

Myotendinous Nerve Endings in Human Infant and Adult Extraocular Muscles

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ABSTRACT

Myotendinous nerve endings in extraocular muscles of some mammals consist exclusively of palisade nerve endings incorporated in myotendinous cylinders. There is evidence for a similar form in man, some doubt remains. The objectives of the present study were to examine the structure and distribution of nerve endings in extraocular muscles of infant and adult human material. Muscles from five infants and six adults aged 3 days to 90 years were prepared for light and electron microscopy. Nerve endings were sparse in a 4-year-old and none were present in the muscles of younger donors. They were present in all adult samples. One group of nerve endings branched from single recurrent nerve fibers and were distributed in the encapsulated tendon of single Felderstruktur muscle fibers. Terminals were varicose and shared certain characteristics of known sensory endings and were similar to those of myotendinous cylinders except that none formed neuromuscular junctions. In other myotendinous complexes capsules were fragmented and nerve endings were dispersed in tendon common to two or more muscle fibers. In the myotendon of two adult donors, a further group of endings issuing from non-recurrent nerves were unencapsulated and distributed randomly in tendon. The frequency of nerve endings varied across myotendon and in some instances, most marked in one case, large areas lacked nerve endings. Golgi tendon organs were not present. The terminals having features characteristic of sensory endings suggest a proprioceptive function, which is apparently unavailable in infancy. In mature muscles, the irregular distribution and variety of terminal form cannot be equated with those found in extraocular muscles of animals. We suggest that these features reflect an aberrant development and conclude that their capacity to fulfil an effective proprioceptive role is open to question. *Anat Rec* 260:132–140, 2000. © 2000 Wiley-Liss, Inc.

Key words: extraocular muscles; myotendinous nerve endings; human; proprioception

In some mammalian species, extraocular muscles (EOM), in common with most skeletal muscles, contain muscle spindles and Golgi tendon organs (GTO). In others, spindles are absent and myotendinous nerve endings lack the classical characteristics of the GTO (Barker, 1974). Whether or not an animal possesses spindles is broadly agreed whereas, the position with regard to GTO and other myotendinous nerve endings remains unresolved in some species. Dogiel (1906) identified GTO in the EOM of several species and he also described various other forms of myotendinous nerve endings including palisade end-

ings, which were predominant. The latter consists of myelinated fibers passing from muscle to tendon and turning back and branching to form palisades surrounding muscle fiber tips. The presence of palisade endings was confirmed

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in monkeys, cats, and rabbits by Tozer and Sherrington (1910), who found all nerve endings to be of this type. Their ultrastructure has been studied in cats by Alvarado-Mallart and Pinçon-Raymond (1979) and in monkeys by Ruskell (1978) who also noted one or two GTO in some, but not all, EOM. The terminals, the single muscle fiber tip they invest, and the attached tendon, are enclosed by a thin fibroblast-like capsule and the complex has been called a myotendinous cylinder (Ruskell, 1978). On the basis of their morphology they are assumed to be sensory nerve endings.

Views on the identity of myotendinous nerve endings in human EOM differ. Dogiel (1906) found palisade endings in each of the six species he examined, which included man. In later studies, the tendon nerve endings in human EOM were regarded as GTO-like (Cooper and Daniel, 1949; Cooper et al., 1955), but a description of their form was not given and an illustrated terminating arborizing nerve fiber in the proximal tendon had more in common with a palisade ending than a GTO. However, Bonavolontà (1956) also considered a rare terminal, which he illustrated, to be a simple version of the GTO. In contrast, distal myotendinous nerve endings with palisade characteristics were identified using silver impregnation technique, in infant and adult material, but they could not be demonstrated in all muscles (Richmond et al., 1984). No GTO were found. Three varieties of nerve fibers were identified with electron microscopy in adult human samples, each of them terminating in partly encapsulated tendon/muscle fiber complexes, but they were not observed in all samples (Sodi et al., 1988). Again, no evidence of GTO could be found. The objectives of the present work were to review the apparent irregularity of the incidence of myotendinous nerve ending, and to compare their structure in human infant and adult muscles. Some of the results were referred to briefly in a recent report (Ruskell, 1999).

MATERIALS AND METHODS

For the study of the distal myotendon of infant EOM, material was first collected from patients undergoing strabismus surgery which, with swift fixation, offered the best opportunity for optimal tissue preservation. Unfortunately, the samples were frequently crushed and rarely contained muscle tissue and this source was abandoned in favor of postmortem material. Seven rectus muscles from five infants aged from 3 days to 47 months were obtained and fixed up to 10 hr after death (Table 1). Death occurred due to failed cardiac surgery, infection, or accident and in each case the muscles were adjudged to be suitable for the study. Eight muscles from six adults were removed during surgery to enucleate blind painful eyes or for choroidal melanoma and none of the patients had a previous history of binocular visual abnormality or neuropathy. Anterior parts of muscles including the tendon were removed and immersed in 5% glutaraldehyde, buffered to pH 7.4 with sodium cacodylate, and stored in a refrigerator for a minimum of 1 week before further preparation. Adult muscles were then cut into three to six longitudinal strips and infant muscles left whole (Fig. 1a) and immersed in cold buffered sucrose overnight. After washing, tissues were immersed in a 1% solution of unbuffered osmium tetroxide for 1 hr, then dehydrated in graded ethanols, cleared in xylene, and embedded in Araldite. Tissues were placed in a rotator at each of the stages following osmication and

TABLE 1. Sources of Myotendon

Ref.	Age	Sex	Muscles*	Interval before fixation
HC8	3 days	M	MR	7h (est.)
HC4	6 days	M	IR	10h
HC2	5 months	M	MR, IR	7h
HC6	30 months	M	MR, IR	1h
HC1	47 months	F	IR	3h
HW3	25 years	M	LR (part)	minutes
HW20	35 years	M	MR, LR	—
HS1	52 years	F	MR	—
HW28	73 years	M	SR	—
HW4	74 years	M	MR, SR	—
HW11	90 years	F	SR	—

*MR, IR, LR, SR: medial, inferior, lateral, and superior rectus muscles.

