Electron Microscopy of Nerve Fibers V.
On the Fine Structure of the Small Myelinated Nerve Fibers in the Peripheral Nerve*

by
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Much valuable information on the fine structure of the nerve fibers has already been demonstrated by electron microscopic studies, which have remarkably extended our knowledge on this subject. Nevertheless, detailed observation of all kinds of nerve fibers enclosed in the peripheral nerve bundle has been severely restricted because electron microscopic examination is extremely time consuming and is subject to interference by many artefacts produced in the process of specimen preparation. There seems to exist several structural differences between the large myelinated nerve fiber and the small ones. The purpose of the present paper is to report observations on the fine structure of the small myelinated fiber in the frog's peripheral nerve in comparison with that of the large ones, made with the electron microscope and very thin sections.

Materials and Methods

The observations described here are based on examination of the sciatic nerves of mature frogs (Rana nigromaculata nigromaculata). The nerve was exposed by careful dissection, and ice-cold fixative was injected into the fascial sheaths around the nerve bundle. Then the animals were left on ice for 10 minutes, and small pieces of

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nerve, 2 to 3 mm. in length, were quickly removed from them and rapidly placed in a vial of fixative immersed in ice water. Veronal-acetate-buffered 1% OsO₄ and 0.6% KMnO₄ at pH 7.42 were used as fixative. The fixation lasted 2 to 4 hours in a cold chamber at 0° to 3°C. Four hours’ fixation seemed best for OsO₄ and 3 hours for KMnO₄. After fixation the materials were washed with a few changes of cold distilled water for 1 hour and dehydrated by passage through a graded series of ethanol at 20-minute intervals in a refrigerator. They were then embedded in methacrylate—a mixture of 8 parts n-butyl methacrylate and 3 parts methyl methacrylate containing 2% benzoyl peroxide as catalyst—or Araldite following the procedure described by Glaeber and Glaeber (1958). Polymerization was carried out in gelatin capsules. Sections were cut with a JUM-5 ultra-microtome and glass knives and floated on distilled water. Suitable sections, about 200Å in thickness, were selected by their interference colors and mounted on electron microscope slit grids covered with carbon film. The sections embedded in Araldite were stained with either Pb(OH)₄ (Watson, 1958) or KMnO₄ (Lawn, 1960). Observation was made with an HU-11P electron microscope of 20μ objective aperture. Electron micrographs were taken at original magnifications of 5,000 to 20,000 and thereafter enlarged photographically. Measurement of the fine structural elements was made on a projected image of the electron micrograph at a magnification of 20.

Besides the studies on the thin sections, light microscopic examination was carried out on thicker sections (about 1μ) made from all the embedded blocks and mounted on glass slides with photographic adhesive without removing the plastic.

Results

As demonstrated in a previous paper (Honjin, 1957b), electron microscopy of the sciatic nerve of frogs indicates that the so-called nerve fibers appear as a number of Schwann cell units running parallel with one another and standing close side by side which contain in their cytoplasm one, or less frequently two, myelinated axons, or several, sometimes one, non-myelinated axon. Figs. 1 and 2, plate I are photomicrographs of a cross section of the sciatic nerve fixed with neutral OsO₄ and embedded in methacrylate. A portion of the nerve bundle in Fig. 1 is shown enlarged in Fig. 2.
Numerous large myelinated fibers (4 to 10\(\mu\) or more in diameter) are uniformly distributed in the nerve bundle, appearing as relatively large black circles of myelin, while the small myelinated fibers (less than 4\(\mu\) in diameter) lie in small groups among the large fibers. The location of the non-myelinated fibers is obscure in Figs. 1 and 2. Fig. 3 is an electron micrograph of a cross section of the nerve at a relatively low magnification. There appear about 10 small myelinated axons. In the center of the picture many non-myelinated axons are found in the Schwann cell units which enclose the Schwann cell nucleus as well as the axons. A large myelinated fiber appears in the upper right corner.

