MORPHOLOGICAL CORRELATES OF FUNCTIONAL

DIFFERENTIATION OF NODES OF RANVIER

ALONG SINGLE FIBERS IN THE NEUROGENIC ELECTRIC

ORGAN OF THE KNIFE FISH *STERNARCHUS*

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ABSTRACT

Electric organs in Sternarchidae are of neural origin, in contrast to electric organs in other fish, which are derived from muscle. The electric organ in *Sternarchus* is composed of modified axons of spinal neurons. Fibers comprising the electric organ were studied by dissection and by light- and electron microscopy of sectioned material. The spinal electrocytes descend to the electric organ where they run anteriorly for several segments, turn sharply, and run posteriorly to end blindly at approximately the level where they enter the organ. At the level of entry into the organ, and where they turn around, the axons are about 20 μ in diameter; the nodes of Ranvier have a typical appearance with a gap of approximately 1 μ in the myelin. Anteriorly and posteriorly running parts of the fibers dilate to a diameter of approximately 100 μ, and then taper again. In proximal and central regions of anteriorly and posteriorly running parts, nodal gaps measure approximately 1 μ along the axon. In distal regions of anteriorly and posteriorly running parts are three to five large nodes with gaps measuring more than 50 μ along the fiber axis. Nodes with narrow and with wide gaps are distinguishable ultrastructurally; the first type has a typical structure, whereas the second type represents a new nodal morphology. At the typical nodes a dense cytoplasmic material is associated with the axon membrane. At large nodes, the unmyelinated axon membrane is elaborated to form a closely packed layer of irregular polypoid processes without a dense cytoplasmic undercoating. Electrophysiological data indicate that typical nodes in proximal regions of anteriorly and posteriorly running segments actively generate spikes, whereas large distal nodes are inactive and act as a series capacity. Increased membrane surface area provides a morphological correlate for this capacity. This electric organ comprises a unique neural system in which axons have evolved so as to generate external signals, an adaptation involving a functionally significant structural differentiation of nodes of Ranvier along single nerve fibers.

INTRODUCTION

In the Sternarchidae, a South American family of weakly electric gymnotids or knife fish, the electric organs are derived from peripheral nerve. This neurogenic origin contrasts with that of other electric organs, which are derived from muscle. Comparison to other gymnotids suggests that a myogenic electric organ was originally present, but that its function was taken over by its motor

nerves in the course of evolution (Bennett, 1971 a). In this respect it is interesting that the sternarchids discharge at frequencies much higher than do other electric fish, the rate varying from 700 to at least 1500 per second. The evidence for neural origin is based on light microscope examination of sections and dissection of the organ (Couceiro et al., 1955; de Oliveira Castro, 1955; Bennett, 1966, 1970, 1971 a). Single axons can be followed from the spinal cord into the organ, and are seen to comprise the entire organ, except for connective tissue and blood vessels (Bennett, 1971 a). Furthermore, curare, which blocks neuromuscular transmission and transmission from nerve to electrocyte in all other electric fish, has no effect on sternarchid organ discharge although it does block neuromuscular transmission in this group (Bennett, 1966, 1970, 1971 a).

Light microscope examination reveals characteristic changes in the nodes of Ranvier along the nerve fibers in this electric organ. We describe here two classes of nodes on the basis of differences in fine structure; one of these classes represents a new nodal morphology. The morphological differentiation of nodes is consistent with physiological data indicating functional differences along the fibers.

MATERIALS AND METHODS

Whole Fibers

For examination of single dissected fibers, fish were perfused through the conus arteriosus with a 2.5% solution of glutaraldehyde in Sorensen's phosphate buffer at pH 7.3. After perfusion, the electric organ was exposed or dissected out, and left in a 1% solution of OsO_4 in phosphate buffer for 10–25 min. Single fibers were isolated with watchmaker's forceps. They were mounted in distilled water on glass slides under cover slips, where they were examined and photographed with conventional bright-field optics. Some fibers were stained with dilute solutions of toluidine blue (0.1–0.5% in 0.5% borax), which preferentially stains nodes of Ranvier (Hess and Young, 1952).

Sectioned Material for Light and Electron Microscopy

Two fixation procedures yielded generally similar results: (a) topical application of 1% OsO_4 in Millonig's buffer (pH 7.3) to the exposed electric organ, which was removed and left in this fixative for a total of 1 hr; (b) perfusion through the conus arteriosus with 2.5% glutaraldehyde in Sorensen's buffer (pH 7.3) for 15 min, followed by removal of the organ

and immersion in this solution for a total of 2 hr, washing for 12 hr in fresh buffer, and postfixation in 1% OsO_4 in Sorensen's buffer for 45 min to 1 hr. All tissue was dehydrated in graded ethanol solutions and embedded in Epon 812. The pieces of electric organ removed for study included short lengths of the efferent spinal nerves, and they were embedded so that sections could be cut along all three major axes. The efferent nerves from some segments were embedded separately. Thick sections (1 μ) for light microscopy were cut from all blocks on Porter-Blum MT-2 and LKB ultramicrotomes and were stained with 1% toluidine blue in 0.5% borax. Thin sections for electron microscopy were cut with glass and diamond knives, and were stained with lead citrate for 2–4 min, followed by 20% uranyl acetate in absolute methanol for 10–15 min. These sections were examined and photographed with a Philips 200 electron microscope operating at 60 kv.

RESULTS

The electric organ consists of paired midline structures, located ventral to, and running parallel with, the spinal cord from the small caudal fin to just behind the head (Fig. 1). In the abdominal region, the organs lie separated just medial to the rib cage. Caudal to the abdominal cavity, the medial surfaces of the two halves of the electric organ are closely apposed, separated only by a thin connective tissue septum, ventral spinous processes, and segmental nerves running to ventral muscles and skin. The organs are covered by a connective tissue sheath and are distinctly separate from the neighboring muscle, which lies dorsally, ventrally, and laterally.