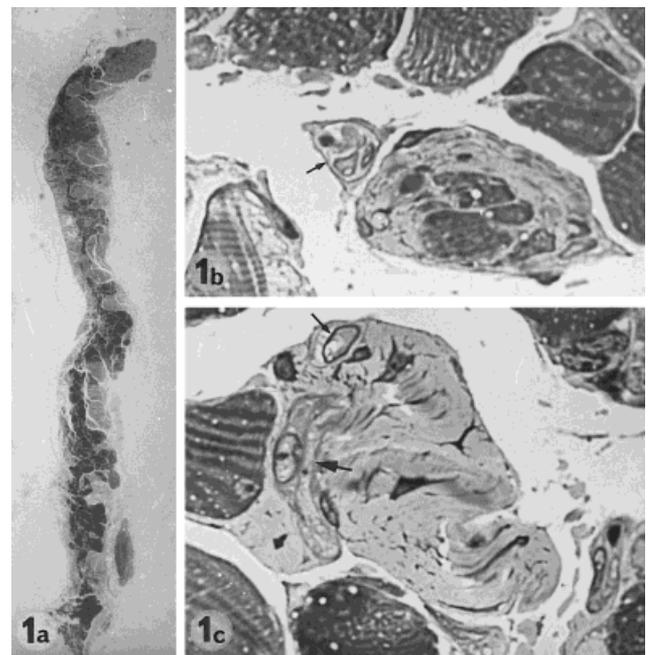


Fig. 1. **a:** Transverse section of a whole medial rectus muscle at the distal myotendinous junction. The termination of the dark muscle fibers occurs irregularly across the width of the muscle, age 5 months. $\times 20$. **b:** The split tip of an encapsulated muscle fiber with an adjacent small nerve (arrow). Inferior rectus, age 47 months. $\times 390$. **c:** A myelinated nerve fiber (small arrow) and a preterminal axon (large arrow) in myotendon. The axon is enclosed by a Schwann cell sheath with a prominent nucleus. Inferior rectus, age 47 months. $\times 390$.

the embedding procedure began by rotating tissues overnight at room temperature and completed by incubation in fresh Araldite-filled trays at 60°C in an oven for 48 hr.

Serial transverse sections 0.75 μm thick were prepared from infant samples and all sections were collected. Sections were collected at approximately 100 μm intervals in the adult samples progressing from muscle to tendon and on reaching the first evidence of tendon, every fifth section, and in areas of special interest, all sections were collected. Ultrathin sections were prepared for electron microscopy at varying intervals. Semi-thin sections were stained in equal parts of 1% toluidine blue and 2.5%