Cross sections of the small myelinated fibers fixed with OsO\(_4\), are shown in Figs. 4 and 5. The axoplasm contains within itself many neurofilaments, tubular or vesicular components of the endoplasmic reticulum and mitochondria. The axoplasm is limited by an axon membrane which is enveloped by the myelin sheath. The myelin sheath appears as alternating concentric dark (dense period) and light layers with a characteristic repeating period of about 120\(\AA\) in thin sections fixed with OsO\(_4\) and embedded in methacrylate (Figs. 6 and 10). The myelin lamellar membrane is connected with the outer surface membrane of the Schwann cell the outer connecting membrane (outer mesaxon) as shown in Fig. 10; the myelin lamellar membrane is closely wound about the axon in a spiral. There are usually fewer myelin lamellar layers in the small fiber than in the large one. The thickness of the myelin sheath, however, is not always in proportion to the fiber diameter. The outer cytoplasm of the Schwann cell contains many mitochondria, membrane system of Golgi apparatus, rough surfaced endoplasmic reticula, and large special electro-dense granules. These granules are spherical or elliptic and have diameter of 0.1 to 0.3\(\mu\). They show a tendency to accumulate in the cytoplasm near the nucleus. Around the outer surface membrane of the Schwann cell, there is seen a relatively dense basement membrane (Figs. 4, 5 and 6). Many collagen fibrils of the endoneural sheath are found in the space between the Schwann cell units (Figs. 5, 6 and 7). Many of these structural features in the small myelinated fibers are in accord with those in the large ones reported by many earlier researchers (Fernández-Morán, 1952; Hess and Lansing, 1953; Honjii, 1955, 1957a, b, c; Robertson, 1955, 1957).

The myelin sheath fixed with KMnO\(_4\) reveals a dense line, inter-
period line, in the middle of the light layer, besides the dense period layer or line. The myelin fixed with OsO₄ and stained with Pb(OH)₂ also shows both the dense period and interperiod lines, but the interperiod line appears less dense than in the former case (Fig. 11).

Text-fig. 1. Diagramatic cross section of the internodal portion of the large myelinated fiber in the peripheral nerve. The myelin sheath is composed of a myelin lamellar membrane which is spirally wound about the axon. The outer end of the myelin membrane is connected with the Schwann cell surface membrane (Sm) by an outer connecting membrane (oc), and the inner end is connected with the outer layer of the axon-Schwann membrane (a-Sm) by an inner connecting membrane (ic). The myelin sheath appears as alternating dark and light layers by the close packing of spiral myelin membrane. The dark layer, which is denoted by the solid line in the diagram, is nothing but the dense period line, and is in continuous connection with the inner dense layer of the Schwann cell surface membrane. The interperiod line, which is denoted by the dotted line, appears in the middle of the light layer when fixation by KMnO₄ or electron staining by KMnO₄ and Pb(OH)₂ is carried out and is in continuous connection with the outer, less dense layer of the surface membrane of the Schwann cell. Mauthner's sheath (Ms) lies between the myelin sheath and axon-Schwann membrane and contains the cytoplasm of the Schwann cell. The axon-Schwann membrane is composed of an axon membrane of nerve axon origin and an infolded Schwann cell surface membrane of Schwann cell origin. A 100 to 150 Å gap is present between them in the internodal portion. There is a dense basement membrane (b) immediately outside the Schwann cell. a, axon; n, Schwann cell nucleus; S, Schwann cell cytoplasm.
The interperiod line is obscure in the myelin treated with OsO₄, but not receiving the after staining (Fig. 10).

In the large fiber, the deeply infolded Schwann cell surface membrane envelops the axon to form the axon-Schwann membrane in conjunction with the axon membrane. A gap of 100 to 150Å is usually present in the axon-Schwann membrane (Text-fig. 1). The innermost lamellar membrane of the spiral myelin is connected with the outer layer (Schwann membrane) of the axon-Schwann membrane through the inner connecting membrane (inner mesaxon). There is usually found a thin cytoplasmic layer between the axon-Schwann membrane and the lamellar myelin sheath. This layer corresponds to the so-called Mauthner's sheath (Text-fig. 1).

