multiple sites of initiation? Regarding the primitive nature of cnidarian nervous systems, distinct neuronal systems exhibit some adaptations that are well known in higher animals, such as the use of oversized neurons with increased speed of conduction, and condensation of neurites into nerve-like tracts. A comparison of neural control of two-dimensional muscle sheets in a mollusc and jellyfish suggests that a possible primitive feature of cnidarian neurons may be a lack of regional specialization into conducting and transmitting regions.

Introduction

Cnidarians are frequently referred to as "nerve net animals," even though the majority of extant species show some form of centralization of the nervous system in addition to the acknowledged organization of a nerve net in many areas of the body (Mackie 2004; Garm et al. 2006, 2007; Skogh et al. 2006; Satterlie 2011, 2015). The phylogenetic position of cnidarians has driven speculation that the nerve net represents a key position in the evolution of multicellular nervous systems, particularly since many cellular components of basic excitability and cell communication apparently did not originate within the phylum (e.g., Anderson and Greenberg 2001; Moran et al. 2015). At least three possibilities can explain the appearance and persistence of nerve nets within cnidarian nervous systems, none of which should be considered exclusive. First, the nerve net may well represent a primary component of nervous systems of ancestral forms at, or near, a stage representing the origin of multicellular nervous systems. Second, the nerve net may be an adaptation to radial or biradial symmetry and its developmental history. Third, the nerve net simply may be the most efficient way to innervate broad, two-dimensional sheets of effectors in which multiple, spatially-separated sites of excitation can activate the effectors.

While molecular and genetic studies have opened new analytic doors to address questions about the origin of neurons and multicellular nervous systems (Moroz 2009; Watanabe et al. 2009), more traditional electrophysiological and morphological investigations can highlight interesting properties of the nervous systems of extant basal groups, and thus provide foci for future molecular and genetic work. In particular, important properties of nerve nets and compressed nets of cnidarian species highlight neural adaptations found in other animal groups, and a few examples are presented here. In addition, activation/coordination of muscle sheets of medusoid cnidarians are compared with that of a molluscan species that uses two-dimensional sheets of striated muscle for locomotion (the pteropod *Clione limacina*). This comparison will suggest what may be a primitive characteristic of the neurons that comprise cnidarian nerve nets.

Why nerve nets?

Two important aspects of medusoid motor systems include the need for rapid conduction of impulses in a circular direction (around the bell), and in a radial direction (from margin toward bell's apex), to ensure coordination of widely-separated muscle cells throughout the two-dimensional muscle sheets that make up the musculature used in swimming (hereafter "swim musculature"). This rapid conduction is necessary to produce a coordinated contraction throughout the subumbrella for efficient ejection of water from the cavity of the bell.

In all three classes of cnidarians that have medusoid members, activation of the swim musculature originates in marginal nervous tissues: the marginal rhopalia in scyphomedusae and cubomedusae, and a compressed network in the inner nerve ring of hydromedusae (see Satterlie 2002). In all three groups, excitation can originate from multiple sites around the margin of the bell from these neural structures. This organization should rule out use of polarized (unidirectional) conducting systems for distribution of excitation through the muscle sheets, which would require multiple, parallel systems, one associated with each potential pacemaker site around the bell. A non-polarized, diffuse conducting system (Fig. 1) appears to be the most efficient fit for the unique issues related to excitation of swim musculature in medusae. However, the nerve net is not the only solution. Another form of non-polarized conducting system is found in the hydromedusae (Satterlie and Spencer 1983; Satterlie 2002). The widespread use of electrical conduction, via gap junctions, allows multidirectional conduction throughout the muscle sheets. While the subumbrellar muscle sheets of some hydromedusae are aneural, others use both electrical conduction and neuronal input from nerve nets (Spencer 1978; Spencer and Satterlie 1981; Satterlie and Spencer 1983; Satterlie 1985, 2008).