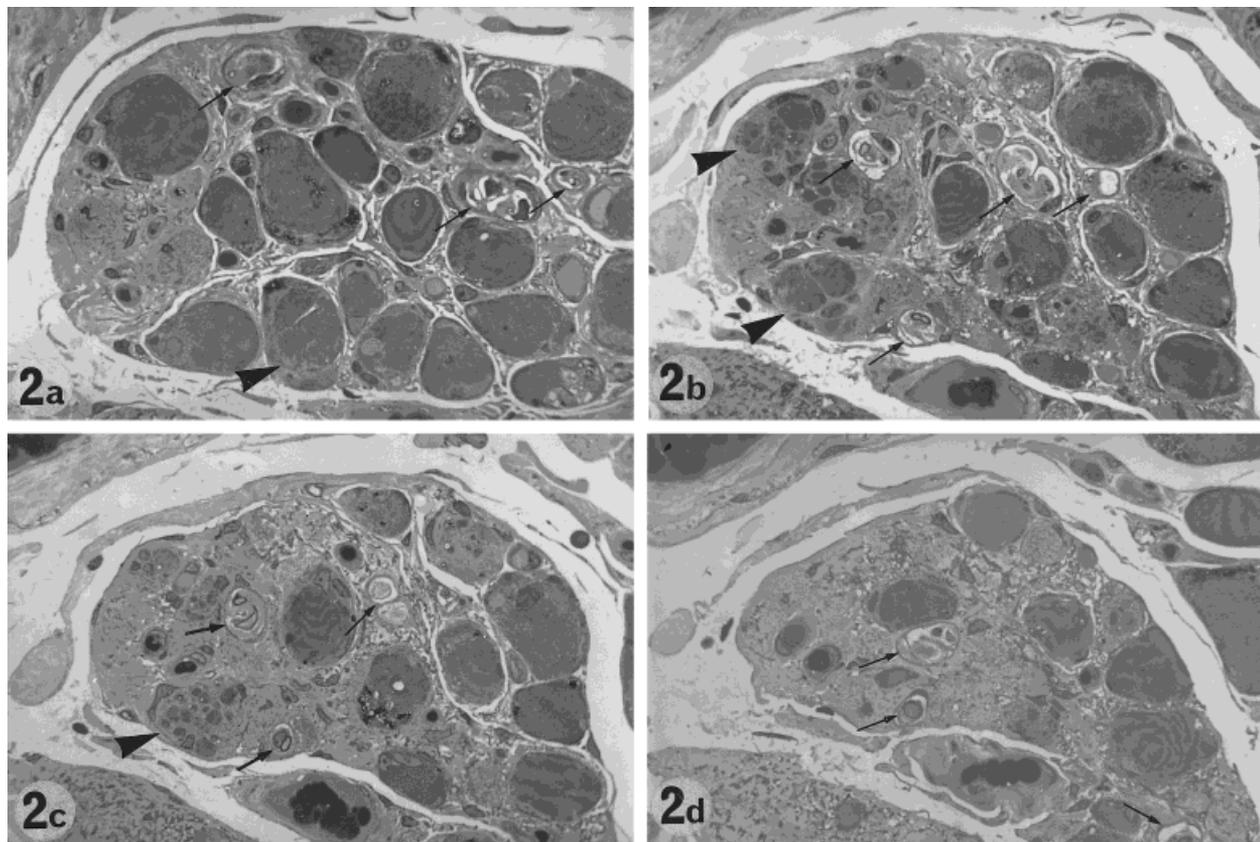


Fig. 2. Four sections of a myotendinous region taken at intervals of approximately 50 μm . Muscle fibers split into several processes (arrowheads) before terminating and myelinated nerve fibers, pass from muscle into tendon (arrows). All muscle fibers are of the Felderstruktur type. Medial rectus, age 74 years. $\times 445$.

sodium carbonate and those for electron microscopy were collected on unfilmed copper grids and immersed in a saturated solution of uranyl acetate in 70% ethanol for 20 min followed, after washing, by immersion in a solution of lead citrate in 0.1 M sodium hydroxide. A few longitudinally cut sections were prepared.

RESULTS

Infant Myotendon

With one exception, no nerve fibers were found in the myotendon of infant muscles. There were a few small nerves in the distal halves of the muscles with an average content of two myelinated and two unmyelinated fibers and the anterior-most nerves were usually a substantial distance from tendon. The absence of tendon terminals

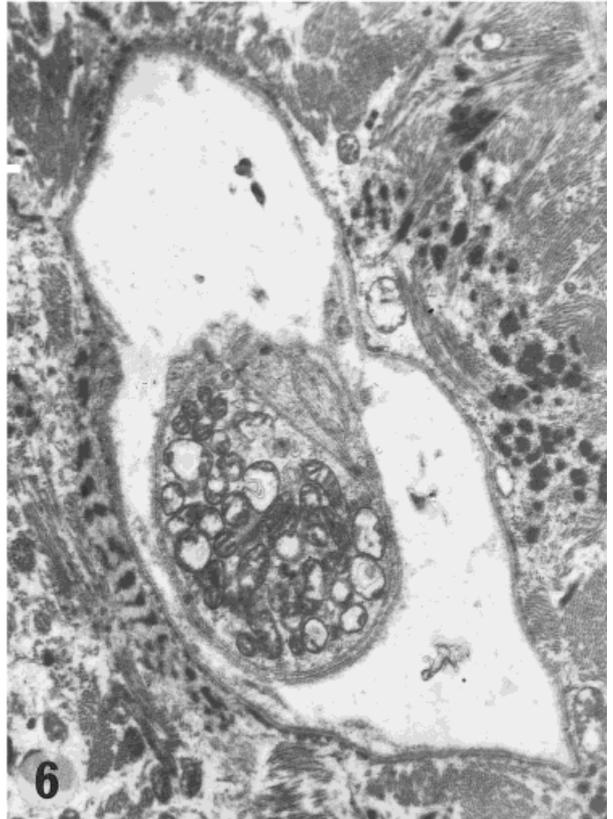
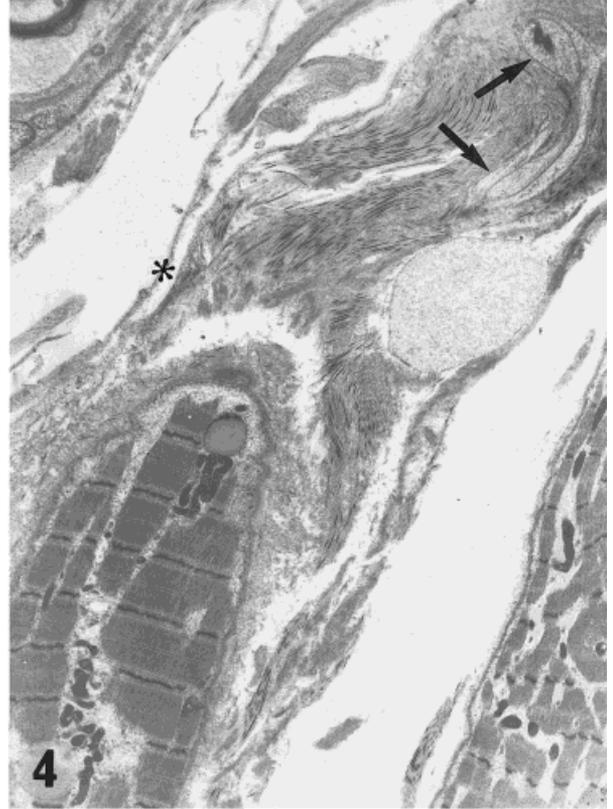
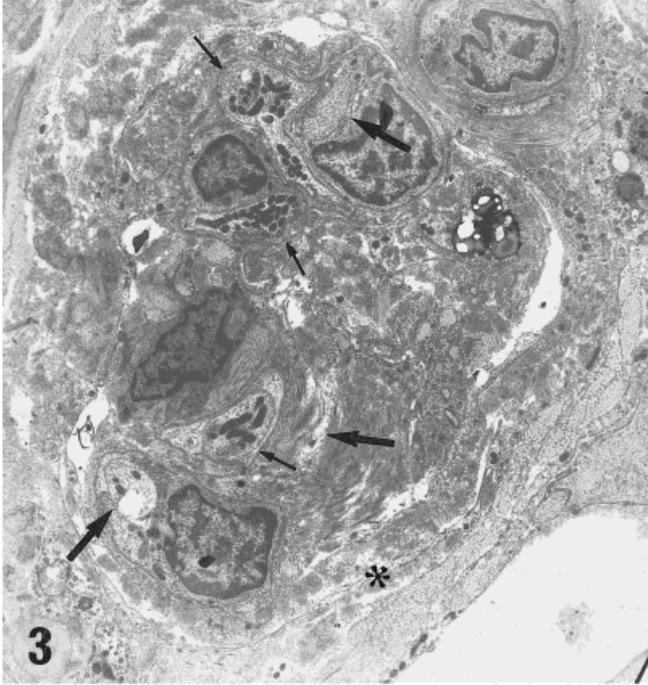
was unexpected and the few nerves present were presumably motor serving multi-innervated Felderstruktur fibers or precursors of tendon terminals. The 47-month preparation provided the single exception. In this case a few scattered myotendinous nerves were present, each one with one or two nerve fibers (Fig. 1). Eight small areas of the muscle containing nerves reaching tendon were identified, with one to three nerves in each. Large areas of tendon had none. On reaching myotendon they immediately turned into tendon associated with single split muscle fiber tips (Fig. 1b) and sometimes with more than one muscle fiber. Such myotendinous units or complexes were partly encapsulated by thin fibroblast-like processes, and in two instances the encapsulation was complete. Myelin was shed on reaching tendon and terminals were buried in

