sponding in short bursts of impulses, (*b*) initial frequency of responding as a function of the intensity of the stimulus, (*c*) probability of at least *n* impulses as a function of intensity, (*d*) average number of impulses in response to brief stimuli as a function of the intensity of the stimulus, and (*e*) latency of response as a function of the duration and intensity of the stimulus.

* This work was supported by a contract between the Office of Naval Research and Columbia University.

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*THE STRUCTURE OF THE SCHWANN CELL AND ITS RELATION TO THE AXON IN CERTAIN INVERTEBRATE NERVE FIBERS**

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So far as we are aware, it is a general rule that, in all types of peripheral nerve fibers capable of conducting propagated impulses, the axon (axoplasm) is separated from the exterior by Schwann cells. In heavily myelinated vertebrate fibers, Schwann cell constituents can be recognized chiefly by the nucleus which lies exterior to the myelin and by the cytoplasmic inclusions and limiting membranes visible at the node of Ranvier.[1, 2] In myelinated invertebrate fibers, such as those of prawns and shrimps, the nucleus and cytoplasmic constituents lie on the inside surface of the myelin;[3] so far as we know, no electron microscope description of these fibers has as yet appeared. Unmyelinated vertebrate fibers, particularly the very thin "C" fibers, were shown by Gasser[1, 4] to lie within the protoplasm of the Schwann plasmodium. The smaller fibers of squid and lobster nerves appear to resemble the vertebrate "C" fibers in that a number of fibers share common Schwann cells. In the squid giant and medium-sized fibers and in larger lobster fibers the Schwann cells lie around the axon, the nuclei indenting the axon.

The bioelectrically active surface membrane, whose properties have long been the object of study by electrophysiologists, would appear to be a constituent of the Schwann cell or to bound this cell. Accordingly, the detailed structure of this region of the fiber is of interest not only to the morphologist but also to the physiologist. Detailed description of our own studies of invertebrate nerve fibers, as viewed in thin sections with the electron microscope, will be given elsewhere. In the present brief report we wish to stress the membranous structures which occur in the Schwann cell and particularly the axon–Schwann cell interface, the special properties of which suggest that it may play an important role in the active processes of nerve.

METHODS

The squid giant fibers and the nerves of the walking legs of the lobster were excised in chilled sea water and immediately fixed in 1 per cent OsO_4 in buffered sea water (artificial sea water, according to Hodgkin and Katz[5] or Harvey[6]). Imbedding was in normal butyl methacrylate (occasionally mixed with 5 per cent methyl methacrylate). Sectioning was done with the Minot microtome as modified by Geren and McCulloch.[7] An RCA Model EMU-2 electron microscope equipped with an objective aperture was used.

RESULTS

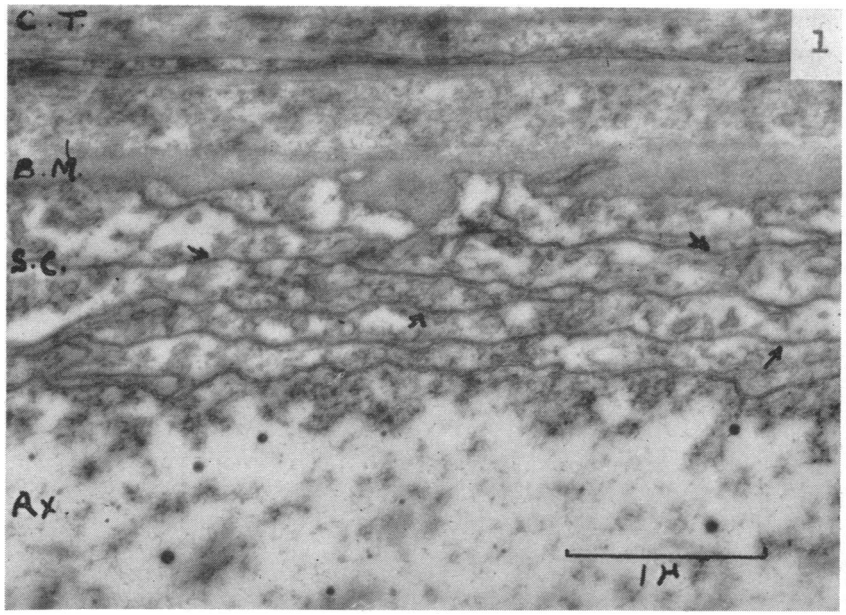
The Schwann cell may be extremely thin (except, of course, in the neighborhood of the nucleus). In the squid giant fiber it is of the order of 0.5 μ (0.2–1.0 μ) thick. In the lobster fibers the thickness may be similar, although in some cases the cell may be only 0.1 μ or less in thickness. The surface-to-volume ratio of these Schwann cells is obviously very high. In the squid giant fiber the volume of the Schwann cell is of the order of 1 per cent of that of the axon. However, this small protoplasmic mass and its limiting membrane may play a highly important role in nerve-fiber activity.