In scyphomedusae and cubomedusae, gap junctions have not been found (Mackie et al. 1984; Satterlie 2002), and if rapid conduction through the subumbrella is the goal, why use a network of small neurons? A network with a random orientation of neurons originating with some set of marginal sites of initiation, ensures both circular and radial conduction of excitation throughout the muscle sheets regardless of which site of origination is active. Furthermore, the large number of circular muscle cells that must be activated requires a large number of sites for neuromuscular output throughout the network, particularly since scyphomedusae and cubomedusae utilize chemical synapses for
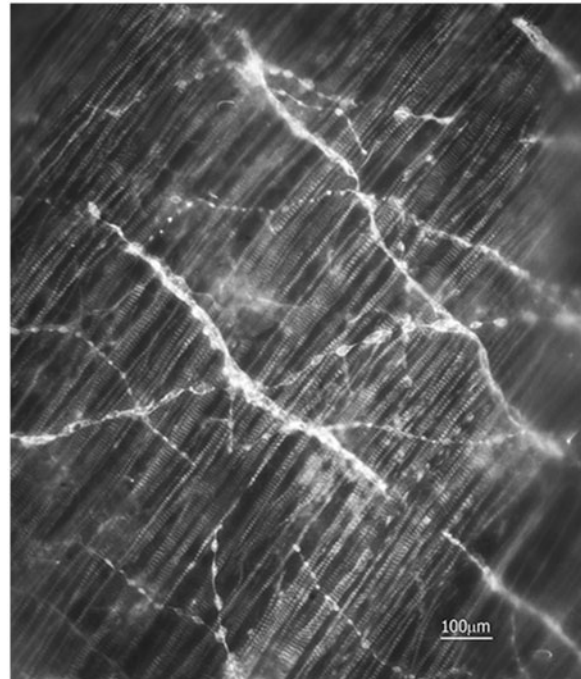

Fig. 1 Double immunohistochemical stain of the subumbrellar motor nerve net of the cubomedusa *Tripedalia cystophora* (tubulin antibody), and the striated swim muscle (actin antibody). Note the random orientation of the neurites and their blebbed appearance.

neuromuscular conduction. Under these conditions, the use of unpolarized nerve nets is likely the most efficient system for circular and radial coordination of these two-dimensional muscle sheets.

One disadvantage of using nerve nets for the excitation of muscle sheets is the relatively modest velocities of conduction found both in circular and radial directions (range: 30–100 cm/s for scyphozoan and cubozoan swim-systems) (Horridge 1954; Passano 1965; Satterlie 1979). Yet, two adaptations help achieve velocities of conduction at the higher values within this range, and also ensure that widely separated segments of the muscle sheet are activated with reasonable latencies that ensure a coordinated wave of contraction throughout the sheet.

First, in the nerve rings of hydromedusae and cubomedusae, neurons that make up the conducting systems for motor excitation around the margins (in the circular direction) are oversized relative to other neurons in the nerve rings (Fig. 2; Table 1). This suggests that the use of oversized neurons in behavioral systems that require fast conduction of excitation is a well-established property of cnidarian nervous systems. This is further supported by the use of giant neurons in the escape systems of siphonophores (Mackie 1973, 1978) and the hydromedusa
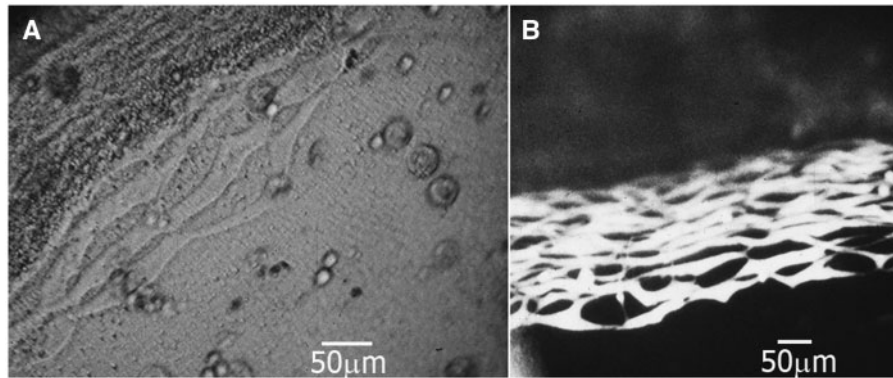
Fig. 2 Inner nerve ring of the hydromedusa *Polyorchis penicillatus*. (**A**) Live preparation with oblique substage illumination showing oversized motor network (banana-shaped cells). (**B**) Lucifer Yellow injection of one neuron resulted in movement of the dye throughout the network. Electrophysiological and electron microscopical examination confirmed that the dye-coupling was accompanied by electrical coupling via gap junctions.