Fig. 3. A richly innervated tendon compartment of an encapsulated (asterisk) complex. Preterminal axons (large arrows) and mitochondria-filled varicose terminals (small arrows) infiltrate the collagen. Medial rectus, age 74 years. $\times 4,800$.

Fig. 4. Longitudinal section through a myotendinous complex. Note the merging of the myofibrils in the encapsulated (asterisk) Felderstruktur muscle fiber compared with the separate, less densely stained myofibrils of the Fibrillenstruktur fiber (right). Nerve fibers (arrows) are directed towards the muscle fiber. Superior rectus, age 90 years. $\times 2,270$.

Fig. 5. Muscle compartment of a myotendinous complex. The muscle fiber has several processes and a single large invagination. Typically, the nerve preterminals (arrows), or palisade endings, infiltrate between the fiber tip processes. The fine capsular sheath (asterisk) is incomplete. Medial rectus, age 35 years. $\times 4,100$.

Fig. 6. A Nerve fiber at a large preterminal varicosity within a muscle fiber invagination. The preterminal has a complete Schwann cell sheath and does not contact the muscle fiber. Superior rectus, age 90 years. $\times 14,170$.



Figures 3-6.

the tendon, none reaching the level of the muscle fiber tips.

Adult Myotendon

Numerous small nerves, mostly containing one or two myelinated nerve fibers and rarely more than six, and usually fewer unmyelinated fibers, passed forward from distal muscle towards tendon. Many of them continued into tendon for a short distance but none were present beyond approximately 100 μm (Fig. 2). Nerves shed their perineurium and most of the nerve fibers looped back towards muscle before losing their myelin sheath, branching, and terminating in the tendon of single muscle fibers or in tendon common to several muscle fibers. Only tendon of darkly-stained muscle fibers with poorly defined myofibrils and limited sarcoplasmic reticulum received terminals; these were recognized as the slow Felderstruktur multi-innervated type that do not generate an action potential. The muscle fibers were split into several finger-like processes and invaginations at their terminations (Fig. 2), and each fiber tip, together with its attached tendinous collagen, was partly or completely enclosed by thin fibroblast-like capsular cells, lacking a basal lamina, to form myotendinous complexes (Figs. 3 and 4). While complete encapsulation was rare in the infant sample, it was quite common in adults.

The recurrent path of the myelinated nerve fibers could be followed with facility in the serial sections. The preterminal/terminal branches consisted of fine unmyelinated axons containing neurofilaments and microtubules with large varicosities containing, in addition or exclusively, numerous mitochondria with or without small clusters of small agranular vesicles (Fig. 3). The terminals had a Schwann cell investment which was continuous except at infrequent sites opposite the varicosities. Most of the varicosities were located in the tendon compartment of the complexes and others penetrated further to lie among the muscle fiber tip processes (Fig. 5) or within muscle invaginations (Fig. 6). They frequently lay very close to muscle without making direct contact with muscle cell plasma membranes. Direct contacts were expected as they are known to be present in cat and monkey EOM myotendon, but careful examination revealed none. Where encapsulation was incomplete, nerve endings were still related to single muscle fibers in many instances but often they were spread more broadly in tendon relating to two or more muscle fibers.

Another distinct group of nerve terminals was noted. Rather than taking a recurrent course, on reaching tendon, nerve fibers branched and were distributed laterally among the collagen and elastic fiber bundles forward of the muscle fiber tips (Fig. 7). They were therefore unrelated to individual muscle fibers and apparently randomly distributed. Their structure was similar to nerve endings of the complexes except that mitochondria-rich varicosities were more frequent and variable in shape. They widened and were constricted according to the constraints imposed by the surrounding connective tissue, particularly the numerous elastic fibers (Fig. 8). The intervaricose axons and most varicosities had a Schwann cell investment but occasionally the varicosities were exposed to the surrounding tissues, separated from them by the basal lamina alone. Where this occurred, vesicles were aggregated opposite foci of increased plasma membrane density

(Fig. 9). This feature was not seen in the terminals of recurrent nerve fibers.

Innervation Density

There was a substantial difference within single adult muscles in the frequency of nerve endings in the complexes. In some they were numerous (Fig. 3) with up to ten profiles in single cross sections, while many others contained only one or two, when varicosities were often not observed. Complexes without nerve endings were very common and were disposed among the innervated complexes or were aggregated. Tendon areas up to twice that illustrated in Figure 2 without innervated complexes were frequent and in some muscles they were substantially larger. In one exceptional case (Table 1—HW20,LR), about 80% of the myotendon was uninnervated and complexes containing nerve endings were confined to a single area (Fig. 12).