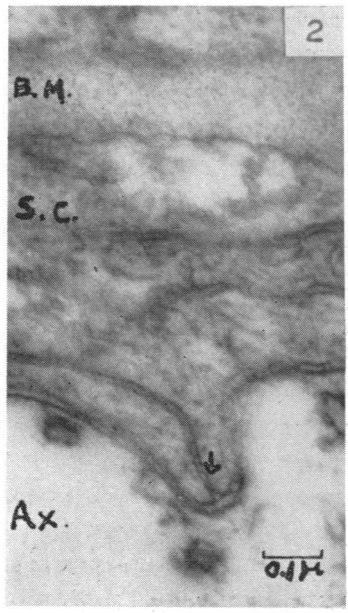
Despite its thinness, the Schwann cell protoplasm contains occasional spheroidal mitochondria having structures similar to that to be described below. Other structures commonly observed in active cells, such as endoplasmic reticulum (either as diffuse lacework or as a tubular apparatus), Golgi material, etc., were not conspicuous, although no careful study has thus far been made of the Schwann cell protoplasm as such.

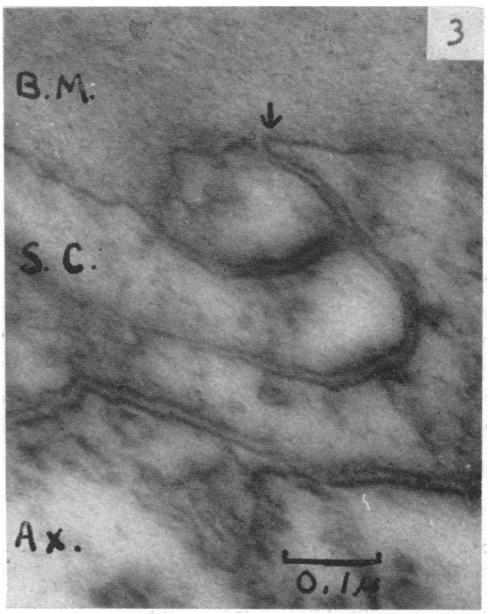
1. *Intracellular Dense Membranes.*—Within the Schwann cytoplasm of the squid giant fiber there are several (3–6) layers, each about 150–250 A thick and showing a double-contoured structure with dense osmiophilic borders (Pl. I, Figs. 1–3). A similar layer can usually be seen at the axon–Schwann cell interface. The intracellular layers may appear to be rather convoluted, arising from the single dense membrane at the outer surface of the Schwann cell (Pl. I, Fig. 3) and, by a tortuous

FIGS. 1–3.—Transverse sections through Schwann cell region of squid giant fibers. Fig. 1, note dense, osmiophilic layers (*arrows*). Fig. 2, continuity of intracytoplasmic membrane with limiting membrane at axon–Schwann cell interface. Fig. 3, continuity of intracytoplasmic membranes with dense layer (single) at outer surface of Schwann cell. Abbreviations: *Ax*, axoplasm; *B.M.*, basement membrane; *C.T.*, connective tissue; *C.T.C.*, connective-tissue cell; *M*, mitochondria; *S.C.*, Schwann cell cytoplasm.