Isolated Fibers

The cell bodies of the electrocytes are located in the spinal cord. Axons descend vertically from the cord to the electric organ, where they run anteriorly for several segments (5–10 mm in a fish 15 cm long). They then turn sharply around, and run posteriorly to end blindly at about the same level at which they entered the organ or somewhat anteriorly (Fig. 1; Bennett, 1971 a). The morphology of the fibers changes characteristically along their course in the organ, as may be seen from the single dissected fiber shown in Fig. 2. At the level of entry into the organ from the spinal cord, the axon is about 20 μ in diameter, and the nodes of Ranvier have the appearance of nodes normally observed in peripheral nerve. The gap in the myelin appears about 1 μ long, and the axon is slightly constricted at the node (Fig. 2 a). The distance between nodes is 150–200 μ. As the
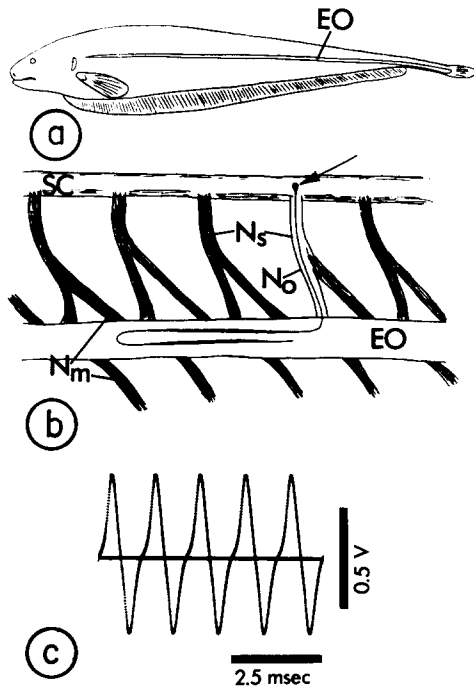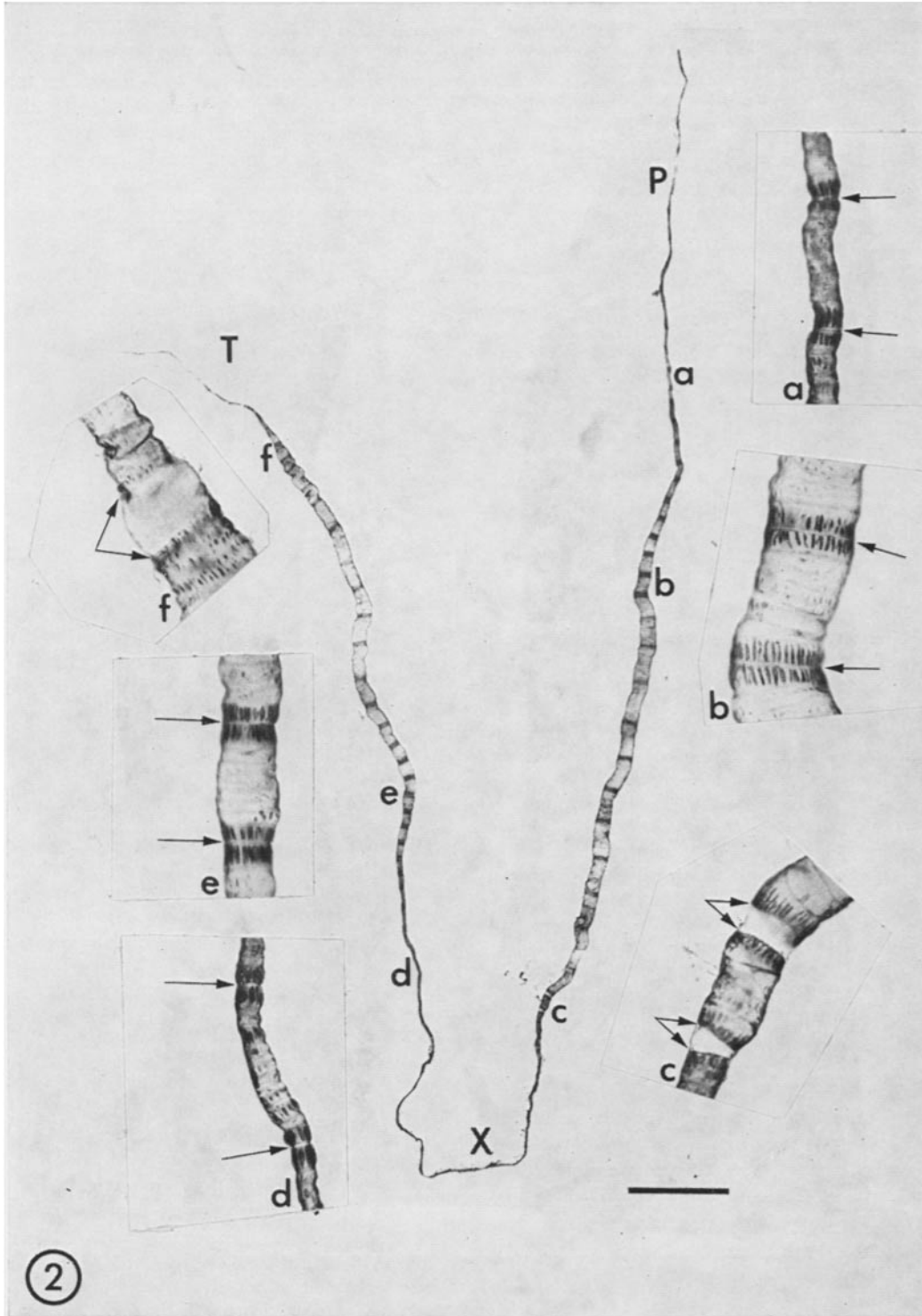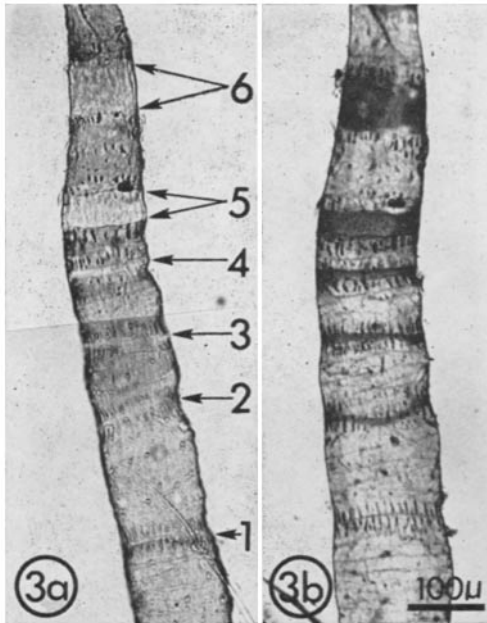
fiber runs anteriorly, it becomes dilated to 100 μ or more in diameter, and then tapers again to 10–20 μ where the fiber turns around. In the proximal, expanding region and in the central region of the anteriorly running portion, the gap at the nodes is narrow (Fig. 2 *b*). Internode distances increase to 400–500 μ in the thickest part of the fiber. In the distal tapering region (Figs. 2 *c*, 4), there are three to five nodes that are long, up to 50 μ or more measured along the axis of the fiber. The axons do not appear constricted at these large nodes. The nodes become normal again where the fiber becomes thin (less than 20 μ in diameter) and turns around. The sequence is repeated in the caudally running segment of the fiber. Anteriorly the axon is about 20 μ in diameter, with nodes about 1 μ long (Fig. 2 *d*). As the fiber continues to run caudally, it expands to a diameter of about 100 μ, and the nodes remain narrow. In the most caudal region, the nodes are very large (Figs. 2 *f*, 3) and the fiber tapers and ends blindly. A thin connective tissue strand runs somewhat farther (Fig. 5) and often ends in the sheath of the organ. Oval creaselike depressions in the myelin, with their long axes parallel to the axis of the fiber, are present in the paranodal regions at all of the nodal types described above. A fibrous sheath can be seen surrounding the axon at nodes (Fig. 4) and in internodal areas.

Visualization of large nodes in dissected fibers is enhanced by staining with dilute solutions of toluidine blue (cf. Hess and Young, 1952). Over a period of 5–10 min, the axon at the node becomes deeply stained, in contrast to myelinated regions, which take up the stain only faintly. In these preparations, nodes stand out as dense transverse bands around the axon. Fig. 3 shows part of a fiber before and after staining with toluidine blue (see also Fig. 5).