Motor Nerve Fibers

A proportion of the nerve fibers present in the anterior parts of muscles proximal to myotendon were predicted to be motor, terminating on multi-innervated Felderstruktur muscle fibers and numerous examples were found, sometimes very close to muscle fiber tips (Figs. 10 and 11). They invariably contained large numbers of synaptic vesicles and aggregated mitochondria. An unexpected finding was the occasional presence of much larger motor end-plates on Fibrillenstruktur fibers, again sometimes quite close to tendon; motor end-plates are generally considered to form a band located across the posterior part of the middle third of EOM in man.

DISCUSSION

The results show that myotendinous nerve endings were absent from the youngest muscles, sparse and apparently immature at 47 months, and present in adult muscles. Assuming the seven muscles studied from five young individuals to be representative, we conclude that development of the nerve endings is delayed until after infancy. The possibility that terminals were overlooked was reduced by preparing complete serial sections, and identification of nerve fibers and myotendinous complexes presented little difficulty.

In the context of present understanding of muscle receptor development this result is extraordinary. Sensory nerve fibers generally appear in muscles prenatally during myotube development with end-organs showing recognizable characteristics at birth and maturing within 2–3 weeks. For example, the GTO of skeletal muscle tendon are present at birth; nerve terminals, in contact with muscle fibers in the newborn rat, withdraw at 5 days and the receptors adopt their mature structure at 2–3 weeks (Tello, 1922; Zelená and Soukup, 1977). In the only previous report of human infant myotendon innervation in EOM, terminals were found in three specimens obtained from 12 children aged 9 months to 10 years undergoing surgical correction for strabismus (Richmond et al., 1984). Some of the resected specimens were composed only of tendon and it was not made clear whether this factor explained why terminals were found in only three specimens. In light of our results, it is possible that some of those in which terminals were not found were myotendon specimens lacking terminals and that the three inner-

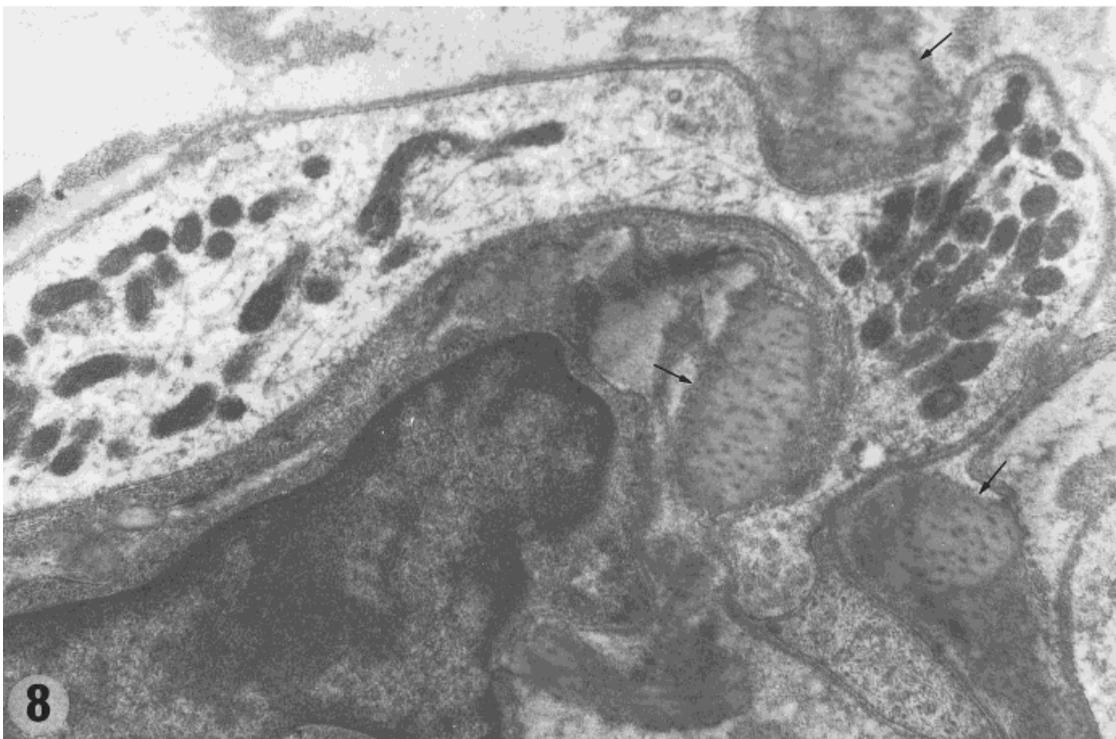
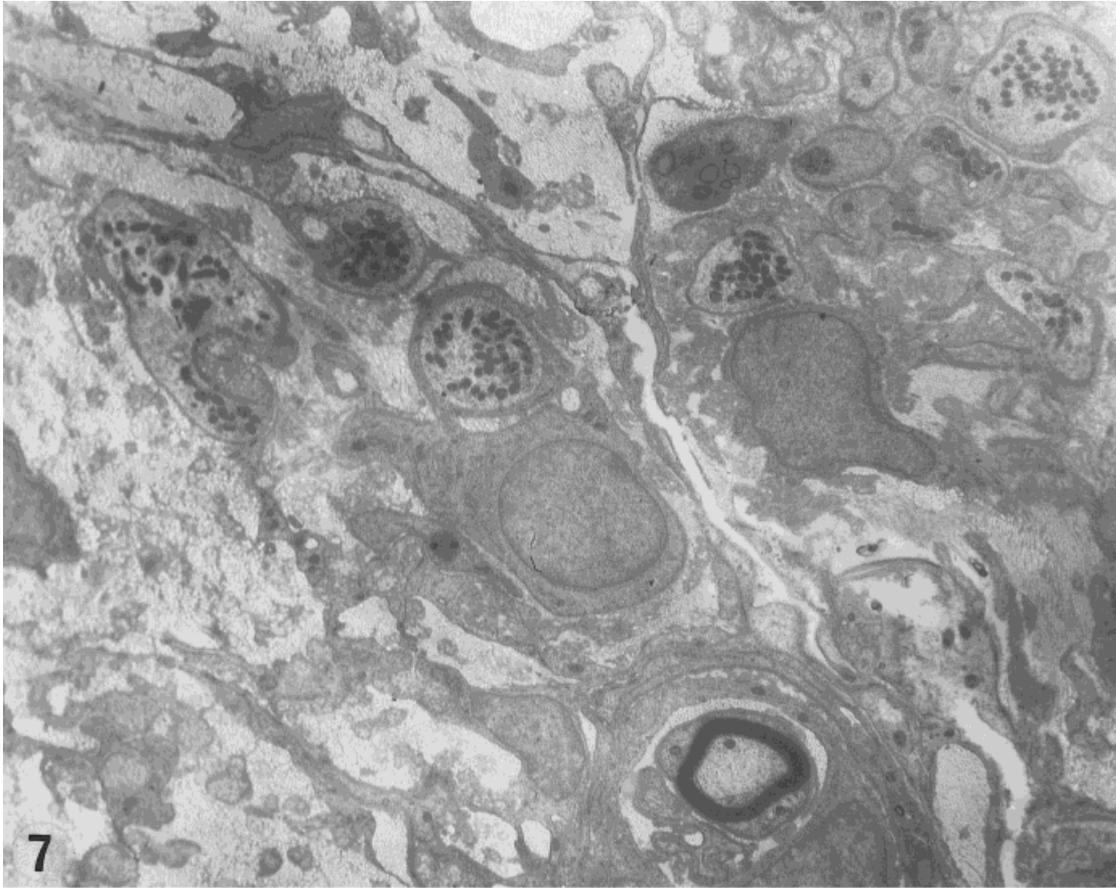