PLATE I







course, reaching the axon–Schwann cell boundary (Pl. I, Fig. 2). Such cases may, in fact, represent the junction of two Schwann cells. Except for the outer boundary, beneath the basement membrane, the layers are double-contoured. In the lobster fibers usually only the double-contoured membrane at the axon–Schwann cell interface and the thin membrane at the outer boundary may be seen, although occasionally one other intracytoplasmic dense, double-contoured layer may be seen.

It seems reasonable to identify these layers with lipid-protein, myelin-like layers. Their borders are osmiophilic, and they have a thickness equal, within the resolution available, to those of the myelin sheath as demonstrated by X-ray diffraction methods[8, 9] but different from the layer thickness observed by electron microscopy.[10] They may be similar in nature to those recently observed within the cytoplasm of various types of cells.

If squid nerve fibers are immersed in an artificial sea water devoid of Ca or Mg ions and are fixed in 1 per cent osmic acid in this medium or if, to the fixative, sufficient versene is added to deionize the divalent cations in sea water and in the nerve fiber, the dense-edged double membranes are observed to be spread apart. Thus divalent cations are implicated in the structural integrity of the intracytoplasmic dense-edge membranes, and the apparent width and shape of such membranes in sections is dependent on the local ionic environment. X-ray diffraction studies[11] of nerve lipid double layers in dispersions of univalent and divalent cations at varying ionic strengths have shown marked differences in the effects, on the distances between double layers, of sodium or potassium ions as compared with calcium ions. Since one can observe, in electron micrographs of fixed and sectioned preparations of purified lipids, spacings comparable to those obtained from X-ray diffraction data,[12] it should soon be possible, by detailed studies of model systems, to clarify the molecular composition of the dense-edged lipid-protein double layers as seen in the electron micrographs (see also Finean[13]).

2. *The Metatropic Reaction.*—As a result of a study of the so-called "metatropic" reaction of Göthlin,[14] Bear and Schmitt[15] showed that the relationship between the sign and magnitude of birefringence manifested by the exterior region of invertebrate nerve fibers and the refractive index of the immersion media indicated the presence of lipid and protein molecules oriented in the same manner as in the myelin sheath of vertebrate fibers; a difference was that the lipid was present in very much lower concentration. The oriented lipids were thought to exist in a "sheath" surrounding the axon. These studies were extended to the squid giant fiber by Bear, Schmitt, and Young,[16] who interpreted their results to indicate the existence of a myelin-containing layer analogous to the "metatropic sheath" of crustacean fibers, "lying immediately next to the axis cylinder, as belonging to cells presumably analogous to the Schwann sheath cells of vertebrate fibers. As in the fibers of prawns and shrimps and opposed to the relation in vertebrate axons, these cells lie inside the myelin-containing layer, being placed between it and the axis cylinder." The thickness of the metatropic sheath in the squid giant fiber was estimated to be of the order of 3–4 μ. In their illustrations (Pl. I, Figs. 1 and 2) Bear, Schmitt, and Young indicated that the "myelin-containing" layer surrounds the Schwann cell.

Examination of thin sections of invertebrate fibers with the electron microscope has greatly extended these observations and has permitted a more accurate description of the structural basis of the metatropic reaction. As a result of eary studies of thin sections of squid giant nerve fibers in this laboratory,[7, 17] it was observed that the Schwann cell is bounded on the peripheral side by a layer 0.1–0.2 μ thick which could be readily differentiated structurally from the surrounding connective tissue. Because it was located in the region expected of the metatropic "sheath," this rather amorphous, somewhat dense layer was tentatively known among ourselves as the "M" layer.

Further study caused us to regard the rather amorphous "M" layer as a kind of basement membrane of the Schwann cell, having no obvious relation to oriented lipid-protein layers or to the metatropic reaction as observed in the squid giant fiber. At its outer surface, bounding the connective tissue, this layer has a smooth contour, while the inner boundary is markedly contorted (Pl. I, Fig. 1) Lobster fibers (of a size in which the metatropic reaction may readily be demonstrated) possess no such basement membrane or any other "sheath"-like structure belonging to the nerve fiber itself, peripheral to the Schwann cell. What, then, is responsible for the metatropic reaction in such fibers?

