A COMPARISON OF THE FINE STRUCTURES OF FROG SLOW AND TWITCH MUSCLE FIBRES

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ABSTRACT

The organisation of the myofibrils and the sarcoplasmic reticulum in frog slow muscle fibres has been compared with that in twitch fibres. It has been found that the filaments have the same length in the two types of fibre, but that there are differences in their packing: (a) in contrast to the regular arrangement of the I filaments near the Z line in twitch fibres, those in slow fibres are irregularly packed right up to their insertion into the Z line; (b) the Z line itself shows no ordered structure in slow fibres; (c) the fine cross-links seen between the A filaments at the M line level in twitch fibres are not present in slow fibres.

The sarcoplasmic reticulum in slow fibres consists of two separate networks of tubules. One set of tubules (diameter about 500 to 800 A) is oriented mainly in a longitudinal direction. The tubules of the other network (diameter about 300 A) are oriented either transversely at approximately Z line level or longitudinally, connecting the transverse tubules. Triads are very rarely found, occurring at only every 5th or 6th Z line of each fibril. The central element of these triads is continuous with the thin tubules. Slow fibres from muscles soaked in ferritin-containing solutions contain ferritin particles in the network of thin tubules, the rest of the sarcoplasm remaining free of ferritin.

INTRODUCTION

As is well known, there are two types of skeletal fibre in the frog: the fast fibres which respond to a single motor impulse to give a propagated action potential followed by a twitch, and the slow fibres, unable to propagate action potentials and requiring a series of impulses to give a contraction (Kuffler and Vaughan Williams, 1953 a; Burke and Ginsborg, 1956; Orkand, 1963). In the latter, both the development and the relaxation of tension are slower than in twitch fibres, whether the contraction is initiated through nerve stimulation or by a uniform depolarisation of the excitable membrane due to increasing the potassium concentration in the external fluid (Kuffler and Vaughan Williams, 1953 b; Lüttgau, 1963). These findings imply not only that the two types of fibre differ in the nature of the excitatory mechanism, but also that differences exist either in the process by which contraction is activated, or alternatively, or perhaps in addition, in the contractile apparatus itself.

In view of these physiological differences it is of interest that structural differences between the two types of fibre have recently been described (Peacgey and Huxley, 1962) in both the contractile apparatus, i.e. the myofibrils, and the sarcoplasmic reticulum, which is believed to play an important part in the process activating contraction (Huxley and Taylor, 1958). The aim of the present work has been to extend the comparison of the fine structure of the two fibre types, particularly with respect to their myofibrils and sarcoplasmic reticulum. At the same time, some information has been obtained on the structure of the motor endings on slow fibres.
**MATERIALS AND METHODS**

**Electron Microscopy**

Toe muscles (extensor longus digitorum IV--17 muscles) and rectus abdominis muscles (5 muscles) from the frog (*Rana temporaria*) were tied onto rods or pinned onto polythene sheets to prevent them from shortening during fixation. They were either fixed in a 1 per cent solution of OsO4 buffered at pH 7.2–7.4 with Veronal-acetate (Palade, 1952) for 30 minutes to 1 hour at 0°C or at room temperature, or first fixed in a 6 per cent solution of glutaraldehyde (Sabatini et al., 1962) buffered at pH 7.0–7.4 with a phosphate buffer (0.085 M) for 2 hours at 0°C or at room temperature, then washed for 1 hour in the phosphate buffer, and further fixed for 30 minutes in a 1 per cent solution of OsO4 buffered with phosphate at pH 7.0–7.4. The tissues were dehydrated in an alcohol series, and in some cases stained overnight with a 1 per cent solution of phosphotungstic acid (PTA) in absolute alcohol. The unstained blocks were transferred to propylene oxide and then embedded in Araldite; the stained blocks were not treated with propylene oxide as this reacted with the stain (Luft, 1961), but were left for a longer time in the Araldite mixture before polymerisation.

Some muscles were kept in Ringer's solution containing 5 to 20 per cent ferritin for 1 hour before fixation in glutaraldehyde and OsO4 as described above. The ferritin solution was prepared by centrifuging the commercial solution of ferritin (L. Light & Co., Slough, Buckinghamshire, England), and resuspending the resulting pellet of ferritin particles in the appropriate volume of Ringer's solution (Huxley, 1964).