FIGURES 3 a and b Effect of staining on nodes of Ranvier in an isolated fiber from *Sternarchus* electric organ. Fig. 3 a shows the distal region of the posteriorly running part of an unstained dissected fiber. The morphology of the nodes changes in a characteristic manner. The most proximal node (*1*) measures about 1 μ along the axis of the fiber. Gaps in the myelin at the node appear as light areas. The nodes increase in size (*2–6*) along the course of the fiber, the largest nodes (*5, 6*) being located in the most distal portion (at the upper part of the figure). Fig. 3 b shows the same region from the same fiber, after staining with 0.25% toluidine blue for 5 min. The nodes appear as densely stained transverse bands on the fiber; internodal regions stain only lightly. The fiber was rotated and flattened somewhat during the staining procedure, so that it appears to have a slightly increased diameter. × 100.

Sectioned Material

Examination of sectioned material of *Sternarchus* electric organ with the light- and electron microscopes reveals that the nodes fall into two classes corresponding to the two types of nodes seen in isolated fibers. The first, those with narrow gaps, resemble typical nodes of peripheral nerve. The second, those with large gaps, exhibit a distinctive morphology involving a great elaboration of the nodal surface.

NODES WITH NARROW GAPS: The first type of node is found in both small diameter and dilated regions of the fibers. Fibers entering the

organ were identified from their small diameter (*circa* 20 μ), orientation, and medial position with respect to the organ (Fig. 6 a). They were also examined in isolated efferent nerves. Similar fibers are also present in sections through the body of the organ. Some of these fibers are oriented
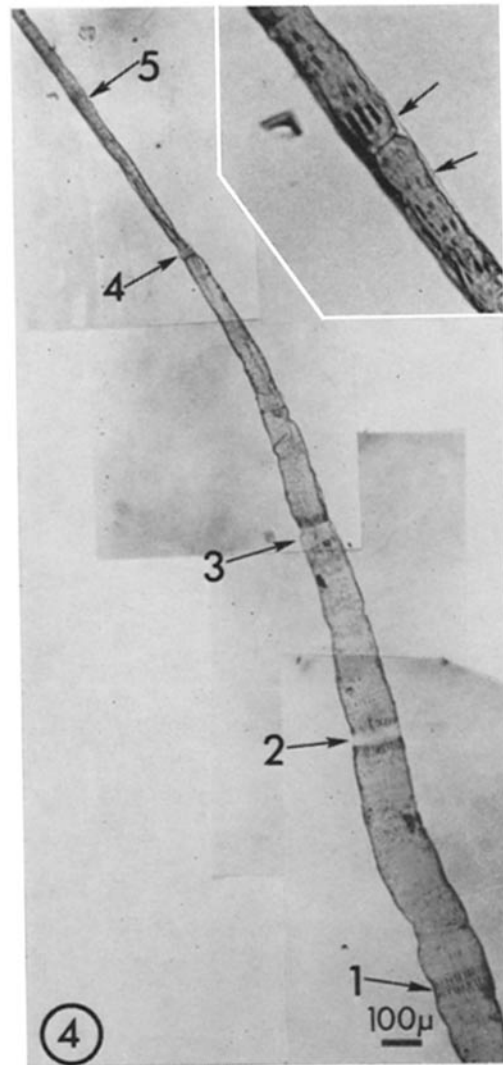
FIGURE 4 The distal part of the anteriorly running segment of an isolated fiber from *Sternarchus* electric organ. Five nodes of Ranvier are present (*1–5*). Node *1* has a narrow gap; nodes *2–4* are large; node *5*, from the region where the fiber becomes thin and turns around, is narrow. Node *5* is enlarged in the *inset*. The connective tissue sheath surrounding the fiber can be seen over the node and adjacent myelinated regions (arrows). Photomontage, × 55; *inset*, × 175.
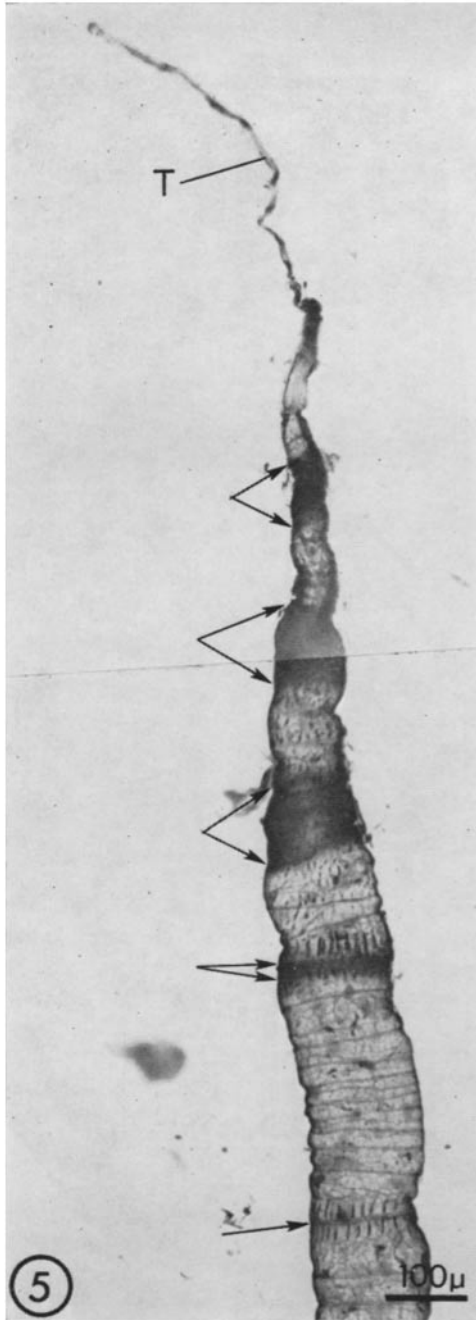
FIGURE 5 Photomontage of the terminal part of an isolated fiber from *Sternarchus* electric organ. This preparation has been stained with toluidine blue. The most proximal node (bottom arrow) is narrow. Subsequent nodes (double arrows) are enlarged, measuring from 20 μ to about 100 μ along the axis of the fiber. The fiber tapers and ends in an extension of its connective tissue sheath (T). × 100.

at approximately right angles to the large longitudinally running fibers, which indicates that they are fibers which have become thin and are turning around (Fig. 6 b). Where the fibers enter the organ and where they turn around, light micrographs show the nodes as gaps of about 1 μ in the myelin, associated with constriction of the axon (Figs. 6 a, b). The myelin in these regions is about 1 μ thick, which is somewhat greater than elsewhere along the fiber. The longitudinally oriented depressions in the myelin seen in isolated fibers near nodes frequently appear in section as deep indentations or isolated ovals.