Bear, Schmitt, and Young[16] estimated the thickness of the metatropic sheath to be about 3 μ. From electron micrographs of transverse sections of squid giant fibers we see that the Schwann cell is but about 0.5 μ in thickness and, outside the basement membrane of the Schwann cell, collagen filaments of the connective tissue are closely packed. Between layers of collagen filaments are also seen the thin processes of the elongate connective-tissue cells. If Bear, Schmitt, and Young were correct about the thickness of the metatropic sheath, the connective tissue would seem to represent the major fraction of the "sheath."

The collagen filaments obviously contribute to the birefringence of the sheath, the sign being negative with respect to the radial direction (due to negative form birefringence and the positive birefringence of the collagen filaments which are oriented tangentially and longitudinally). Dense, double-edged, osmiophilic intracytoplasmic layers (Pl. II, Fig. 5, *b*) are also frequently observed running parallel with the elongate processes of the connective-tissue cells. Quite possibly these, like their equivalents in the Schwann eells, may contribute birefringence positive with respect to the radial direction and hence may play a role in the metatropic reaction observed in the usual preparation.

While the above points bear in a practical sense on the metatropic reaction, the aspect which is of primary interest to the nerve physiologist is the evidence which the highly sensitive polarization optical method throws on the presence of oriented lipid and protein molecules in the nerve fiber itself. Because of the thinness of the Schwann cell (about equal to the wave length of light) and the very large diameter

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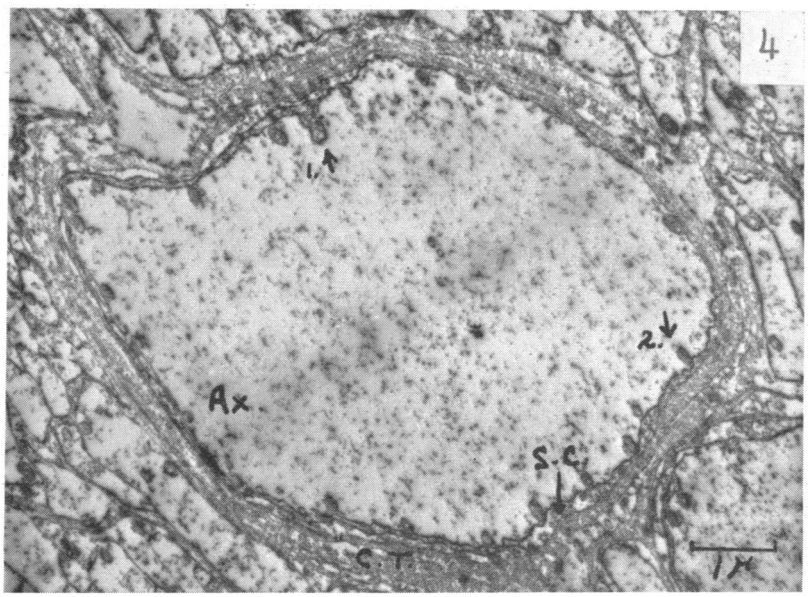
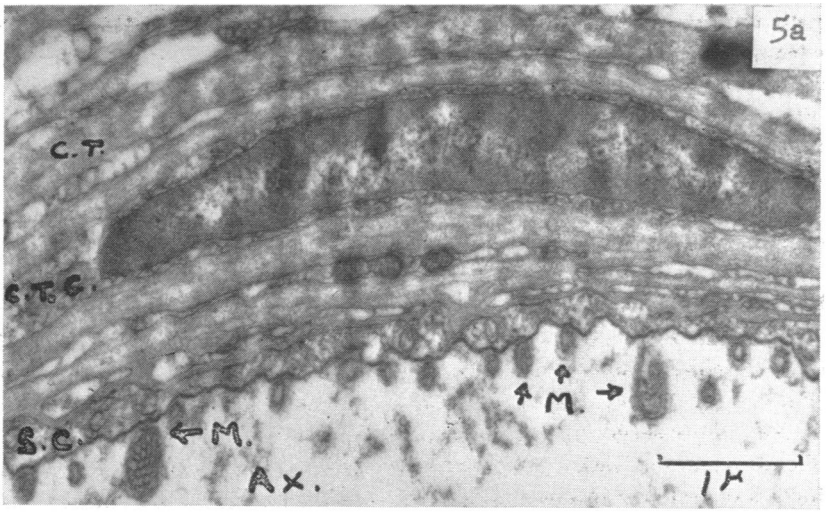
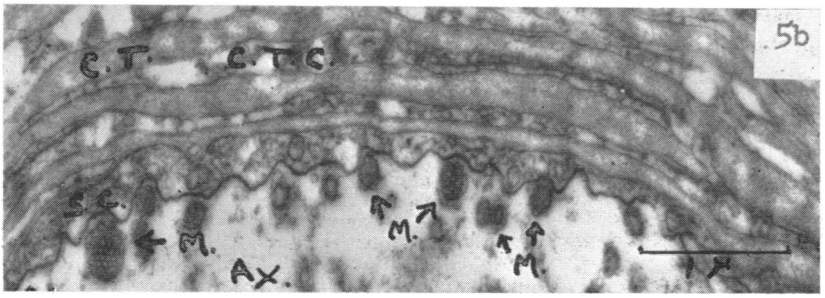
FIGS. 4–5.—Fig. 4, transverse section through fibers of lobster leg nerves, showing peripheral distribution of mitochondria just under Schwann cell interface. Note outpocketing of Schwann cell cytoplasm marked by arrow (*1*). Enlargement of marked areas is shown in Figs. 7 and 8. Fig. 5, *a* and *b*, transverse section through fibers of lobster leg nerves showing mitochondria clustered under axon-Schwann interface. Note internal structure in mitochondria. Also note alternate layers of collagen filaments and connective-tissue cells (one with nucleus). Fiber diameter about 40 μ.