Table 1 Maximal diameter of oversized neurons in the inner nerve ring of hydromedusae, and in the nerve ring of cubomedusae

| Hydrozoa		
Aequorea victoria	22 µm	Satterlie and Spencer (1983)
Cladonema californicum	7 µm	Satterlie and Spencer (1983)
Eutonina indicans	10 µm	Satterlie and Spencer (1983)
Gonionemus vertens	16 µm	Satterlie and Spencer (1983)
Muggiaea atlantica (swim bell)	7 µm	Satterlie and Spencer (1983)
Phialidium hemisphericum	9 µm	Satterlie and Spencer (1983)
Polyorchis penicillatus	30 µm	Satterlie and Spencer (1983)
Proboscidactyla flavicirrata	4 µm	Satterlie and Spencer (1983)
Aglantha digitale (ring giant)	20 µm	Singla (1978)
Aglantha digitale (radial giants)	40 µm	Weber et al. (1982)
Nanomia cara (stem giants)	30 µm	Mackie (1973)
Cubozoa		
Tripedalia cystophora	10 µm	Garm et al. (2007)
Carybdea marsupialis	5 µm neurites, 40 µm somata	Satterlie (1979)

Aglantha digitale (Singla 1978; Weber et al. 1982; Mackie 2004) (Fig. 3).

Second, a coordinated squeeze-type contraction is required of the subumbrellar musculature to ensure an efficient ejection of water from the subumbrella. While the oversized neurons help with rapid circular conduction, what about conduction in the radial direction? This second adaptation is found in the action potentials of the muscle cells. Efficient ejection of fluid from a biological pump requires long-duration contractions in the musculature that decreases the volume of the pump chamber (excellent examples are vertebrate hearts). In both hydromedusae and cubomedusae, the action potentials of muscle cells have been measured in hundreds of milliseconds (Table 2; Fig. 4), and these durations are reflected in the duration of contractions of the muscles used in swimming. These long-duration action potentials, however, have another important consequence. Despite the relatively slow radial conduction of excitation in subumbrellar muscle sheets, the conduction latencies for excitation of widely separated muscle cells will be within the duration of single action potentials in those muscle cells, thereby aiding in the coordinated contraction of the entire muscle sheet. For example, in the cubomedusa *Tamoya haplonema*, the swim muscles' action potentials are 200–250 ms in duration, and the conduction velocity within the
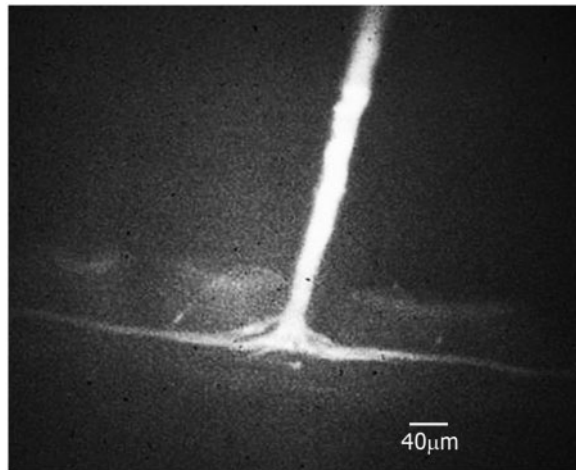
Fig. 3 Lucifer Yellow fill of a motor giant neuron overlying the radial canal of the hydromedusa *Aglantha digitale*. The lateral branches run in the inner nerve ring.
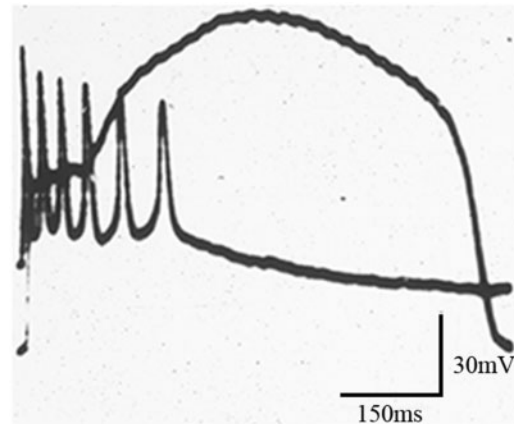
Fig. 4 Dual intracellular recording of a neuron from the inner nerve ring's motor network (burst of action potentials) and a subumbrellar muscle cell of the hydromedusa *Aequorea victoria*. The muscle's action potential is 650 ms in duration, and 120 mV in amplitude.