In both regions where the fibers are of small diameter, electron micrographs show the nodes as abrupt interruptions in the myelin sheath (Fig. 7). The paranodal region (the region in which the myelin lamellae terminate) usually extends for less than 3 μ along the axis of the fiber on either side of the node. The paranodal Schwann cell cytoplasm contains mitochondria and microtubules which run circumferentially around the axon (cf. Fig. 8, inset). The axon is usually constricted slightly at the node. Stacked desmosomes are sometimes present (cf. Harkin, 1964). The axon membrane is in direct contact with the extracellular space at these nodes. The gap in the myelin at the node measures about 0.5 μ along the length of the fiber, but the extracellular channel is somewhat narrower because it is lined with the outermost layer of paranodal Schwann cytoplasm (Fig. 7, arrow). Small microvillous processes may be present within the extracellular channel, and in some sections these can be seen to originate from the Schwann cells (cf. Robertson, 1959; Elfvin, 1961). The axon membrane at the node has an irregular contour and occasionally bulges outward. Associated with the axon membrane at the node is a dense layer of cytoplasmic undercoating less than 300 A wide (Fig. 7, inset; cf. Elfvin, 1961; Peters, 1966). Elements of a tubular reticulum and some vesicles are usually present in the nodal axoplasm. A basement lamina of intermediate density extends over the nodal gap. Collagen fibers and occasionally fibroblasts are located outside the basement lamina.

Both light- and electron micrographs show the nodes with narrow gaps in dilated portions of the axons to be of similar morphology to the other narrow nodes (Fig. 6 c, Fig. 8). The narrow nodes in dilated regions must include ones from both anteriorly and posteriorly running segments of the fibers, as they comprise a single class found in
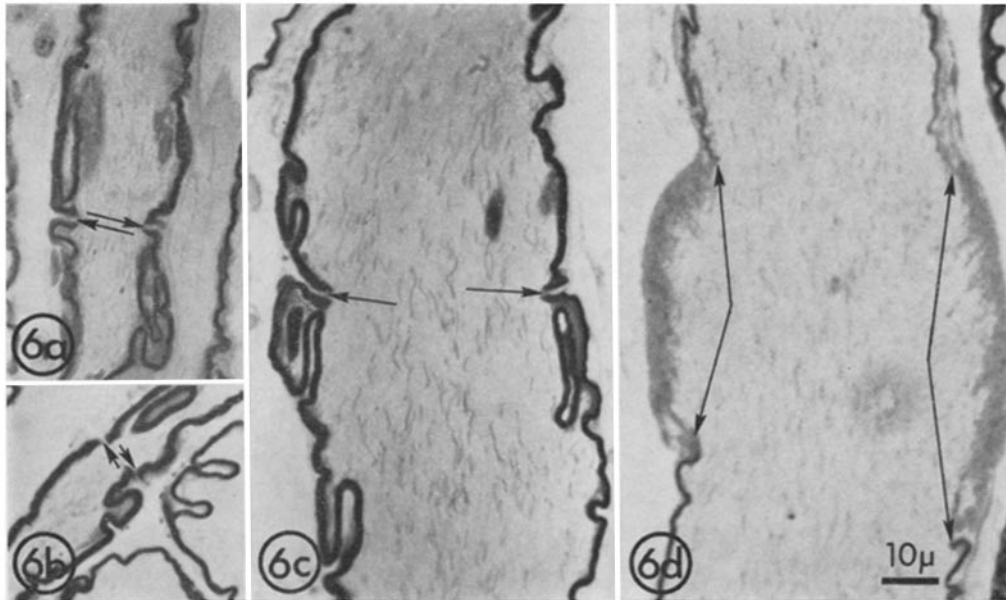
FIGURES 6 a–d   Light micrographs of thick (1 μ) sections through several types of nodes of Ranvier in *Sternarchus* electric organ. All figures show the nodes in longitudinal section. Fig. 6 a: a fiber at its site of entry into the electric organ. The nodal gap in the myelin extends for about 1 μ (arrows). Fig. 6 b: part of a thin fiber within the body of the organ. Because the fiber runs perpendicular to the other fibers in the organ, one can conclude that the section is from the region in which the fiber narrows and turns around. The arrows indicate the nodal gap. Fig. 6 c: a typical node with a narrow gap in a dilated part of the fiber (arrow). Note the folds in the paranodal myelin. Fig. 6 d: a large node, with an unmyelinated region extending for more than 40 μ, as indicated by the arrows. The surface region of the axon at the node is diffusely stained, with a suggestion of a striated appearance. × 700.

all parts of the organ. The myelin is usually about 0.5 μ thick, somewhat thinner than in the small diameter regions of the fibers. Constriction of the axon at the narrow nodes is more marked in dilated parts of the fibers, and the myelin can give the appearance of abruptly indenting the axon in the paranodal region. Indentations or ovals from sectioning of the longitudinal depressions in the paranodal myelin are a common feature. As at the nodes in small diameter regions, a distinct channel from the axon membrane to the extracellular space is always present (Fig. 8, arrow).

FIGURE 7   Electron micrograph of a section through a node of Ranvier, from a 15 μ diameter fiber in the efferent nerve to the electric organ. In this and all subsequent micrographs, the axis of the fiber runs vertically from top to bottom of the page. The axoplasm (a) contains neurofilaments, vesicles, and elements of a tubular reticulum. Associated with the axon surface at the node is a dense cytoplasmic layer about 200 A thick. A distinct extracellular channel, less than 0.5 μ wide, runs to the axon membrane (arrow). The *inset* shows the axon membrane at a node from a larger fiber within the electric organ. Note the dense cytoplasmic undercoating associated with the axon membrane at the node (arrow) Glutaraldehyde-OsO₄ , × 27,000; *inset*, × 42,000.