PLATE II







of the giant fiber, it would be impossible to establish the precise locus of the oriented molecules by this method.

However, certain observations help localize the oriented lipid molecules. Bear, Schmitt, and Young[16] noticed that squid giant fibers which had been immersed in 1 *M* NaOH showed positive birefringence at the outer edge of the axon, presumably owing to radially oriented lipids. This relatively high concentration of alkali not only disoriented the connective-tissue constituents but possessed a refractive index sufficiently high to reduce or cancel any negative form birefringence. The inference is that the optical positivity originates in the Schwann cell. This is supported by our own observation that careful treatment of giant fibers with a bacterial proteinase[18] caused disintegration and disorientation of the connective tissue sufficient to reduce greatly or to abolish the negative birefringence of the connective tissue. Nevertheless, in glycerinated sea water such proteinase-treated fibers manifested positivity at their surface, presumably owing to the presence of oriented lipid molecules in the dense, osmiophilic layers in the cytoplasm of the Schwann cells and at the axon–Schwann cell interface.

The question may be raised whether there is sufficient lipid material in the Schwann cell to produce a readily measurable positive birefringence and to make up the osmiophilic layers seen in the Schwann cell. Mitchison[19] stated that, if all the lipid in the sheath of the squid giant fiber were concentrated in a continuous layer, that layer would have a thickness which could not be greater than about 15 A and might be as low as 5 A. Mitchison therefore claimed that the interpretation of the metatropic reaction given by Bear *et al.*[15, 16] must be incorrect and suggested that his own interpretation, offered to explain the birefringence of the red cell ghost, be applied also to the metatropic sheath of the nerve fiber.

Mitchison based his calculations concerning the squid sheath on the lipid analyses of McColl and Rossiter.[20] Unfortunately, the values quoted in that paper should be multiplied by 1,000 because of a typographical error.[21] Estimation of the amount of lipid present in the Schwann cell from the data of McColl and Rossiter depends upon the average thickness of connective tissue estimated to have remained on the fibers used for the analysis. However, on any reasonable assumption there would be more than sufficient lipid to make up half a dozen of the layers observed[22] (assuming that they were composed entirely of lipid).