Table 2 Duration muscle cell action potentials from the swim system of medusae

Hydromedusae	
Polyorchis penicillatus	200 ms
Stomotoca atra	200 ms
Catablema sp.	300 ms
Euphysa japonica	200 ms
Aequorea victoria	700 ms[a]
Gonionemus vertens	200 ms
Cubomedusae	
Tamoya haplonema	250 ms

Notes: Values are maximal measured durations (see Satterlie and Spencer 1983). Value for *Tamoya* is previously unpublished.
[a]Range = 200–700 ms, and positively correlated with bell diameter.

motor nerve net is 50 cm/s. For a specimen with a subumbrellar muscle sheet that measures 5 cm from nerve ring to the top of the sheet, a muscle cell activated near the nerve ring will still be in the contraction mode when the most distant muscle cells are beginning to contract. While an initiation wave can be detected in large medusae, the long duration of action potentials (and contractions) will ensure that lags in contraction between distant muscle cells will be minimal.

Some motor nerve nets do have a directional bias (Satterlie 2002, 2008) that allows a greater velocity of conduction in the preferred anatomical direction. Even more directionality is seen in compressed nets, such as those associated with strips of radial muscle that frequently overlie radial canals (Fig. 5). In these cases, the nerve nets can function as motor nets, and also for communication between marginal nerve elements and those of the manubrium. In this way, these compressed networks may function as equivalents of nerves.