FIGURE 8   Electron micrograph of a section through a node of Ranvier from a dilated (60 μ) part of a fiber within the electric organ. The axoplasm at this node (a) contains neurofilaments oriented parallel to the axis of the fiber. Microtubules within the paranodal Schwann cell cytoplasm (enlarged in *inset*) run circumferentially around the axon. The arrow indicates the extracellular gap at the node. Glutaraldehyde-OsO₄, × 27,000; *inset*, × 52,000.
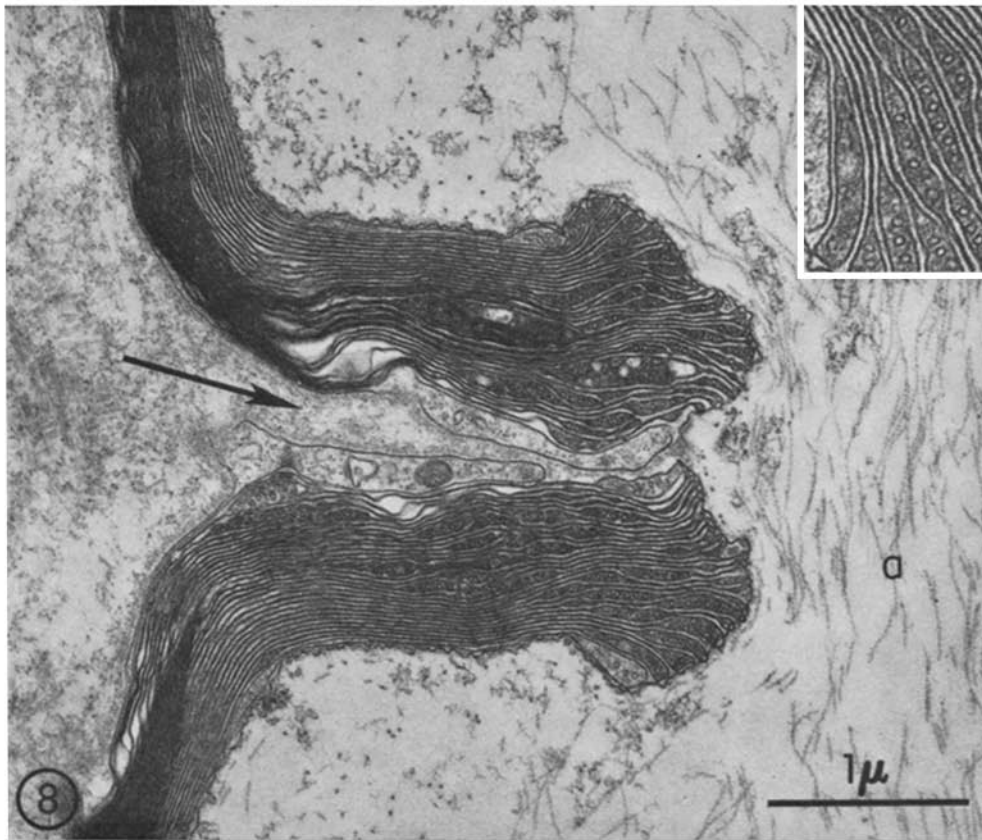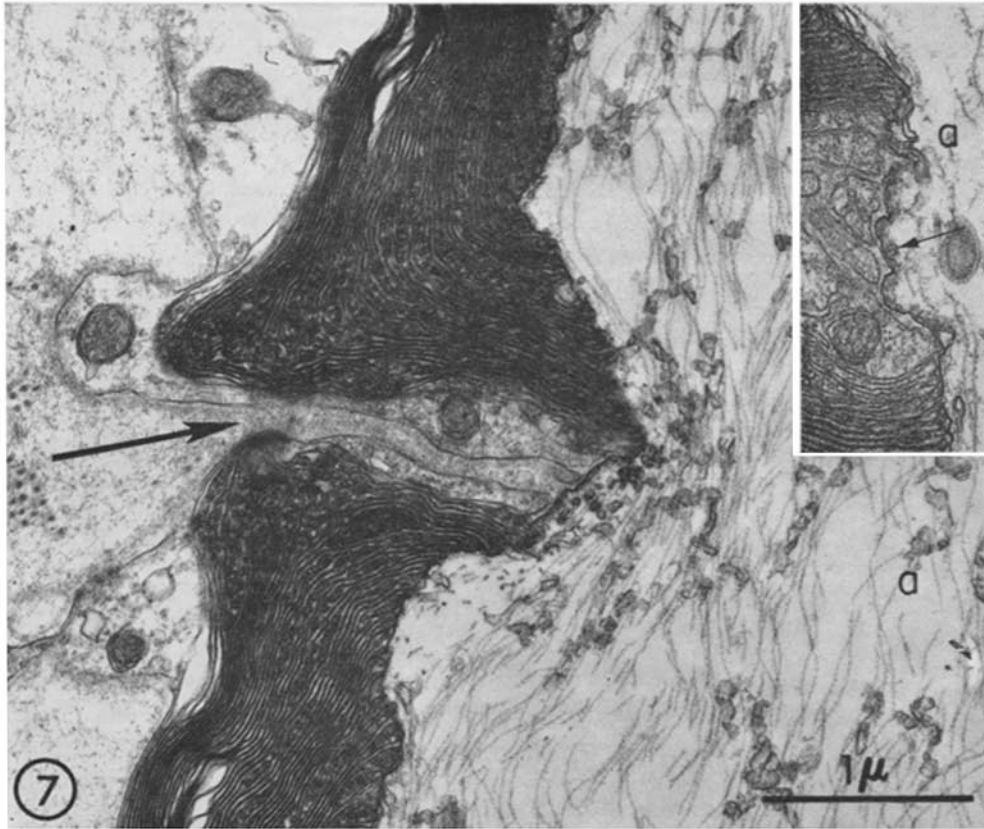
NODES WITH LARGE GAPS AND SURFACE ELABORATIONS: A second type of node is present in sections of dilated regions of the fibers; these correspond to the large nodes seen in isolated fibers. Again, the distribution indicates that these nodes are from both anteriorly and posteriorly running segments of the fibers. In light micrographs the axonal surface exhibits a thick layer of denser staining with poorly defined striations perpendicular to the axis of the fiber (Fig. 6 d). In electron micrographs this layer is revealed as a striking proliferation of the axon membrane, which is elaborated to form a large number of irregular polypoid processes over the entire unmyelinated nodal surface (Figs. 9, 10). In cross-section these processes are roughly circular in outline and between 800 A and 5000 A in diameter. Examination of serial sections indicates that each process is in continuity with the axon. Although the protrusions themselves run irregular courses, they are separated from each other by narrow regions of extracellular space, and form a discrete layer, usually less than 5 μ thick. Parts of the outer layer of axonal processes are covered by a basement lamina, and some of this material extends into the spaces between the processes. Fibroblasts and collagen fibers in turn surround the outer margin of the basement lamina.

The myelin is thinner near the large nodes than in other regions of the fiber. The paranodal regions can extend relatively great distances, at least as far as 40 μ (Fig. 9). A further specialization at these nodes is the increased frequency with which mitochondria are present in the axoplasm immediately subjacent to the nodal elaborations. The core of the axon at the node contains numerous longitudinally oriented neurofilaments, mitochondria with a similar orientation, and elements of a tubular reticulum. This reticulum is more prominent in nodal than in internodal axoplasm. Occasional clear membrane-bounded vesicles, 400–800 A in diameter, are also present in the nodal axoplasm. While mitochondria within the core of the axon are oriented parallel to the axis of the fiber, mitochondria subjacent to the nodal surface have no simple orientation. The irregular axonal processes contain electron-lucent cytoplasm. Rarely, the profiles of small mitochondria or multivesicular bodies are present within the axonal processes. The dense cytoplasmic material associated with the axon membrane at narrow nodes is not present at the enlarged nodes after fixation with either osmium tetroxide or glutaraldehyde, although its presence can be demonstrated in the same specimens at the nodes with narrow gaps.

DISCUSSION

The present study demonstrates a structural variation in nodes of Ranvier along single fibers from *Sternarchus* electric organ. Two types of nodes may be distinguished on the basis of fine structure; one of these represents a new nodal morphology. The structural differentiation of nodes is consistent with physiological differences that will be described below.

The fibers described in this report comprise a neurogenic electric organ. The fine structural studies confirm and extend earlier light microscope data indicating that the fibers are modified axons which end blindly (Bennett, 1970, 1971 a). Although we have not studied the morphology of the blind endings in a definitive manner, we have encountered, in studies of sections through the organ, processes which appear to be the terminations of these fibers. We have also seen bundles of collagen fibers that apparently represent the connective tissue strands extending beyond the blind tips of the axons (Figs. 2, 5). The structure of these unique nerve endings will be the subject of a future report.

As in other electric fish, the electric signal from *Sternarchus* represents the summated activity of many electrocytes which discharge synchronously. The discharge in *Sternarchus* consists of diphasic pulses (initially head-positive). Physiological data indicate that impulses propagate to involve both anteriorly and posteriorly running segments of the axons, the first generating the head-positive phase and the second generating the head-negative phase of the discharge (Bennett, 1971 a).