It is probable that the layered structures depicted by the electron microscope to exist within the Schwann cell would constitute a Wiener mixed body of the type originally proposed to explain the metatropic reaction. If we assume that the dense-bordered layers paralleling the surface of the film seen in sections of the giant fibers have dimensions similar to those existing in life and that they are myelin-like, lipid-protein structures having a birefringence of about 0.011 (as found for myelin by Schmitt and Bear[23]), it may be shown that retardations may be expected which are similar to those which are actually observed.

3. *The Axon Surface of the Schwann Cell and Its Relation to Mitochondria.*— The mitochondria of the nerve fiber resemble those found in the perikaryon[24] and in other tissue cells. They are ovoid structures of widely varying size. Indeed, in the axon of the squid giant fiber some of the mitochondria (Pl. III, Fig. 6) are as large as the sarcosomes of insect flight muscle (2–4 μ). They also manifest various types of internal fine structure which may reflect real differences in architecture or

may depend on differences in response to the fixative. The most commonly observed structural types are those with internal honeycomb structure, those with internal lamellae, those consisting of concentric or helical membranes, and those with irregularly shaped inclusions (Pl. II, Fig. 5, *a* and *b*, and Pl. III, Figs. 6, 8, and 10).

To call these particulates "mitochondria" seems justified on structural grounds; definitive proof would require studies of their chemical properties. Such studies are under way, employing extruded axoplasm of squid giant fibers. This material has unique experimental advantages because no harsh mechanical treatment, such as the use of homogenizers and other devices to disintegrate cells, is necessary.

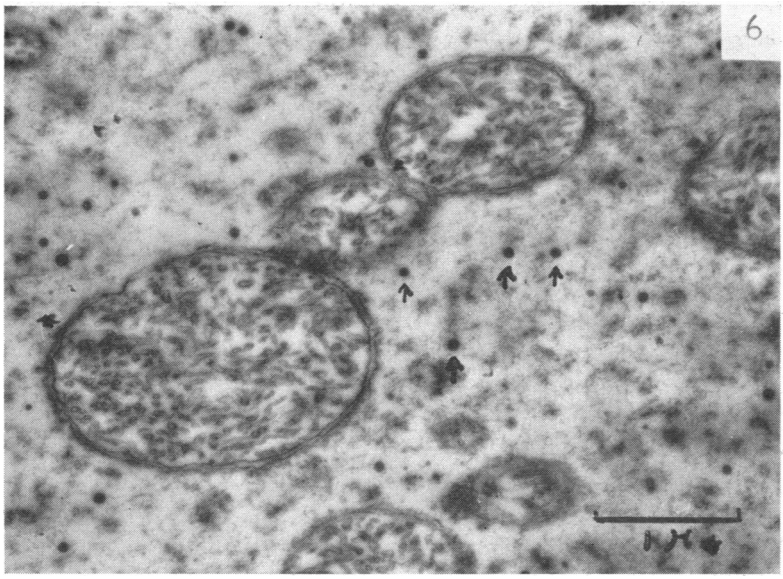
The differential distribution of the axonal mitochondria near the surface of the Schwann cell may have peculiar significance. In squid giant fibers the mitochondria are found in the body of the axoplasm as well. However, in lobster fibers, especially the larger ones, and in the medium-sized squid fibers, the mitochondria are almost exclusively clustered just below the surface of the Schwann cell (see Pl. II, Fig. 4 and Fig. 5, *a* and *b*).

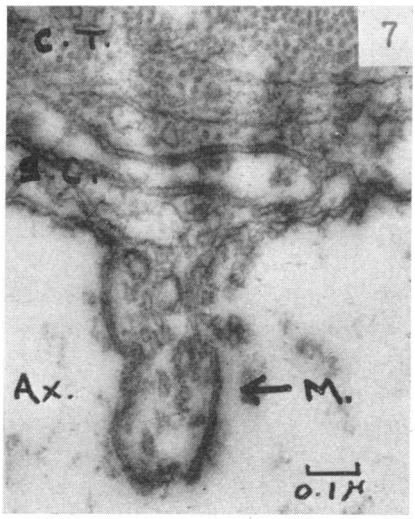
The concept of mitochondria as the power plant of the cell[25] has led morphologists to associate the presence of large numbers of mitochondria in tissue situations with the expenditure of large amounts of metabolic energy. The orientation of the sarcosomal mitochondria about the myofibrils is an example of such a case. If such a morphological diagnosis of function were applied to lobster and squid nerve fibers, one might suppose that the Schwann cell, spread out in a very thin layer around the axon, may be the site of high metabolic activity. The highly contorted axonal surface of the Schwann cell is in agreement with such a possibility. The high surface-to-volume relation in the Schwann cell in itself suggests high energy expenditure and the diffusion into the surface film of molecules presumably from Schwann cell protoplasm.