Control of two-dimensional muscle sheets—the cnidarian nerve net

The apparent lack of gap junctions in scyphozoans and cubozoans suggests that each muscle cell in the subumbrella may be activated by a motoneuron. This requires that component neurons have synaptic sites along the length of their neurites for activation of multiple muscle cells as well as for synaptic interactions with crossing neurons. Evidence in support of this morphology comes from immunohistochemical staining of the subumbrellar motor nerve nets of cubomedusae and scyphomedusae (Fig. 6). Neurites have a "blebbed" structure, sometimes having a "string-of-pearls" appearance. In the cubomedusa *Tripedalia*, the density of blebs, measured from six tubulin-immunohistochemical preparations like those shown in Figs. 1 and 6A, is similar to the estimated density of striated muscle cells, measured from four actin immunohistochemical preparations like that shown in Fig. 1 (R. A. Satterlie, unpublished data). Furthermore, electron microscopical examination of neuromuscular junctions indicates that single neurites have multiple synaptic sites, including some presynaptic elements that align with more than one postsynaptic muscle cell (Satterlie 1979) (Fig. 6). The blebs are not apparent in live carboxyfluorescein-injected neurons, suggesting they are a result of fixation-related shrinkage of the neurites.
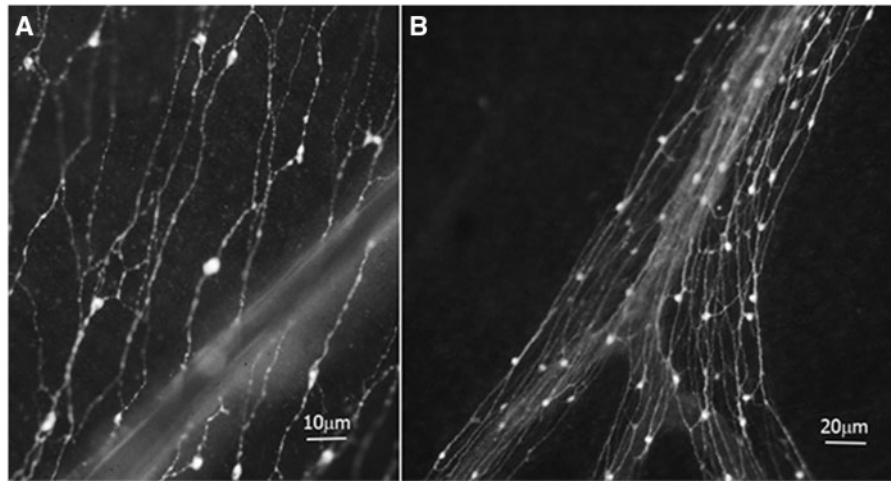
Fig. 5 (A) Directionally-biased nerve net from the subumbrella of the hydromedusa *Phialidium* sp. The primary orientation of the network is in a radial direction. (B) Compressed nerve net running along a radial canal of the hydromedusa *Proboscidactyla* sp.

## Control of two-dimensional muscle sheets—a molluscan example

In the pteropod mollusk *C. limacina*, tissue in the foot is modified into a pair of wing-like parapodia (called wings). Two layers of dorsal muscle bundles produce dorsal bending of the wings, while two layers of ventral muscle bundles produce ventral bends (Fig. 7; Satterlie 1993). Each layer of bundles forms a two-dimensional sheet, and thus presents similar issues for activation as seen in cnidarian systems of swimming, with one exception. Only one source of excitation is present—the ipsilateral pedal ganglion via the wing nerve.

The motoneurons that innervate the swim musculature have their cell bodies in the ipsilateral pedal ganglion, which is some distance from the muscle sheet (Satterlie 1991, 1993). The primary neurites that exit the pedal ganglion and run through the wing nerve to the wing, branch extensively within the appropriate muscle sheet. Slow-twitch muscle cells, which are active during slow swimming, are electrically coupled; however, both physiological and structural evidence suggests that they are individually innervated (Satterlie 1991). The fast-twitch muscle cells are recruited into activity during fast swimming, and are innervated by oversized neurons that have innervation fields throughout the entire muscle sheet (Satterlie 1991, 1993). These latter muscle cells are not electrically coupled, so individual synaptic activation is required.

The primary neurites of the motoneurons do not show evidence for synaptic contacts within the wing nerve or its primary branches (Fig. 8), so a significant portion of these neurons is specialized for rapid conduction. Once in the wing, the extensive branching gives rise to a dense array of terminals so this portion of the neurons is specialized for synaptic transmission. In contrast, the neurites of cnidarian motoneurons (those neurons that make up the motor nerve nets) simultaneously function both in conduction and in synaptic transmission. This lack of regional specialization (possibly an example of multifunctionality) may represent a significant difference between cnidarian motoneurons and those of higher invertebrates, like molluscs.