Sections were cut on a Porter-Blum microtome using glass or diamond knives. If the tissue had not been stained before embedding, the sections were stained with a 1 per cent aqueous solution of KMnO4 for 1 hour, or with lead hydroxide (Karnovsky, 1961) for 10 to 15 minutes, or with an alcoholic solution of uranyl acetate for 15 minutes at 50°C. The microscope used was a Siemens Elmiskop I, operated at 60 or 80 kv with a 50 μ objective aperture.

**Tension Measurements**

The toe muscle (extensor longus digitorum IV) was mounted vertically and the tension from it recorded by means of an RCA 5734 mechano-electric transducer valve connected to a pen recorder. For the experiments in which the muscle was stimulated directly, the level of the bath fluid was lowered to the bottom tendon, and electrical stimuli applied between a Ag/AgCl wick electrode at the top of the muscle and the bath. Stimulation was effected by means of a train of square wave pulses, each 1 msec. in duration, 1 1/4 times the strength required to give maximal response, and of a frequency to induce a smooth tetanus. For the contracture experiments, the bath was drained and refilled either with an isotonic solution of potassium methyl sulphate or with Ringer's solution containing 10⁻⁴ gm/l acetylcholine. The experiments were done at room temperature; between periods of tetanic stimulation or contractures, the muscles were bathed in oxygenated Ringer's solution containing 3 ml NaHCO₃.

**RESULTS**

In material from both the toe muscle and the rectus muscle, the two types of fibre could be distinguished in longitudinal sections by the following features. One type of fibre has relatively few mitochondria, no M lines, ill defined H zones and thick Z lines when compared with the other type (Fig. 1). These properties have already been described as characteristic of the slow fibres (Peachey and Huxley, 1962), and the absence of M lines will be used in this paper as a criterion for identifying a slow fibre. Moreover, in cross-sections as Peachey and Huxley (1962) showed, the slow fibres have large ill defined fibrils, whereas the twitch fibres as a rule contain smaller, more circular fibrils. However, in the present study, a few fibres, identified as twitch fibres by the presence of M lines and ordered Z lines (see next section), were found to have large and ill defined fibrils. Thus, the shape of the myofibrils does not provide an unfailing criterion for distinguishing between the two fibre types.

**FILAMENT ARRANGEMENT IN SLOW AND TWITCH FIBRES:** While studying the structure of the myofibrils in greater detail, further differences between the two types of fibre were observed at the level of the Z line. In twitch fibres...
there is a thickening of the I filaments on either side of the Z line (Figs. 2 a and 3 a) which extends for about 150 A. Within this region the I filaments are organised in an approximately square lattice close to their insertion into the Z line, which itself has a regular and, in part, filamentous structure (Knappels and Carlsten, 1962; Franzini-Armstrong and Porter, 1964 a; Reedy, 1964).

In contrast, no such regular organisation was observed in the neighbourhood of the Z lines of slow fibres, in which the packing of the I filaments appears to be irregular right up to the Z line (Figs. 2 b and 3 b); moreover, neither filaments nor any other internal structure can be seen within the Z line, which appears in cross-section as a dense amorphous region (Fig. 3 b).
This absence of a regular arrangement of the I filaments is probably not due to an artifact since it was quite consistently observed in the slow fibres, i.e. both when the Z lines looked quite straight, and when they appeared, as more frequently, to have a "wavy" course across the fibril (Fig. 11). These wavy Z lines, on the other hand, may well be a result of distortions in the tissue occurring at some stage of the preparative procedure. As the Z lines are always straight in twitch fibres, such distortions are apparently confined to the slow fibres. Possibly this difference may be due to the regular lattice structure in the twitch fibres providing greater mechanical resilience.

Little difference was observed in the organisation of the A filaments in the two types of fibre. (a) In both, the filaments are arranged in an hexagonal array, although this appears to be distorted more frequently in the slow fibres. (b) The interfilament distance was found to be the same in the slow and twitch fibres taken from the same muscle where the extent of shrinkage would be approximately the same. (c) In both, the I filaments occupy approximately the trigonal points in the A filament lattice.