Fig. 7. Tendon beyond the muscle fiber tips with a non-recurrent myelinated nerve and numerous dispersed terminal varicosities containing large numbers of mitochondria. Medial rectus, age 74 years. $\times 6,780$.

Fig. 8. Detail of a dispersed preterminal branching and threading between elastic fibers (arrows). The Schwann cell investment is discontinuous, exposing much of the preterminal axon to the surrounding collagen. Medial rectus, age 74 years. $\times 21,100$.

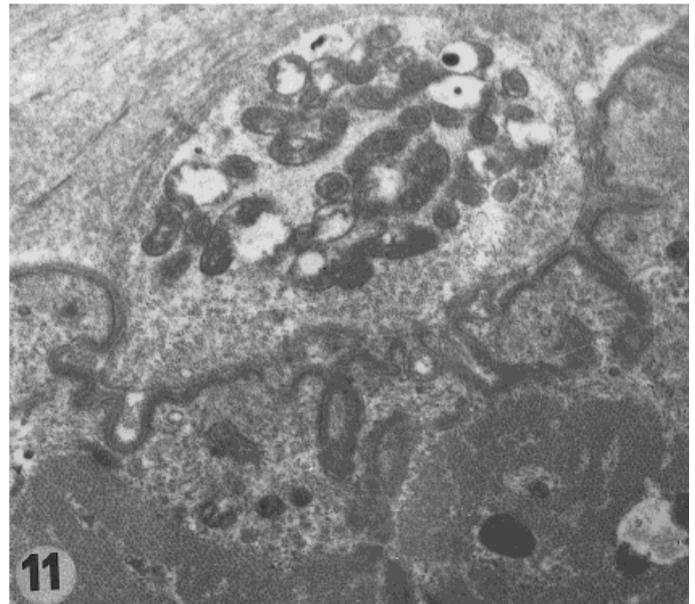
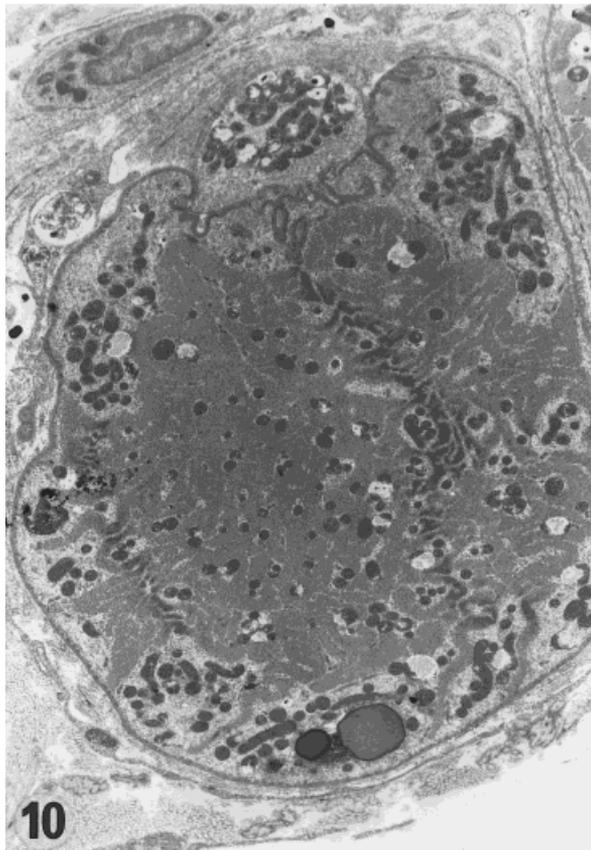
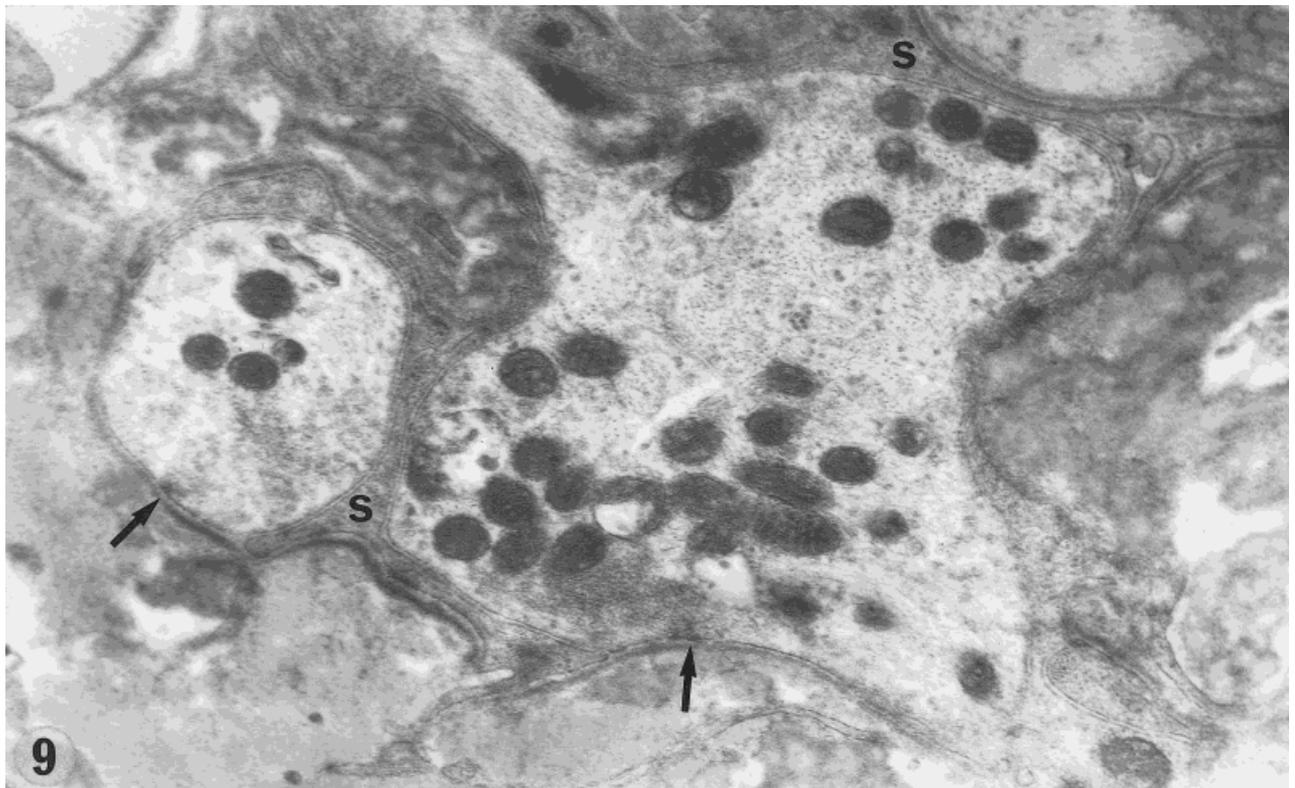