The lack of regional specialization in cnidarian neurons may represent a primitive condition and/or it could be a consequence of the unique demands of radial symmetry. With regard to the latter instance, cephalization in bilateral animals has resulted in an accumulation of anterior sensory structures, and a concomitant anterior concentration of associated neural tissue (frequently referred to as the "brain"). The close association between sensory and neural structures frequently results in a significant distance between the neural centers and the appropriate effectors. As a result, a portion of the neurites must be specialized for rapid conduction in the absence of transmission. Since excitation of broad muscle sheets in some molluscs involves a peripheral neural plexus (see Moroz et al. 1997; not seen in the *Clione* swim system), further examination of such plexuses in relation to the conduction/transmission question, is warranted. Similarly, some neurons within the cubomedusan nerve ring may function purely in transmission, although this, too, requires further examination. Certainly, the oversized neurons of the motor network within the inner nerve ring of hydromedusae also perform both conduction
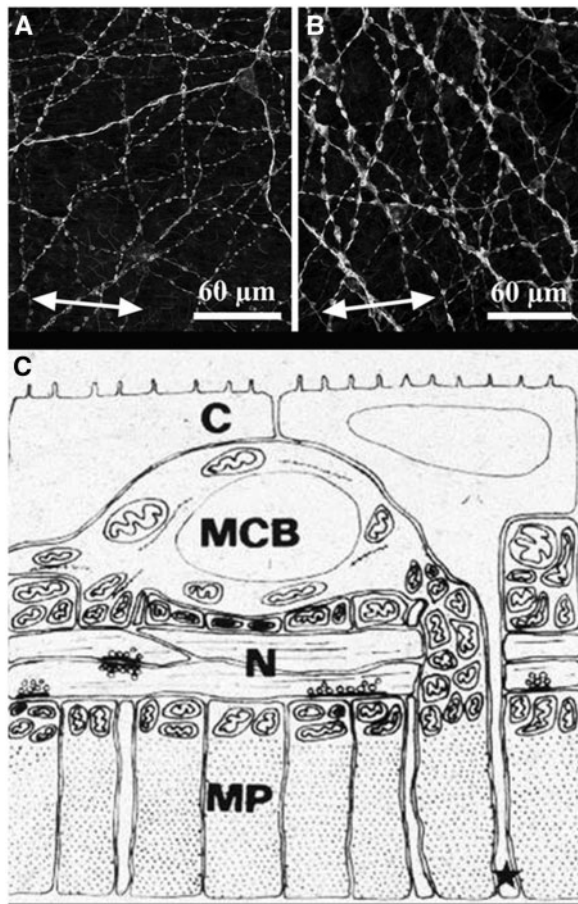
Fig. 6 Subumbrellar nerve elements of cubomedusae. (A, B) Tubulin immunoreactive neurons of the subumbrella (A) and velarium (B) of *Tripedalia cystophora*. Note the blebbed appearance of the neurites. The arrows indicate the orientation of the cells of the striated swim muscle. (C) Schematic of the innervation of swim musculature from the subumbrella of *Carybdea marsupialis* (based on electron microscopical examination). Note that a layer of neurons (N) run between the muscle cell bodies (MCBs) and the contractile processes (MPs), and that individual neurites have multiple synaptic outputs, including presynaptic terminals with more than one postsynaptic process of the muscle cell. (C) Covering cells send processes between the processes (star) of the muscle cells.

and transmission without regional specialization (Spencer and Satterlie 1980; Satterlie and Spencer 1983). Yet, other conducting systems within the nerve rings may be purely conductive (see Mackie 2004). Finally, the highly-specialized giant neurons of siphonophores and *Aglantha* should be similarly evaluated with this question in mind.

Summary

Three possibilities are considered for the origin and successful utilization of nerve nets in extant animals, and they will be considered in reverse order.

Unfortunately, the nature of the questions render them untestable by direct experimental manipulations.