Text-fig. 2. Diagramatic cross section of the internodal portion of the small myelinated fiber in the peripheral nerve. The fine structure of the myelin sheath is similar to that in the large fiber. The spiral myelin membrane is connected with the Schwann cell surface membrane (Sm) at the outer end by the outer connecting membrane (oc) and forms the inner myelin loop (iml) at the innermost end. The inner myelin loop contains a small amount of Schwann cell cytoplasm in the interior. There is found no Mauthner's sheath; the axon membrane (am) borders on the innermost myelin lamellar membrane. a, axon; b, basement membrane; n, Schwann cell nucleus; S, Schwann cell cytoplasm.

Mauthner's sheath, which is usually present in the bulk of circumference of the axon in the large fiber, has not been found in the small fiber. The innermost myelin lamellar membrane of the small fiber forms a small loop termed 'inner myelin loop.' In other words the myelin lamellar membrane is composed of double layers derived from the infolded Schwann membrane, and separated along the dense period line to form the inner myelin loop.
at the innermost end of the spiral myelin membrane. The inner myelin loop is limited by these separated membranes, contains the cytoplasm within itself, and is situated in intimate contact with the outer surface of the axon membrane (Figs. 5, 6, 7 and 8). Thus the innermost myelin membrane of the small fiber is in direct contact with the outer face of the axon membrane, except in the region of the inner myelin loop; no Mauthner's sheath is found in the small fiber (Text-fig. 2).

The Schmidt-Lanterman cleft is a well known feature of the myelin sheath. Robertson (1958) has demonstrated that the clefts are shearing defects in myelin in which the lamellae are widely separated at the dense period lines and the layers between the lamellae are continuous with the outer layer of Schwann cytoplasm and Mauthner's sheath. According to the present observation, the cleft structure can not be seen in the myelin sheath of the small fiber less than 4μ in diameter, though many definite cleft structures have been observed in the large fiber in the same materials. It is worth pointing out here that in the earlier studies both the light and electron microscopic observation of the Schmidt-Lanterman cleft was limited to the large fibers.

As regards the fine structure of the nodes of Ranvier, electron microscopic observations have been reported by Hess and Lansing (1953), Honjin (1957 a, b, c), Uzman and Nogueira-Graf (1957), Robertson (1959), Uzman and Villegas (1960), and Honjin, Takahashi and Nishi (1961). According to the present study, intended to clarify the structural differences between the large and small myelinated fibers, the axon of the myelinated fibers is more or less constricted near the termination of the myelin sheath at the node. This feature is remarkable in the largest fibers, in which the axon is reduced in the node to about one-third in diameter, while the axon of the small fiber less than 4μ in diameter is scarcely constricted at the node. On the other hand, the length of the non-myelinated nodal axon of the myelinated fiber is much shorter in the large fibers (0.5μ or less) than in the small ones (2μ or more). (Compare Fig. 9 in this paper with Figs. 1 and 2 in the report by Honjin, Takahashi and Nishi, 1961). At the nodal termination of the myelin sheath, each lamellar membrane of myelin is separated at its dense period line to form a small nodal myelin loop, which contains Schwann cytoplasm in its inferior and lies on the outer surface of the axon membrane roughly perpendicular to
the fiber axis in the juxta-terminal myelin region. There are found in the cytoplasm of the nodal myelin loop a small tubular or vesicular structure probably representing components of the endoplasmic reticulum (Fig. 9). The nodal myelin loop is helically arranged near the node and closely envelops the axon. The nodal myelin loop appears in the longitudinal section of the node as a number of rings lying side by side on the outer margin of the axon membrane of the juxta-terminal myelin region (Fig. 9 and Text-fig. 3).

The Schwann cell forms in the nodes small finger-like nodal processes about 500Å in diameter, as suggested by Robertson (1959) and Honjin, Takahashi and Nishita (1961). The nodal axon is surrounded by nodal processes of the two, proximal and distal, Schwann cells, but there is a gap of considerable width between the nodal processes. The nodal processes are much more numerous in the large fibers than in the small ones. This indicates that the axon membrane is directly exposed to the outside in the nodal region. The length of the non-myelinated nodal axon indicates that a smaller proportion of axon membrane is exposed to the outside in large fibers than in small ones.