The conclusions from microelectrode studies are summarized in Fig. 11 a. Intracellular recordings are diagrammed in the center column as they would be obtained at the sites indicated in the diagram of the electrocyte on the left. The directions of current flow during the two successive phases are indicated for the electrocyte drawn on the right, the light areas of which represent nodes of Ranvier. A single cycle of externally recorded organ discharge is shown in the uppermost trace of the center column. During the head-positive phase the narrow nodes at the posterior of the anteriorly running segment become active, and pass inward current. Large nodes at the an-
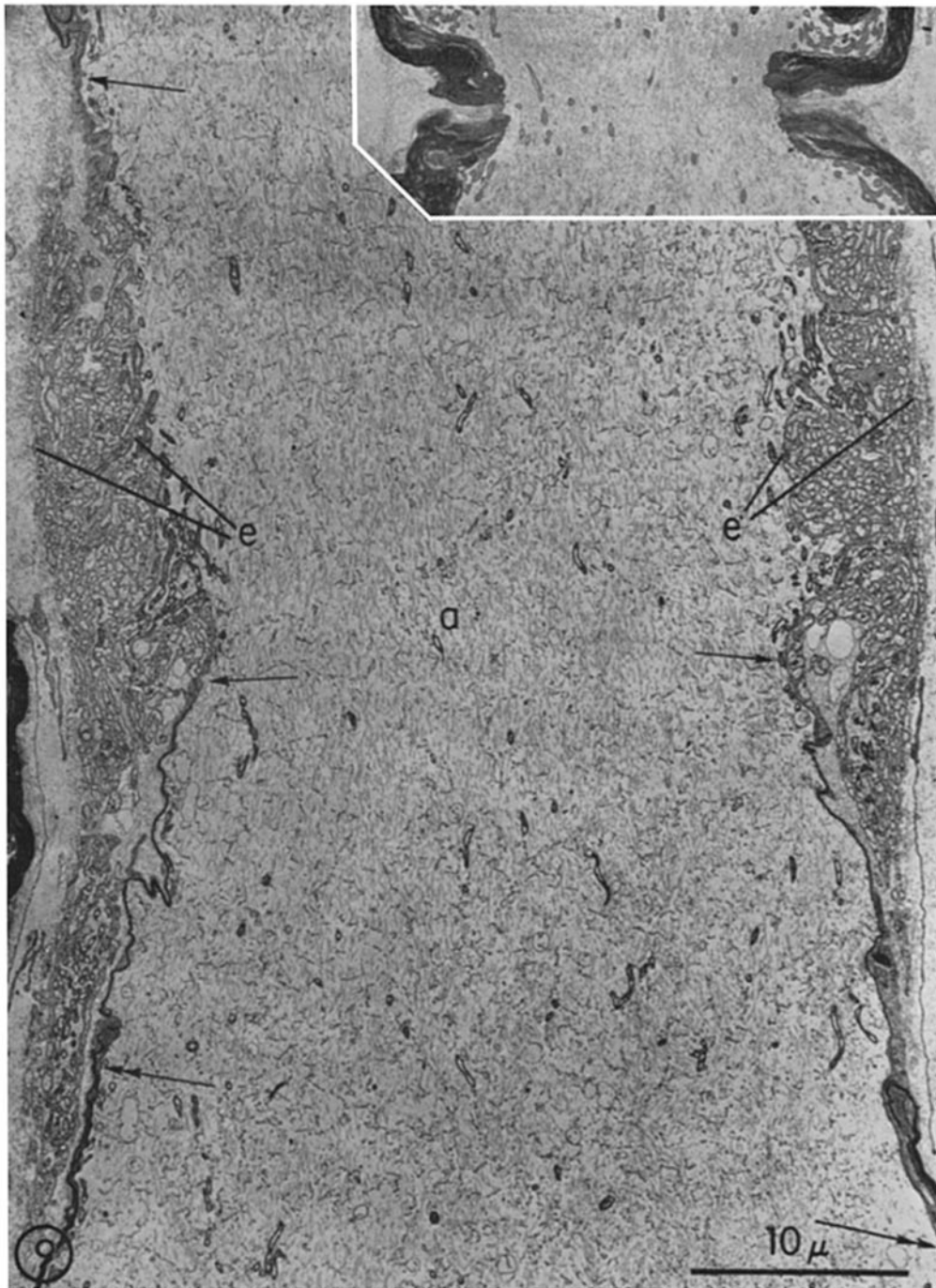
FIGURE 9 Electron micrograph of a large node with surface elaborations. Numerous polypoid processes from the axon surface (a) form a layer about 5 μ thick around the unmyelinated region at the node (e). The terminations of the myelin sheath are indicated by arrows. The paranodal region (in which the myelin terminates layer by layer) extends to the double-headed arrows. The unmyelinated area extends for approximately 30 μ along the axis of the fiber. The *inset* shows, for comparison, a node of Ranvier from a fiber near its site of entry into the organ, at the same magnification. The gap in the myelin measures less than 1 μ along the axis of the fiber. OsO₄; × 3000.

terior of this segment are inexcitable and pass only outward current (arrows on left part of the right diagram). During this phase a large action potential is recorded in the proximal region of the anteriorly running segment and the potential becomes markedly smaller and somewhat delayed more anteriorly. Thus, during this phase current runs anteriorly through the core of this segment of the electrocyte and from head to tail in the external circuit, thereby generating head positivity. The reduced spike at the anterior end of the anteriorly running segment is able to excite ordinary narrow nodes in this region and the impulse propagates around to invade the posteriorly running segment of the fiber. The head-negative phase is then generated in the same manner as the head-positive phase. Active narrow nodes at the anterior of the posteriorly running segment pass inward current and the inexcitable large nodes at the posterior pass outward current. The action potential is large at the proximal end of the posteriorly running segment and decrements markedly in reaching the distal end. Current flows caudally in the fiber core and from tail to head in the external medium to generate the head-negative phase. (During each phase some "external" current flows back through the segment which is inactive during that phase; the external potentials are small enough that these currents have no effect on organ function and they constitute only a small fraction of the total current.)

As would be expected the space constant is quite large in the dilated regions of the fibers, which must increase the generation of external fields. It is not clear whether narrow nodes in the dilated regions become active. The reduction in spike amplitude moving distally along each segment could represent loading by the large area of the inexcitable nodes as well as decrement in passive propagation from active nodes restricted

to the proximal regions. In the earlier light microscope studies, it appeared that nodes in the proximal portion of the anteriorly running and posteriorly running segments were somewhat larger (Bennett, 1971 a). Although there may be some differentiation of nodal regions in these parts of the fibers, gap width is not markedly greater. Gap width varies somewhat at single nodes and it is still possible that there is a modest difference in area at these nodes. However, narrow nodes in the large diameter regions certainly have a considerably greater area than narrow nodes in small diameter regions.