The nerve net may be the most efficient way to innervate broad, two-dimensional sheets of effectors in which multiple, spatially-separated sites of excitation can activate the effectors. The lack of cephalization, or any form of circular polarity for locomotion or environmental sensing, has resulted in the appearance of multiple swim pacemakers and multiple sensory structures around the full circumference of the medusoid bell. The active pacemaker site for individual contractions used in swimming thus can shift around the bell, typically due to localized or asymmetric sensory inputs to the system. These multiple pacemaker sites activate what is essentially a single subumbrellar muscle sheet. If each pacemaker had its own dedicated, polarized conducting system for activation of the muscle sheet, such as seen in the swim system of the mollusc, *Clione*, the result would be multiple, parallel conducting routes to activation of the singular muscle sheet. The efficiency of using a single, non-polarized nerve network that allows entry of excitation from any one of a number of spatially-separated pacemaker sites is apparent. Furthermore, the organization of individual neurons within the nerve net enhances this efficiency. The non-polarized nature of the neurons and their connections, specifically symmetrical synapses, allow each individual neurite to conduct meaningful information in either direction. Furthermore, the presence of synaptic sites all along the neurites allows neuromuscular output regardless of the direction of conduction through the neurite.

The nerve net may be an adaptation to radial or biradial symmetry and its developmental history. There is no doubt that nerve nets are well suited for effector excitation in medusae for reasons mentioned above. In addition to cnidarians, nerve nets are well represented in ctenophores, which are proposed to be the most basal metazoans that have multicellular nervous systems (Moroz 2009; Watanabe et al. 2009). The suggestion of independent origins of nervous systems in these basal phyla speak to the utility of nerve nets in motor control of radially symmetrical animals (Moroz 2009). However net-like nerve plexuses are found in bilateral animals from flatworms to vertebrates, where they are used to innervate broad effector sheets or muscular layers in the walls of enteric tubular structures (e.g., Chien and Koopowitz 1977; Furness et al. 1988; Moroz et al. 1997). This suggests that the nerve net/plexus may be an adaptation to specific effector organizations regardless of body symmetry.
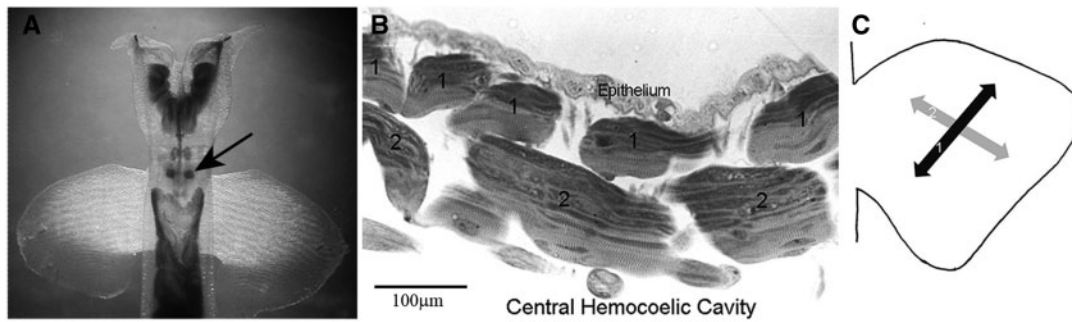
Fig. 7 (A) Live, pinned specimen of the pteropod mollusc *Clione limacina*. The wings show a cross-hatched pattern from the two layers of oblique muscle bundles (swim musculature). The arrow indicates the right pedal ganglion. (B) Histological section of the dorsal layer of swim musculature. Two layers of muscle bundles are found under the dorsal epithelium and run at nearly right angles to one another. (C) Outline of a wing with the arrows showing the orientation of the two oblique layers of muscle bundles of the dorsal swim musculature. The numbers correspond to the numbered layers in B.
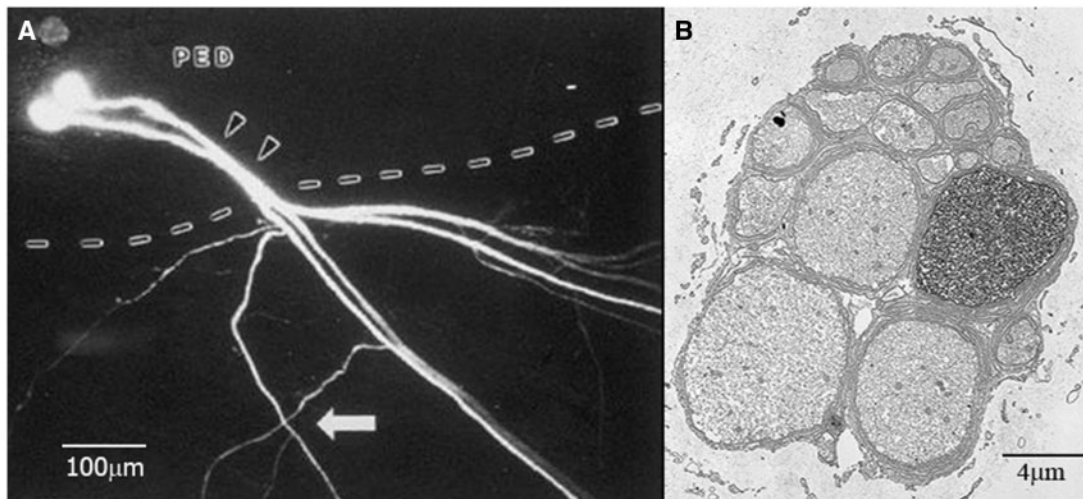
Fig. 8 Swim motoneurons of the pteropod mollusc *C. limacina*. (A) Carboxyfluorescein injection of two large motoneurons which innervate the ipsilateral wing (anterior border of the wing indicated by the dashed line). The cell bodies of the neurons are in the pedal ganglion (PED). Secondary branches of the axons of motoneurons are shown by the arrow. (B) Electron micrograph of a nerve containing a secondary branch of a large motorneuron, which was filled with Neurobiotin (dark reaction product). The filled process is 4 μm in diameter.