The spiral myelinogenesis concept of Geren (1954), Robertson (1955) and Honjin (1957 a, b) is useful in understanding this complicated geometrical arrangement of the membrane system in the myelinated nerve fibers. Text-fig. 3 presents a diagramatic interpretation of the findings on the small myelinated fiber. A cylindrical piece is taken to represent the axon which is stripped off the spiral Schwann cell. An idealized Schwann cell which is separated along the interperiod line of the myelin lamellae and uncoiled to a sheet, is shown in A together with the cross section by the plane of the arrows. One idealized node of Ranvier in longitudinal section is shown in B. In the sheet of the Schwann cell, the myelin part which is composed of adherent double layers of membrane, is shown as a white area, while the cytoplasmic part which holds the Schwann cell cytoplasm between two cell membranes, is stippled. As is clearly shown in the diagram, the Schwann cell uncoiled to a sheet is composed of the central membranous myelin part (mlm) and the peripheral cytoplasmic part. The latter is divided into three subdivision: the outer cytoplasmic part containing the Schwann cell nucleus (oSc), the inner cytoplasmic part next to the axon (iml) and the cytoplasmic edge of the sheet directed toward the node (nml). The nodal tip of the outer
Text-fig. 3. (A) is a diagramatic interpretation of the small myelinated nerve fiber in which the Schwann cell is uncoiled and expanded into a sheet (Schwann cell sheet). The cross section by the plane of arrows is shown underneath. A cylindrical piece is taken to represent the naked axon (a) which is scarcely constricted at the node of Ranvier (nR). The large central part of the sheet is occupied by the myelin lamellar membrane (mlm) which is composed of adherent double layers of membrane.
The small myelinated fibers are characterized by the very thin inner cytoplasmic part and the central part of the Schwann sheet consisting entirely of membranous myelin; there is found no cytoplasmic cord communicating the outer and inner cytoplasmic parts across the myelin part. When this sheet is rolled around the cylinder representing the axon, the inner cytoplasmic part becomes the inner myelin loop, and the nodal cytoplasmic edge is coiled around the axon to form the nodal myelin loop. The fine processes at the nodal tip of the outer cytoplasmic part then appear as nodal processes.

Text-fig. 4 presents a diagramatic interpretation of the findings on the large myelinated fiber. It is similar to Text-fig. 3 in construction, but the scale is reduced and a part of the Schwann sheet and the axon has been cut off from the drawing as indicated by the wavy lines. As shown in the diagram, there are thin cytoplasmic cords running across the myelin part (SLc). These cytoplasmic cords are nothing but of the Schmidt-Lanterman clefts in the uncoiled state and connect the outer cytoplasmic part with the inner. When the Schwann sheet is rolled around the axon, these thin cytoplasmic cords are coiled around the axon together with the myelin lamellar membrane to form the Schmidt-Lanterman clefts. The inner cytoplasmic part in the large fiber (Ms) is far wider than that in the small one. This part corresponds to Mauthner's sheath. The nodal cytoplasmic edge of the large fiber is much longer than that of the small fiber and the nodal processes are much more numerous. Moreover the constrictions.

A considerable amount of cytoplasm exists in the outer Schwann cell layer (oSc), while the inner edge of the sheet next to the axon (iml) and the nodal edge of the sheet directed to the node (nml) contain only a small amount. They correspond respectively to the inner myelin loop and the nodal myelin loop in the coiled nerve fiber. There exists a cytoplasmic connection in the periphery of the sheet, which surrounds the central myelin lamellar membrane. At the nodal tips the Schwann cell provides many fine processes (np) which correspond to the nodal processes. n, Schwann cell nucleus. (B) is a diagramatic longitudinal section of the node of Ranvier of the small fiber. The myelin lamellar membrane forms the nodal myelin loop (nml) at its juxta-terminal part. The outer Schwann cell cytoplasm (oSc) provides the nodal process (np) at its nodal end. A relatively large extent of the nodal axon (a) is exposed to the outside in the node of the small myelinated nerve fiber. am, axon membrane; i, interperiod line of myelin sheath; m, myelin sheath; p, period line of the myelin sheath; Sm, Schwann cell surface membrane.
Text-fig. 4. Diagramatic interpretation of the large myelinated nerve fiber. The Schwann cell is uncoiled into a sheet (Schwann cell sheet). The cross section by the plane of the arrows is shown underneath. The scale is smaller than in Text-fig. 3, and moreover a part of the Schwann cell sheet and the naked axon has been omitted as indicated by the wavy line, because in large fiber the internodal length and the myelin lamellar membrane are too great. The axon (a) is remarkably reduced at the node (nR). The inner cytoplasmic part next to the axon is wide enough to form Mauthner's sheath (Ms). The nodal myelin loop (nml) is thin and long. There is also found a peripheral cytoplasmic connection in the Schwann cell sheet among Mauthner's sheath, the nodal myelin loop and the outer Schwann cytoplasm (oS) containing the nucleus (n). Moreover, many cytoplasmic cords (SLc) are present across the myelin lamellar membrane (mlm), connecting Mauthner's sheath with the outer Schwann cell cytoplasm; they correspond to the Schmidt-Lanterman cleft in the coiled large myelinated fiber. The nodal processes (np) at the tip of the outer Schwann cytoplasmic part are large in number.
tion of the axon at the node is more conspicuous in the large fiber.