However, there is the feature already mentioned that the M line is absent in the slow fibres (Peachey and Huxley, 1962). In twitch fibres the A filaments are thicker in the middle of the H zone, as can be seen in Fig. 4, and there are also thin, well defined cross-links between them at this level (Fig. 4) which are similar to those described in certain fish muscles (Franzini-Armstrong and Porter, 1964 c). Neither the thickening of the A filaments nor the cross-links between them have been observed in slow fibres; and possibly the frequent distortion of their filaments is related in part to the absence of such links.

**Filament lengths:** The length of the A bands is the same in the two types of fibre after the same preparative procedures (1.45 to 1.5 µ after OsO₄ fixation). Comparison of the I filaments in the slow and twitch fibres is complicated by the fact that neither fresh nor glycerinated slow fibres show sharp H zones (Fig. 1), which would mark the ends of the I filaments. A possible explanation for this could be that the I filaments are not all of the same length, and so do not produce a sharp contrast at the boundary of the H zone. To test this possibility, muscles were fixed after stretching them beyond the length where overlap occurs between A and I filaments in twitch fibres. In slow fibres, this usually results in a distortion of the Z

Figure 4 Cross-section through the M line in a twitch fibre, showing fine cross-bridges between the thick filaments at this level (arrows). Glutaraldehyde and OsO₄ fixation; uranyl acetate stain. X 107,000.
FIGURE 5 Longitudinal section through a slow fibre in a very stretched muscle, showing the gap between the A and I filaments, with its boundary nearer the I filaments roughly parallel to the Z line. (The section was cut with the knife edge parallel to the fibre axis so that there is no compression in the direction of the fibre axis.) In places the fine periodicity along the length of the I filaments can be seen (arrow). Note region of low density in the middle of the A band. Its origin is unknown, but at this sarcomere length it is clearly not the equivalent of the H zone in twitch fibres. OsO₄ fixation; PTA stain. × 22,000.

lines and of the other striations, making it difficult to measure filament lengths accurately. However, a few sarcomeres with relatively undistorted striations were found, and in these there was a region of low density between the A band and I band (Fig. 5) very similar to that observed in twitch fibres stretched to the same extent. The outline of these gaps is roughly parallel to the Z line, suggesting that the I filaments attached to these Z lines are of approximately equal length. The length of the I filaments in such preparations is found to be the same as that of the I filaments in twitch fibres after the same preparative procedure. Moreover, 24 fine periods can be counted along the length of the I filaments on either side of the Z line, (Fig. 5), i.e. the same number as in the twitch fibres, which is further evidence to suggest that the I filaments have the same length in slow and twitch fibres; i.e., 2.05 μ (Page and Huxley, 1963).

Sarcomere Lengths: In the toe muscle, the sarcomeres of the slow fibres have been found to be approximately 2/3 to 3/4 times as long as those of the twitch fibres (Fig. 1). Since, as shown above, the filament lengths are the same in the two types of fibre, the sarcomere length at which overlap is optimal for tension development (Gordon, Huxley, and Julian, 1964) should also be the same. As a consequence, the maximum in the curve relating active tension to muscle length would be expected to lie at shorter lengths for slow fibres than for twitch fibres. To test whether this is in fact true, experiments were made on three toe muscles in which the tension, developed by either the slow or the twitch fibres, was measured at various lengths of the muscle. A short tetanus was used as an index of the tension developed by the twitch fibres, whereas the maintained tension in an acetylcholine contracture was taken to represent the response of the slow fibres (Kuffler and Vaughan Williams, 1953 b). The results in all three experiments showed that the length at which maximum tension occurred was indeed shorter by about 10 per cent in the case of the slow fibres as compared with that of the twitch fibres. For example, in one experiment the ratio (optimum length for twitch fibres)/
(optimum length for slow fibres) was 1.11. In comparison, the ratio (sarcomere length of slow fibres)/(sarcomere length of twitch fibres) for the same muscle was 1.14, a result which clearly is in good agreement with prediction.

A similar difference in the optimum muscle length for tension development by the slow and twitch fibres, respectively, had already been reported for the iliofibularis muscle (Kuffler and Vaughan Williams, 1953 a), and in this muscle, too, the sarcomere lengths of the slow fibres are longer than those of the twitch fibres (unpublished observations). It may be mentioned, however, that such a difference in sarcomere length is not invariably observed in muscles containing the two types of fibre, for in the rectus muscle the sarcomere lengths of twitch and slow fibres were found to be equal.