Fig. 9. Detail of a branching tendon preterminal containing neurofilaments, microtubules, mitochondria, and clusters of small agranular vesicles. The vesicles are aggregated close to the surface opposite plasma membrane densities (arrows). In these positions the terminals are exposed to the surrounding collagen. s; Schwann cell investment. Medial rectus, age 52 years. $\times 18,480$.

Fig. 10. A motor nerve terminal (en grappe) on a Felderstruktur muscle fiber close to myotendon. Superior rectus, age 90 years. $\times 6,730$.

Fig. 11. Detail of the nerve terminal of Figure 10. $\times 17,500$.



Fig. 12. Montage of a lateral rectus muscle with an outline drawing to show the single area with myotendinous nerve endings (circles). The section corresponding to the indicated area is largely of myotendon. Other areas, composed of either muscle (right) or tendon (left), when sectioned at myotendon level bore no terminals. Age 35 years, marker: 1 mm.

vated specimens (age not stated) were taken from older members of the group.

The lack of terminals in the early years is of particular interest because it has implications for the potential role of muscle receptors in visual development. Binocular visual development is considered to be dependent upon proprioceptive feedback from the extraocular muscles in cats. For example, following interruption of feedback by sectioning the ophthalmic nerve, deficits in visually guided behaviour were noted, but only in the developing animal (Hein and Diamond, 1983; Trotter et al., 1987). In another study, again using cats, it was shown that muscle proprioception was necessary for the development of normal depth perception (Graves et al., 1987). Cat EOM lack spindles (Maier et al., 1975), but have many myotendinous nerve endings, and it is argued that they are the receptors providing proprioceptive feedback, although it is worth noting that nerve endings have not been studied in kittens. During the crucial years for binocular visual development, our results show that myotendinous nerve endings are not present in man so, if a similar function obtains, proprioception must be the responsibility of other terminals. Muscle spindles are present, but following detailed structural analysis, their viability as proprioceptors in adult and infant specimens was considered doubtful (Ruskell, 1989; Bruenech and Ruskell, 1993). Consequently, these anatomical studies offer no support for the involvement of proprioception in binocular visual development in man.