The above are the marked features of large myelinated fibers. The diagramatic representation of the node of Ranvier in large fibers in longitudinal section is given in a previous report (Hon-jin, Takahashi and Nishi, 1961).

Discussion

The thin cytoplasmic layer next to the axon known as Mauthner's sheath is a well-known feature of the myelinated fiber. It was discovered by light microscopy in large myelinated fibers of the peripheral nerve. It is, however, worthy of remark that Mauthner's sheath is not always found in all of nerve fibers; its existence is rather inconstant. According to the present study, it has become clear that Mauthner's sheath is not present in the small myelinated fibers less than 4μ in diameter, but there exists an inner myelin loop in the form of a slender tube which contains cytoplasm and is limited by the infolded Schwann cell membrane. It is oriented along the long axis of the fiber on one side of the axon. Mauthner's sheath is usually found in the large fibers, but even in some of the fairly large fibers, it does not always appear as a circular cytoplasmic layer enveloping the entire circumference of the axon. It is often absent on one side of the axon in large fibers. The inner myelin loop of the small fibers is apparently equivalent to Mauthner's sheath of the large fibers. The inner cytoplasmic layer in central nerve fibers is usually similar in form to the inner myelin loop of peripheral small fiber in the present study (Hon-jin, 1959, 1961, 1962; Maturana, 1960; Peters, 1960; Bunge, Bunge and Ris, 1961). This indicates that Mauthner's sheath found in the large fibers may be a special case of inner myelin loop, in which it has become large enough to envelop the entire axon.

The cytoplasm in the interior of the inner myelin loop is connected with the cytoplasm in the nodal myelin loop in the nodal region. After going through a spiral pathway at the node, the nodal myelin loop joins with the outer cytoplasm of the Schwann cell, viz. the inner myelin loop shows a cytoplasmic connection with the outer Schwann cytoplasm through the nodal myelin loop. This gives an important suggestion for discussing the question of the node of Ranvier. It appears that the nodal myelin loop has two essential meanings: one is from nerve function and the other
from cell metabolism. In the first place, the nodal end of the myelin sheath closely ties up the axon in the juxta-terminal myelinated region of the node. This may be due to the turgor of the nodal myelin loop which contains the cytoplasm in its interior and is arranged in a spiral. Consequently the spiral nodal myelin loop and the axon membrane are in intimate contact with each other and the 100 to 150Å gap, which is usually present in the internodal axon-Schwann membrane as well as other paired membrane structure between cells, can not be found near the node. This is very important in connection with the rôle of the myelin sheath as insulator during conduction of nerve impulses. The nodal myelin loop probably plays an important rôle in the electro-saltatory conduction of nerve impulses in the node of the myelinated fibers.