**SARCOPLASMIC RETICULUM:** For the comparison of the structures of the sarcoplasmic reticulum in the two types of fibre, the muscle tissue was fixed either in OsO₄ solution or in glutaraldehyde followed by OsO₄. The latter method has been shown to preserve certain membranous structures better than the use of OsO₄ alone (Franzini-Armstrong and Porter, 1964 b). Also, a number of muscles were exposed to concentrated solutions of ferritin before fixation, as it had been previously found (Huxley, 1964; Page, 1964) that ferritin appears to be taken up selectively by, and may then be detected in, certain elements of the sarcoplasmic reticulum of the twitch fibres. Using this method, information could be obtained on the continuity of elements of the reticulum with the extracellular medium, and it also proved useful in clarifying structural relationships of the reticulum within the muscle fibre itself.

The organisation of the reticulum in twitch fibres, which is already known in some detail (Muscato, 1951; Franzini-Armstrong, 1963; Huxley, 1964; Page, 1964), is illustrated by the micrograph of a longitudinal section in Fig. 6. The triad structure, composed of a central element or tubule, flanked by two closely-apposed vesicles or side elements, encircles the fibrils at every Z line level. The central elements in any one sarcomere interconnect with one another to form a continuous, branching network across the fibre, and it is only in these tubules that ferritin may be identified as electron-opaque particles after suitable treatment of the muscle. Occasionally branches of this network run longitudinally from one sarcomere to the next, as can clearly be demonstrated with ferritin-loaded preparations. The side elements of the triads at either end of the sarcomere are connected by longitudinal tubules, approximately 500 to 800 A in diameter. In the middle of the sarcomere these tubules fuse to form an almost continuous sleeve around the fibril. However, in grazing (longitudinal) sections of the reticulum, small circles (approximately 300 to 400 A in diameter) may be seen in this region (Porter and Palade, 1957; Franzini-Armstrong, 1963), probably representing cross-sections through cylindrical channels which traverse the reticulum at this point. That these circles are indicative of cross-channels rather than of pores in the membrane (Franzini-Armstrong, 1963) is suggested (a) by the density and sharpness of their outlines which closely resemble those of sectioned membranes, and (b) by the fact that in longitudinal sections, passing approximately through the axis of the sleeve, the reticulum is frequently seen to be interrupted by narrow transverse gaps of width similar to the diameter of these circles (Fig. 6).

In the slow fibres, the most prominent structure of the reticulum, observable after fixation with

![Figure 6](https://example.com/figure6.png)
either of the two methods described, consists of a network of tubules, approximately 500 to 800 A in diameter, which is rather similar in appearance to the network of tubules connecting the side elements of the triads in twitch fibres. The tubules surround the fibrils and lie roughly parallel to the fibre axis, often continuous from one sarcomere to the next, and with numerous transverse connections between them at the I band level (Fig. 7). However, a fusion to a more continuous structure in the centre of the sarcomere, as in twitch fibres, has not been observed. Ferritin does not appear to be taken up by this system, as may be seen from Fig. 11.

It has been thought (Peachey and Huxley, 1962) that slow fibres do not contain the triad structure characteristic of twitch fibres, and indeed the majority of the slow fibres fixed with OsO4 solutions in the present study did not show any triads. In contrast, however, triads could be found in all those slow fibres (14 fibres from 8 toe muscles; 15 fibres from 3 rectus muscles) which were first fixed with glutaraldehyde. The triads are located at the level of the Z line, with the central element lying either transversely as in twitch fibres or, alternatively, parallel to the fibre axis (Fig. 8). The side elements appear to be continuous with the network of tubules described above. Unlike those of twitch fibres, the triads in slow fibres are not very frequent, being associated with only every 5th or 6th sarcomere of any fibril.