A number of data indicate that the inactive large nodes act as a series capacity. The evidence is essentially that there is no net current flow averaged over a single discharge cycle. How a series capacity prevents net current flow may be understood with reference to the equivalent circuit in Fig. 11 b. During the initial part of an action potential current enters the fiber at active nodes, flows axially along the axon, leaves the fiber through the series capacity, and returns through the low resistance of the external medium across which the external potential is recorded. During this period the charge on the series capacity becomes more positive. At some point on the falling phase of the action potential, the charge on the capacity exceeds the potential generated by the active membrane and current begins to flow in the opposite direction. During firing at a steady frequency the capacity cannot continue to accumulate or lose net charge. Thus, in the steady state the integrated current flows during head-positive and head-negative phases of a discharge must be equal, and when the potential recorded across the external resistance is averaged over a complete discharge cycle, the result is zero (Fig. 1).

A diphasic discharge without net current flow can also result from two successive monophasic

FIGURE 10 a The gap in the myelin at an elaborated node. The axis of the fiber runs vertically, from top to bottom of the page. The paranodal region begins at the double-headed arrows, and the nodal bare area extends between the single-headed arrows. The axon surface is elaborated to form a layer of irregular processes (e). The axon (a) contains numerous neurofilaments, as well as mitochondria (m) which are especially common subjacent to the surface elaborations. Attenuated processes of fibroblasts (f) surround the network of processes at the node. The bar indicates 1 μ. Glutaraldehyde-OsO$_4$; $\times$ 12,000.
FIGURE 10 b Part of the node shown in Fig. 10 a, at the same magnification as Fig. 7 and 8. The polypoid processes contain electron-lucent cytoplasm with few organelles. There is no dense undercoating of the axon (a) membranes in this region. $\times$ 27,000.
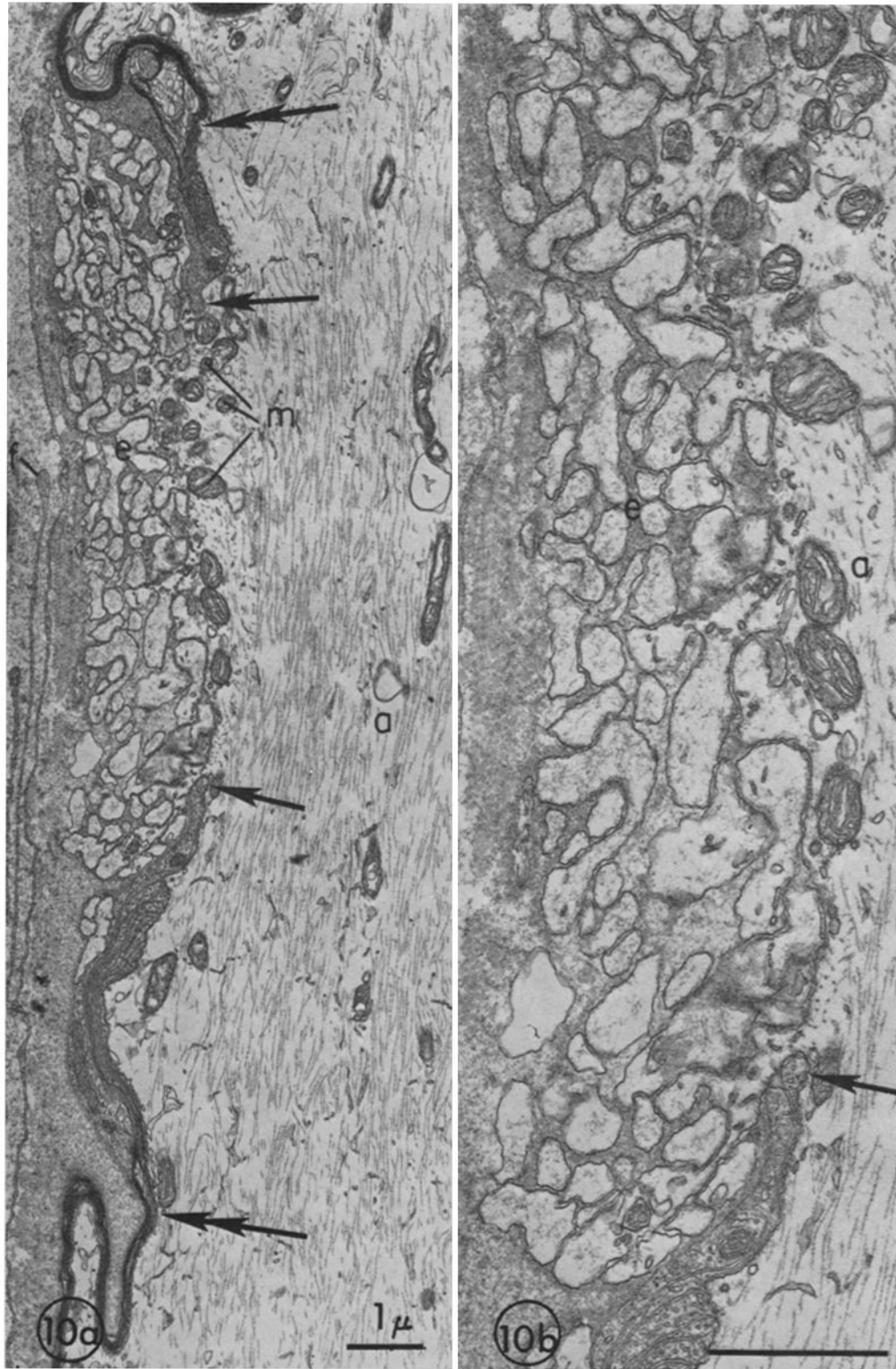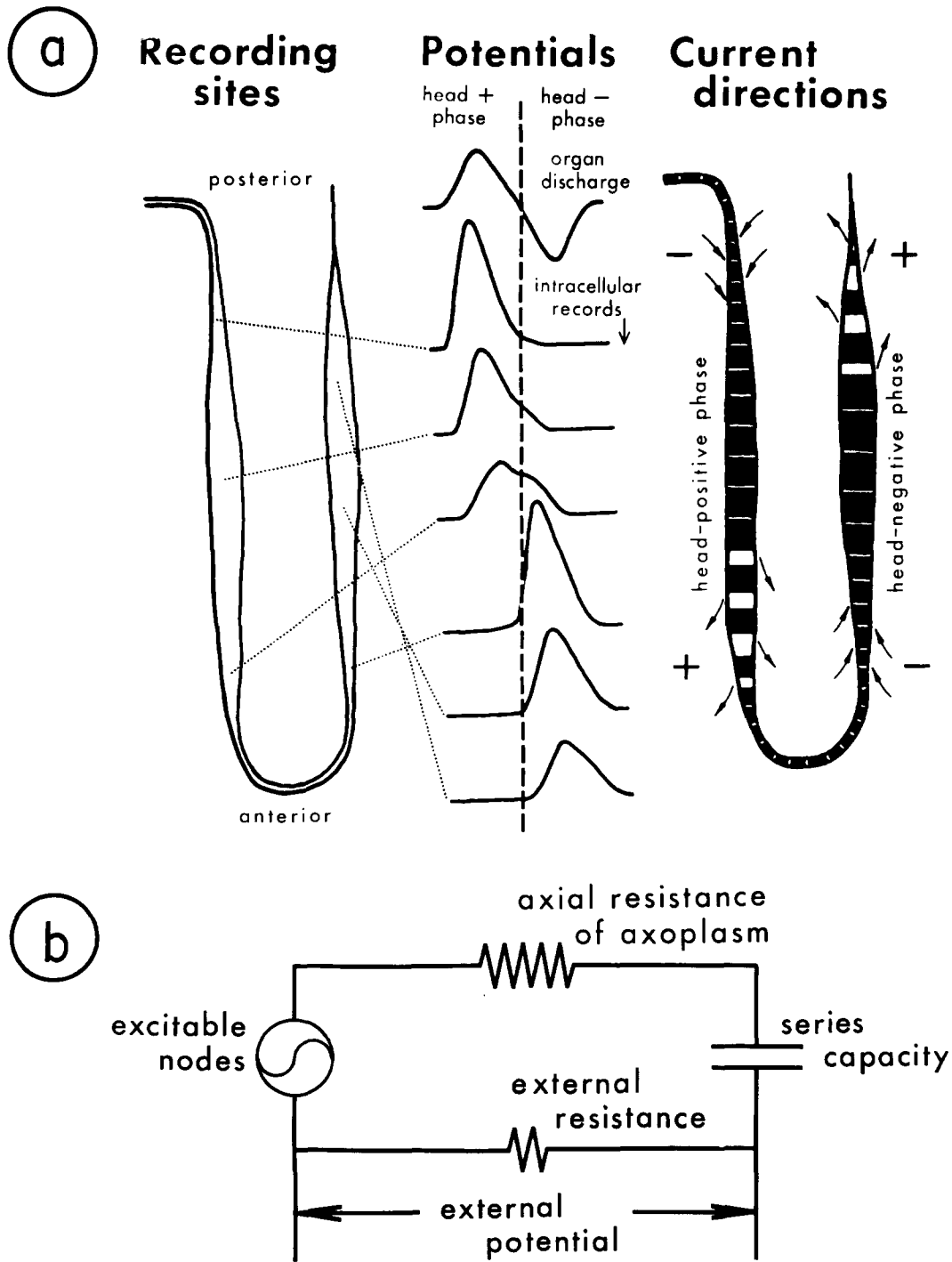
FIGURE 11   Electrocyte function during organ discharge. Fig. 11 *a*: diagrams of intracellular potentials and directions of current flow during electrocyte activity generating the head-positive and head-negative phases of organ discharge. The central column represents organ discharge on the upper line and intracellular recordings on the lower lines at the sites indicated in the diagram of an electrocyte on the left. The directions of current flow during the two phases are indicated on the right diagram. (Modified from Bennett, 1971 *a*). Fig. 11 *b*: equivalent circuit of an electrocyte segment to illustrate the effect of a series capacity.