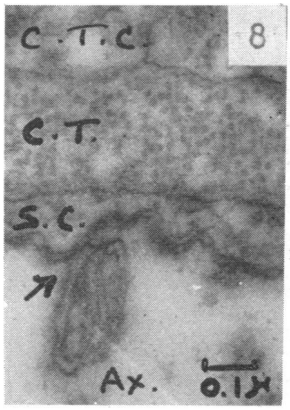
The axon surface of the Schwann cell manifests outpocketings which are highly suggestive. Figures 4, 7, 8, 9, and 10 show structures evidently being produced by an active process of evagination of the Schwann cell membrane which closely resemble the mitochondria lying immediately below the surface. To speculate that these mitochondria may, in fact, have been produced by the Schwann cell would require reliance on highly circumstantial evidence. The implications of this possibility are sufficiently important to make its careful evaluation urgent. If the surface membrane of the Schwann cell actually can participate in the formation of mitochondria, it may be presumed to contain spatially organized enzymes such as are thought to occur in mitochondria. Such a situation would be of the greatest interest to nerve physiologists because of the possibility which it offers of providing a means of chemical coupling of energy-giving reactions with those concerned with the maintenance of polarization potentials and the propagation of action waves. Experiments devised to test the validity of this speculation are in progress.

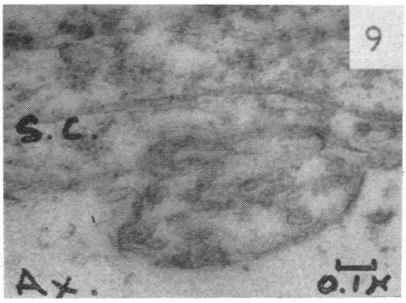
Fig. 6, section through squid giant fiber axon, showing mitochondria containing irregularly shaped inclusions. Note also the dense, osmiophilic granules (*arrows*) characteristic of squid axoplasm. Fig. 7, higher magnification of region of outpocketing of Schwann cell cytoplasm marked with arrow (*1*) in Fig. 4. Fig. 8, higher magnification of region marked with arrow (*2*) in Fig. 4. Note continuity of mitochondrial membrane with membrane at the axon–Schwann cell interface (*arrow*). FIGS. 9 and 10.—Sections through medium-sized squid nerve fibers (*ca.* 20 μ in diameter), showing what appear to be mitochondria connected with the Schwann cell cytoplasm.

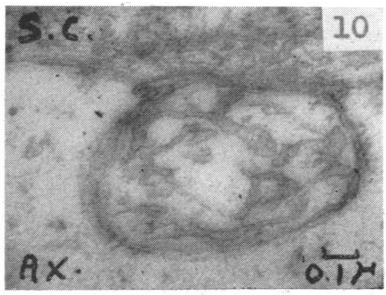
PLATE III











SUMMARY

Attention is called to the existence of osmiophilic layers in, and at the surface of, the Schwann cells of lobster and squid nerve fibers, and the suggestion is made that these are of lipid-protein (myelin-like) constitution and that they manifest the optical properties described as "metatropic." Attention is called also to the highly contorted nature of the axon border of the Schwann cell and to the fact that the mitochondria of the axon (particularly in lobster fibers) are preferentially located immediately below this interface. A speculation is offered about the possible relation between the Schwann cell and certain physiological processes in the nerve fiber.

One of us (B. B. G.) wishes to express her appreciation to Dr. Sidney Farber, scientific director of the Children's Cancer Research Foundation, for his unfailing support of this research.