Secondary, the cytoplasm in the inner and nodal myelin loops may be metabolic pathways. The idealized uncoiled Schwann cell (Text-fig. 3) shows that the large central area is occupied by membranous myelin, while the cytoplasmic part of the Schwann cell is situated in the periphery surrounding the myelin. The inner cytoplasmic part (inner myelin loop), the nodal cytoplasmic part (nodal myelin loop) and the outer cytoplasmic part have cytoplasmic connections as mentioned above, though there are some differences in volume of the cytoplasm among them. The uncoiled pattern of Schwann cell resembles in both form and position of its cytoplasmic parts the light microscopic image of the living onion cells, where the cytoplasm is distributed in the periphery of cells and encloses the central vacuole. It can be seen in the living onion cells under the light microscope that the mitochondria and other cytoplasmic granules are performing protoplasmic movement in the peripheral cytoplasm. It may not be injudicious to expect the same mechanism to be present in the Schwann cell, though it is difficult to examine this mechanism in the living cells. It seems that the cytoplasm in the inner myelin loop is under the metabolic control of the outer cytoplasmic part containing the nucleus through the cytoplasm in the nodal myelin loop.

This concept is probably applicable to the Schmidt-Lanterman clefts, which are sporadically found in the myelin sheath of the large fiber. In the cleft the myelin lamellae are widely separated at the dense period lines. The cytoplasm between the lamellae in the cleft shows a spiral course and is continuous with both the outer cytoplasm of the Schwann cell and the cytoplasm of
Mauthner's sheath, as mentioned above. Generally speaking, the large fiber has thicker myelin sheath and greater internodal length of the myelin segment than the small fiber; hence in the large fiber the myelin lamellar membrane is far larger and the nodal myelin loop is much longer than in the small fiber. The two nodal loops on the proximal and distal edges of each myelin segment seem to be too much separated from each other to serve as connecting pathways for metabolism between the outer cytoplasmic part and the Mauthner's sheath in view of the existence of the relatively large amount of cytoplasm in the Mauthner's sheath of the large fiber. The Schmidt-Lanterman cleft resembles the protoplasmic cords crossing the central vacuole in younger vigorous onion cells and communicating by a short route between the peripheral cytoplasm. The fact, that the Schmidt-Lanterman clefts which are regarded as a metabolic pathway in spiral arrangement, exist in the large fiber and not in the small fiber, seems to be favorable for the metabolism of the long and large Mauthner's sheath and the very wide myelin membrane in the large fiber; they constitute an effective pathway for myelin metabolism. Moreover this suggests that the Schmidt-Lanterman cleft is not a mere artificial product.

Summary

The fine structure of the small myelinated nerve fiber was studied with the light and electron microscopes in thick and thin sections of the sciatic nerves of the mature frog, Rana nigromaculata nigromaculata. The materials were fixed in 1% OsO₄ and 0.6% KMnO₄ buffered with veronal-acetate (pH 7.42), embedded in methacrylate or Araldite, and cut with a glass knife. The thin sections prepared from embedding in Araldite were stained with either Pb(OH)₂ or KMnO₄. The results obtained are summarized as follows:

1. In the small myelinated fiber, the innermost myelin lamellar membrane is separated at its dense period line to form the inner myelin loop which is limited by the separated layers of myelin membrane and contains the Schwann cytoplasm in the interior.

2. The inner myelin loop appears as a small cylindrical tube situated on one side of the axon membrane between the axon and myelin, and running parallel to the fiber axis between the two ends of each myelin segment. At the end of the myelin segment the
inner myelin loop is connected with the nodal myelin loop. In the small fiber, there is no Mauthner's sheath which is usually present in the large fiber.

3. At the node of Ranvier, the helical Schwann cell forms a nodal myelin loop which contains the Schwann cytoplasm in its interior and connects the inner myelin loop with the outer cytoplasmic part of the Schwann cell containing the nucleus. After helically enveloping the axon, the nodal myelin loop closely ties up the axon in the juxta-terminal myelinated region of the node. The nodal myelin loop is shorter in the small fiber than in the large one.

4. The so-called Schmid-Lanterman cleft is absent in the small fiber but is always present in the large fiber. In the cleft the myelin lamellar membrane is widely separated at the dense period line. The layer between the lamellar membrane contains the cytoplasm which connects Mauthner's sheath with the outer Schwann cytoplasm in a spiral pathway.

5. The axon of the small fiber less than 4µ in diameter is scarcely attenuated at nodes. The non-myelinated nodal axon of the myelinated fiber is shorter in the large fiber than in the small one.