The nerve net may represent a primary component of nervous systems of ancestral forms at, or near, a stage representing the origin of multicellular nervous systems. We are limited in drawing conclusions of this type since we only have access to extant species. However, comparative work allows us to suggest what may be primitive features within these nervous systems. One such feature involves the structure of individual neurons. In bilateral animals, anterior–posterior polarity allowed directed locomotion in a preferred plane, and an associated anterior accumulation of sensory structures. In turn, the condensation of neural tissue in association with the sensory structures gave rise to cephalization and the development of a central nervous system.

One can argue that the close association of sensory and neural tissue placed significant distance between the integrating centers and body-wide effectors, particularly those used for movement. This necessitated a need for rapid conduction of electrical information from the central neurons to peripheral effectors (as well as for efferent conduction of sensory information). The classic neuron structure includes a distinct polarity, with one or more processes that are specialized for rapid conduction of action potentials and that lack sites either for input or output. In this case, output (synaptic) sites are restricted to branching axon terminals, so there is an anatomical and physiological specialization within these polarized neurons in which rapid conduction of electrical

information is separated from areas used for transmission of information between neurons. This is seen in the motoneurons of the mollusc *Clione*, which possess axon-like processes that allow rapid conduction between the central components of the neurons (within central ganglia) and the branching terminal processes, which contain the synaptic output sites that activate the appropriate muscle fibers. In contrast, the cnidarian neurons of the motor nerve nets do not have processes that can be considered "classic" axons. These neurons do not show anatomical or physiological polarity, as the neurites function both in conduction of electrical activity and transmission of information between cells throughout their length. This multifunctionality of neuronal processes, and the resulting lack of anatomical and physiological polarity, may be considered a primitive feature of cnidarian, and likely ctenophoran, nerve nets.

Acknowledgments

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