The technical assistance of Miss Phyllis Hoffman and Mr. J. W. Jacques is gratefully acknowledged by the authors.

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[2] A. Hess and A. I. Lansing, *Anat. Record*, **117**, 175, 1953.

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[7] B. B. Geren and D. McCulloch, *Exptl. Cell Research*, **2**, 97, 1951.

[8] F. O. Schmitt, R. S. Bear, and K. J. Palmer, *J. Cellular Comp. Physiol*, **18**, 31, 1941.

[9] J. B. Finean, *Discussions Faraday Soc.*, No. 6 (*Lipoprotein*), p. 134, 1949.

[10] Schmitt, Bear, and Palmer (*op. cit.*) showed that the identity period of the myelin sheath, in the radial direction, is about 186 A in mammalian nerve and 171 A in amphibian nerve. This period involves two double layers of mixed lipids plus a thin layer of protein. F. Sjöstrand (*Experientia*, **9**, 68, 1953) obtained excellent electron micrographs of the layered structure in the myelin sheath. Similar layers have been reported by H. Fernandez-Moran (*Exptl. Cell Research*, **1**, 309, 1950) and by B. B. Geren and J. Raskind (these PROCEEDINGS, **39**, 880, 1953). These layers had a thickness about half that of the X-ray identity period, a situation not unexpected from a consideration of the distribution of electron densities involved. The interpretation of the molecular structure of double-contoured osmiophilic layers, such as those seen in the Schwann cell, is uncertain and will probably remain so until studies of chemical model systems have been made.

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[17] F. O. Schmitt, lecture before the Seventh Congress on Cell Biology, New Haven, Connecticut, 1951.

[18] We are indebted to Dr. John D. MacLennan of the Surgery Department of Columbia University for supplying us with samples of purified collagenase and proteinase. Both enzymes solubilized the collagenous material. The collagenase appeared to be more destructive of the nerve fiber itself and of its ability to conduct impulses than was the proteinase, although this may have been primarily a concentration effect.

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[20] J. D. McColl and R. J. Rossiter, *Nature*, **166**, 347, 1950.

[21] Rossiter (personal communication) explains that, in the paper (*ibid.*) describing the analytical results, the figures were given as milligrams per 100 *gm.* of sheath, whereas they should have been milligrams per 100 *mg.* of sheath (see also McColl and Rossiter, *J. Exptl. Biol.*, **28**, 116, 1951). The latter results for total lipid in extruded axoplasm are similar to those obtained by B. A. Koechlin in this laboratory.

[22] If the connective tissue is considered to be 25 μ thick, the lipid (phospholipid plus cholesterol) would occupy a layer about 0.35 μ thick (or 15–20 of the dense layers). Electron micrographs indicate that in a sheath of this thickness many small fin fibers may be included in the "sheath" tissue analyzed, so that the above figure (0.35 μ thickness) is undoubtedly high if considered as representing only the lipid in the giant fiber Schwann cells.

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[25] F. Lipmann, *Advances in Enzymol.*, **1**, 99, 1941.

ERRATA: Fluctuations in the Space Distribution of the Galaxies

In the article of the foregoing title appearing in these PROCEEDINGS, **40**, 541–549, 1954, the following corrections should be made:

1. Equation (6) should read:

$$N(m') = \omega\bar{\rho} \int_0^A [1 + D(r)]r^2\, dr,$$

2. Equation (7) should read:

$$A = 10^{1/5\,[m' + 5 - M_0]}$$

3. The caption under Figure 1, last two lines, should read:

$$\Gamma = e^{-r^2/r_0^2}\ (\textit{solid line});\ A = 10^{1/5[m' + 5 - M_0]}$$

4. Equation (17) should read:

$$a = 10^{(m' + 5 - M_1)/5}$$

5. Equation (19) should read:

$$N(m') = \frac{\omega\bar{\rho}}{M_2 - M_1} \int_{M_1}^{M_2} dM \int_0^{r'} r^2\, dr\, [1 + D(r)]$$

6. Page 545, ninth line from the bottom, equation at the end of the line, should read:

$$\Delta m = \frac{m_0 - 14.7}{5.7} \pm 0.10$$

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