In addition to these structures bearing some resemblance to those present in twitch fibres, an extensive system of small cylindrical tubules (approximately 300 A in diameter) could be discerned in the glutaraldehyde-fixed slow fibres. A great proportion of these tubules run transversely through the interfibrillar space of almost every sarcomere, encircling the myofibrils at approximately Z line level, as seen in Fig. 9. Others, about one per fibril or every other fibril, are oriented roughly parallel to the fibre axis (Fig. 10), and these can be seen in places to be continuous with the tubules lying transversely. However, connections of this system with that of the larger tubules described above were not observed, although where triads occur, their central elements appear to be continuous with the thin tubules so that the 2 systems of small and large tubules are in close association in such regions. The thin tubules closely approach the surface membrane at various levels of the sarcomere, but direct continuity has not been observed. Nevertheless, in ferritin-loaded muscles (Fig. 11) the ferritin particles could be identified in both the transversely and longitudinally oriented thin tubules and also, as in twitch fibres, in the central elements of the triads. This pattern of distribution confirms the continuity of this system across the fibre and with the central elements of the triads, and also its separateness from the system of larger tubules which, as already mentioned, remain free of ferritin particles.

**MOTOR ENDINGS:** The motor nerve endings on slow fibres are clearly distinguishable from those on twitch fibres which have been described by Birks, Huxley, and Katz (1960). In the region of contact, the small diameter nerve fibres form bulbous structures lying on the surface of the muscle. These are roughly oval in shape, being up to 6 or 7 μ in length with a cross-sectional diameter of 2 or 3 μ, or sometimes more nearly spherical (Fig. 12). These terminals are densely grouped in some areas of the fibre surface; in one section 10 junctional regions were found within a distance of 80 μ along the length of the fibre. In their size and distribution, therefore, the bulbous structures correspond to the "varicosities" of small nerve endings observed in the light microscope (Couteaux, 1952; Gray, 1957).

Another characteristic feature of the slow fibre junctions is the almost complete absence of any junctional folds of the muscle membrane which are present in twitch fibres (Couteaux, 1955; Birks, Huxley, and Katz, 1960). (Only two small folds have been seen when examining the junctions on 15 fibres from 10 muscles.) This confirms Couteaux's (1960) observations on slow fibre endings stained for cholinesterase, viewed in the light microscope.

**Figure 7** Longitudinal section through a slow fibre showing the appearance of the sarcoplasmic reticulum after OsO4 fixation. The tubules are oriented longitudinally (l), with transverse elements (t) at the Z line level. They are frequently seen to be continuous from one sarcomere to the next across the Z line (e.g. at c). OsO4 fixation; PTA stain. × 20,000.
In other respects, the junctional regions are similar to those on twitch fibres (Birks, Huxley, and Katz, 1960). The nerve is covered on one side by a Schwann cell (Figs. 12 and 13) which does not penetrate into the region of contact between the nerve and muscle. The terminals contain mitochondria and the two types of vesicles seen in twitch endings: one group with diameters 350 to 500 A, and another type, of much less frequent occurrence, of 900 to 1100 A diameters which contain small granules (Fig. 12). In the region of contact, the nerve and muscle plasma membranes

**FIGURE 8** Longitudinal sections through slow fibres, showing the presence of triad structures after both OsO$_4$ and glutaraldehyde fixation. The triads lie at the Z line level, oriented either transversely or longitudinally.

Fig. 8a, OsO$_4$ fixation; PTA stain. Fig. 8, b, c, and d, glutaraldehyde and OsO$_4$ fixation; lead stain. X 46,000.
DISCUSSION

The most interesting result of this study is the demonstration that the sarcoplasmic reticulum of the slow fibres, like that of the twitch fibres, consists of two separate networks of tubules, one set lying largely longitudinally and the other, of smaller diameter, being both transversely and longitudinally oriented. In its structural relationships this second set of thin tubules appears to be the counterpart of the tubular system forming the central elements of the triads in the twitch fibres, i.e., the T system (Andersson-Cedergren, 1959); both constitute a continuous network across the fibre, in contact with each fibril, separate from the other elements of the reticulum, and since both take up ferritin, they may have the same relationship to the surface membrane. This close structural similarity suggests that the two systems may have similar functions: e.g., the T system in twitch fibres is thought to be the pathway for the inward conduction of the effect of depolarisation of the surface membrane (Huxley and Taylor, 1958; Andersson-Cedergren, 1959), and the thin tubules may provide the equivalent pathway in slow fibres. Unlike the T system of twitch fibres, however, the thin tubules in slow fibres reach the surface of the fibre at the level of the A band in some sarcomeres, as well as at the Z line level. This difference might account for the finding that in slow fibres a local contraction could be obtained at any level of the sarcomere following depolarisation of a small area of the surface membrane (Peachey and Huxley, 1960), whereas in twitch fibres the sensitive areas were found to be restricted to the Z line level (Huxley and Taylor, 1958).