discharges that are oppositely oriented. In this mechanism each phase is generated as in Fig. 11 except that one surface of the electrocyte behaves as a series resistance instead of a series capacity. It was initially thought that this mechanism might be found in *Sternarchus*, anteriorly and posteriorly running segments generating the two phases. However, when propagation between the two segments is blocked by anoxia, the discharge still exhibits no net current flow, and thus the output of each segment must exhibit no net current flow. Furthermore, in other sternarchid species in which the anteriorly running segments of the electrocytes are reduced or absent, the active head-negative phase of the discharge is reduced or absent, but there is still no net current flow (Bennett, 1971 *a*).

The proposal that one surface of the electrocytes acts as a series capacity is supported by data from the African electric fish *Gymnarchus* (Bennett, 1971 *a*). This species has myogenic electrocytes which are more accessible for microelectrode studies, and one surface of the cell has been directly shown to act as a series capacity.

The large nodes located in the distal parts of the dilated anteriorly running and posteriorly running segments have an extraordinarily large surface. The large area provided by the diameter and length of the unmyelinated region at the node (which can exceed 50 μ along the axis of the fiber) is markedly augmented by the polypoid elaborations of the axon membrane. This extensive area provides a morphological basis for the series capacity indicated by physiological and comparative data. On the reasonable assumption that the capacity per unit area of this membrane is similar to that of other cell membranes (1 μ F/cm^2; cf. Bennett, 1970, 1971 *a*), the capacity of these nodes is greatly increased. For them to act as a series capacity, it is necessary that the membrane time constant be long compared to the duration of the action potential. This requires the membrane resistivity to be high compared to that of ordinary nodes of Ranvier (but not necessarily higher than that of many other membranes). This requirement is not contradicted by the morphological data.

Membranes acting as a series capacity occur in receptor cells of certain electroreceptors and in at least the one electrocyte noted above (Bennett, 1970, 1971 *a*, 1971 *b*). In both electrocytes (Schwartz, 1968; Schwartz and Pappas, 1968) and receptor cells (cf. Bennett, 1971 *b*), the mem-

branes are greatly elaborated as in the *Stenarchus* electrocytes. In fine structural studies of eight different teloest electric organs derived from muscle, it was found that membrane invaginations increased the surface area of all electrocytes, but that the increase in surface area was most marked for electrically inexcitable regions of the cells, those which have a low resistivity and act as a series resistance as well as those which have a high resistivity and act as a series capacity (Schwartz, 1968; Schwartz and Pappas, 1968). Similar findings apply to membranes acting as a series resistance in strongly electric organs (cf. Bennett, 1971 *a*). The morphological techniques available do not yet distinguish between membranes of high and low resistivity.

The role of nodes of Ranvier in saltatory conduction is firmly established. Rushton (1951) has argued that myelinated fibers of ordinary peripheral nerve are "designed" so as to maximize conduction velocity for fibers of any given diameter. However, it is probable that the functions of some nerve fibers require different characteristics. Morphological studies of neuropil from the teleost (Waxman, 1970; Waxman and Bennett, 1970) and mammalian central nervous system (Waxman and Melker, 1971) have demonstrated that the pattern of myelination of preterminal fibers differs from the pattern in peripheral nerve, in that the nodes of Ranvier are closely spaced. Nodal surface area in preterminal fibers may also be somewhat increased, and it has been suggested that variations in patterns of myelination and nodal structure could modulate spatiotemporal patterning of impulses (Waxman, 1971). There is evidence that at some nodes, conduction is blocked at specific frequencies (Wall et al., 1956) and there are some physiological data which suggest that more complex filtering of spike trains occurs at regions of low safety factor, i.e., nodes or branch points (Chung et al., 1970). Axons act as delay lines for synchronization of firing of the electric organ in the electric eel (Bennett, 1971 *a*); in this case the fibers are not myelinated in the manner required for maximal conduction velocity in that the ratios of myelin thickness and internode distance to fiber diameter are too small (Meszler and Bennett, 1972). These ratios of myelin thickness and internode distance to fiber diameter are also considerably smaller along the *Sternarchus* electrocytes than previously reported for most nerves, including teleost lateral line nerves (Thomas and Young, 1949). The function of the

electrocytes is quite different from that of ordinary nerve fibers, and apparently does not require maximization of conduction velocity

The *Sternarchus* electric organ provides an example of a unique neural system in which myelinated nerve fibers act so as to transform action potentials into diphasic external signals, and in which nodes of Ranvier are structurally differentiated in a manner referable to physiological specializations. It also presents interesting problems in developmental neurobiology, particularly with respect to the relations between neurons and glia and the specificity of regional differentiation of the axonal surface.

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