6. The cytological meanings of the inner myelin loop, Mauthner's sheath, the nodal myelin loop and the Schmid-Lanterman cleft are discussed with diagrams of the uncoiled Schwann cell. The nodal myelin loop and the cytoplasmic spiral layer in the cleft are the metabolic pathways which connect the inner myelin loop or Mauthner's sheath with the outer cytoplasm of the Schwann cell containing the nucleus. The nodal myelin loop probably plays an important rôle in the electro-saltatory conduction of nerve impulse by close tightening of myelin as insulator around the axon near the node of Ranvier.

References


Geren, B.B. 1954: The formation from the Schwann cell surface of myelin in
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Explanation of plates

Abbreviations

a: axon of the myelinated fiber.
c: collagen fibril in the endoneural sheath.
iml: internal myelin loop.
Ms: Mauthner's sheath in the large fiber.
m: myelin sheath.
n: nucleus of the Schwann cell.
na: axon of the non-myelinated fiber.
nml: nodal myelin loop at the nodal end of the myelin sheath.
np: nodal process at the nodal end of the Schwann cell.
S: Schwann cell cytoplasm.

Explanation of figures

Plate I

Fig. 1. A photomicrograph of a cross section (about 1μ thick) of the frog sciatic nerve bundle fixed with neutral OsO₄ and embedded in methacrylate. Many large and small myelinated nerve fibers appear as black rings. ×100.

Fig. 2. A photomicrograph of a cross section of the large and small myelinated nerve fibers in a part of Fig. 1 at higher magnification. The small myelinated fibers are situated among the large fibers in small groups. ×690.

Fig. 3. An electron micrograph of a thin cross section of the frog sciatic nerve fixed with OsO₄. There appear about 10 small myelinated axons (a). In the center of the micrograph many non-myelinated axons are found in the Schwann cell units. A large myelinated fiber is seen in the upper right corner. ×5,600.

Fig. 4. An electron micrograph of a small myelinated fiber fixed with OsO₄. The axon (a) enclosing the neurofilaments, fine tubular endoplasmic reticula and mitochondria, the lamellar myelin sheath, and the Schwann cell cytoplasm (S) are shown. A non-myelinated fiber is seen at the upper left corner. ×40,000.

Plate II

Fig. 5. A cross section of the small myelinated fiber fixed with OsO₄. A small circular image of the inner myelin loop (iml) is seen between the lamellar myelin sheath and the axon (a) in the upper left corner. Three non-myelinated axons (na) are found on the right. The Schwann cell surface membrane and the basement membrane of both kinds of nerve fiber are seen. ×48,000.

Fig. 6. The inner myelin loop (iml) in Fig. 5 at higher magnification. The limiting membrane of the inner myelin loop is in continuous connection with the innermost myelin lamellar membrane. ×100,000.

Fig. 7. A cross section of the small myelinated fiber fixed with OsO₄. A relatively large inner myelin loop (iml) is found between the axon (a) and the myelin sheath. A mitochondrion having cristae structure is seen in the Schwann cell cytoplasm (S). ×50,000.
Plate III

Fig. 8. A cross section of the small myelinated fiber fixed with OsO₄. There is seen an inner myelin loop (iml) between the axon membrane and the lamellar myelin sheath. Its limiting membrane is in continuous connection with the innermost myelin membrane. ×100,000.

Fig. 9. A longitudinal section of the node of Ranvier of the small fiber fixed with KMnO₄. The nodal myelin loop (nml) in the juxta-terminal part of the myelin sheath (m) and the nodal myelin loop (nml) are seen. ×60,000.

Fig. 10. A cross section of the small myelinated fiber fixed with OsO₄. The myelin lamellar membrane (m) connected with the surface membrane of Schwann cell by the inner connecting membrane (arrow). In the myelin sheath, the dense period lines are conspicuous, while the interperiod line in the light layers are obscure. ×120,000.

Fig. 11. A longitudinal section of the myelin sheath (m) and axon (a) of the large myelinated fiber fixed with OsO₄ and stained with Pb(OH)₂. The dense period lines and the less dense interperiod lines are seen in the myelin layer. Mauthner's sheath (Ms) is found between the myelin sheath and the axon-Schwann membrane. ×120,000.
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