Previously, when it was thought that there was no transverse tubular system in slow fibres, it was suggested that excitation-contraction coupling might occur by diffusion of an activator from the surface following depolarisation (Peachey, 1961). But as the existence of the thin tubules now suggests the possibility of much faster activation of the whole fibre than by diffusion from the surface, it becomes of considerable interest to know whether the slow development of tension by these fibres is in fact due in part to a slow spread of activation or to a slow rate of the reactions between the filaments which produce the tension. Some of the findings of Kuffler and Vaughan Williams (1953 b) indicate that this latter process is in fact slow, for when they briefly stretched an iliofibularis muscle during a maintained isometric contraction, thereby abolishing tension, they found that the subsequent redevelopment of tension was slow, although the time resolution was not sufficient to determine whether it was as slow as the initial rise of tension.

There is another property of the twitch fibres apparently involving the T system where comparison may be made with the slow fibres and the system of thin tubules. The value obtained for the membrane capacitance of twitch fibres when measured with internal electrodes is high (5 to 8 uF/cm², Fatt and Katz, 1951) compared with squid axon (1 uF/cm², Hodgkin, Huxley and Katz, 1952), for example. Part of this capacitance is thought to arise in the walls of the T system (Falk and Fatt, 1964) whose area may be an estimated 5 to 9 times the fibre surface area. In the slow fibres, on the other hand, the contribution of the walls of the thin tubules to the total surface area is much less, mainly because the fibrils in the slow fibres are much larger. Thus, for a cylindrical fibre (50 µ in diameter) packed with fibrils (1 µ X 2 µ in cross-section) which are surrounded for 3/4 of their circumference at each sarcomere by a transverse tubule (300 Å in diameter) and which have one longitudinally oriented thin tubule per sarcomere (2.5 µ long), the tubular surface area is approximately equal to the surface area of the fibre. This estimate of a small tubular surface area in slow fibres compared with that in twitch fibres agrees with the finding that the slow fibres have a relatively low membrane capacitance (Adrian and Peachey, quoted by Adrian, 1964).

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FIGURE 9 Longitudinal section through a slow fibre fixed in glutaraldehyde and then OsO₄. At each sarcomere there are thin tubules (arrows) which run transversely around the fibrils at approximately the Z line level. In this section the thin tubules are distinguishable from the larger tubules by the presence within them of small dense granules which are occasionally found when the muscle is kept in Ringer’s solution for sometime before fixation, as in this case. The particles, which are also found in the triad central elements of the twitch fibres in the same muscles, are soluble in EDTA, but their constitution and the conditions under which they form are not known. Glutaraldehyde and OsO₄ fixation; lead stain. X 48,000.
Figure 10. Longitudinal section through a slow fibre fixed in glutaraldehyde and then OsO₄. Thin tubules can be seen crossing the fibre at each Z line (vertical arrows) and also lying longitudinally (horizontal arrows). Near the bottom horizontal arrow the longitudinal tubule appears as a row of short tubules, presumably because it runs in and out of the plane of the section. Glutaraldehyde and OsO₄ fixation; lead stain. × 35,000.
Figure 11. Longitudinal section through a slow fibre from a muscle which had been soaked in Ringer's solution containing ferritin before fixation. The small dense dots of ferritin occur within the thin tubules which run longitudinally between the fibrils and transversely at the Z line level (see Figs. 9 and 10). Although their membranes are not very distinct because the section is unstained, it can be seen that the larger tubules do not contain any ferritin (asterisks). Glutaraldehyde and OsO_4 fixation; no stain. × 54,000.
FlavRE 13 Cross-section through a motor nerve ending on a slow fibre, showing the Schwann cell (S) covering the ending, and the single basement membrane (b) between the nerve and muscle. OsO₄ fixation; KMnO₄ stain. × 37,000.

Figure 12 Longitudinal section through two motor endings on a slow fibre. The nerve terminals are covered by a Schwann cell (S) and contain mitochondria and two types of vesicles, one smaller and empty, the other larger and containing granules (arrows). The muscle plasma membrane is thickened beneath the nerve ending (p), but has no infoldings. OsO₄ fixation; PTA stain. × 15,000.