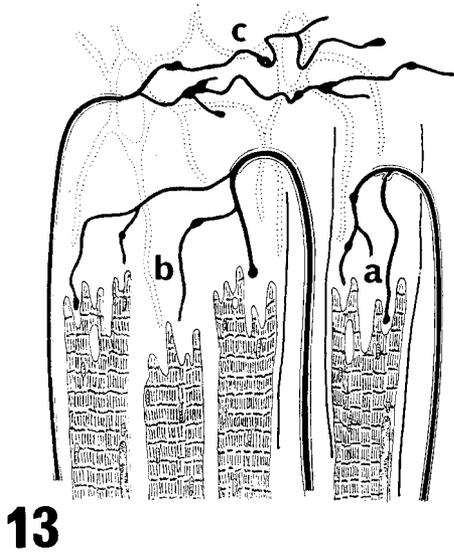
The present results also have relevance for a clinical topic concerning proprioception in the young strabismus patient. It has been shown that patients who have undergone repeated EOM surgery have an altered ability to recognize their eye position (Steinbach and Smith, 1981). Since the surgery damages tendon it has been suggested that the disability might be attributable to the destruction of tendon receptors. However, in the absence of myotendinous nerve endings in the early years, surgical lesion of the myotendinous region clearly could not affect awareness of eye position and visual spatial perception resulting from direct receptor damage, at least not in the younger child.

Turning to the subject of adult human receptors, some variation in form was noted in agreement with the results of the only previous publication on their ultrastructure

(Sodi et al., 1988), but in matters of detail present findings differ. Were EOM representative of skeletal muscle one might expect to find GTO but terminals precisely fitting their description have not been noted in man, although tendon organs resembling GTP were reported (Cooper et al., 1955). However, in more recent work, GTO were not found (Richmond et al., 1984; Sodi et al., 1988), nor were they observed in the present study and it appears safe to conclude that GTO are not present in human EOM. Sodi et al. (1988) observed incompletely encapsulated myotendinous complexes which received a richly arborizing nerve, although they were not found in all samples. Similar complexes are described in this report, but many of them were fully encapsulated and the arbors were often sparse. Where the capsule was incomplete the terminals were often spread broadly in tendon relating to two or more muscle fibers. Many of the complexes contained a blood vessel according to Sodi, whereas in our material, although vessels were frequent, none was seen within fully encapsulated complexes. Another group of terminals, unencapsulated and lying distal to the others were observed regularly in the tendons of two donors, and consisted of randomly distributed terminal arborizations branching from non-recurrent nerve fibers, unrelated to specific muscle fiber groups.

Not all encapsulated single muscle fiber tips and their attached tendon received nerve endings, even in regions rich in nerves. Parts of the tendon were totally free of nerves in most muscles and in some these areas were extensive. This factor is arguably consistent with the statement that 'receptors were found in the majority of samples examined' (Sodi et al., 1988). In one muscle, terminals were restricted to a single small region.

Can human myotendon nerve endings be equated with those of animals, as has been suggested (Richmond et al., 1984)? A proportion of the complexes described here share some key features of animal myotendinous cylinders (MTC)—the muscle fibers were exclusively Felderstruktur, varicose palisade terminals were derived from recurrent nerve fibers and the muscle and tendon compartments were encapsulated. In other respects they differed. Neuromuscular contacts were not present and the capsule was rarely more than one cell thick and was frequently incomplete, whereas neuromuscular contacts were routinely observed in monkeys and cats and the capsule regularly complete and often three to four cells thick (Ruskell, 1978; Alvarado-Mallart and Pinçon-Raymond, 1979). The organelles present in the preterminal/terminal varicosities are the same as those found in myotendinous cylinder terminals in monkeys and cats, but whereas vesicles occupy the greater area in these animals, mitochondria predominate in the human material. The content of the terminals differ little from that found in motor endings, although it is worth noting that a preponderance of mitochondria is more characteristic of sensory endings, as in GTO (Merrillees, 1962) and in muscle spindles (Kennedy et al., 1975). But their content offers a poorer criterion for distinguishing motor and sensory nerve endings than their relationship with target structures, and it was consideration of this factor that promoted the argument that MTC are sensory (Tozer and Sherrington, 1910; Barker, 1974; Ruskell, 1978; Alvarado-Mallart and Pinçon-Raymond, 1979) and, in particular, the absence of sarcoplasmic modification at neuromuscular junctions. In the human material the possibility of a motor identity for



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Fig. 13. Drawing to show the three varieties of nerve termination in tendon. **a**: The myotendinous cylinder; **b**: terminals unconfined or partially confined by a capsule; **c**: dispersed terminals from a non-recurrent nerve fiber.

the myotendinous endings is more remote as contacts between nerve endings and muscle were not found.

The incidence and distribution of MTC in monkeys and cats is substantially different from that of the complexes in man. A small minority of MTC was uninervated in monkeys while, as we have shown, complexes are commonly lacking nerve endings in human muscles and large areas may be without nerves. But the departure from the animal model is most apparent in the targeting of terminals. Apart from the rare presence of GTO in monkey myotendon, all terminals of the region are housed in MTC, which was not the case in man, with the result that many were related to more than a single muscle fiber. Further, targeting was not uniform; all samples contained encapsulated complexes and also partly encapsulated complexes with broader spread of terminals, but in the muscles of two of the six donors many terminals spread transversely across tendon distal to the other terminals and were not encapsulated. The three variants are summarized in Figure 13.

Given that a proportion of the nerve endings described conform approximately to the MTC pattern of monkeys, and cats, many of the remainder may be regarded as fundamentally the same but lack the constraint on terminal distribution imposed by a complete capsule. Consequently the terminals have spread in tendon across the heads of several muscle fibers. Accepting the premise that the nerve endings are sensory, the MTC system is presumably organized to monitor single muscle fiber activity, a role denied the unencapsulated and many of the partly encapsulated nerve endings. The randomly dispersed terminals clearly have little in common with MTC, but their appearance in the tendons of only two of the six individuals suggests an aberrant development where terminals have advanced and spread laterally. Although there is no reason to doubt that all the terminals are functional and respond to muscle contraction, assuming these speculations are valid, when coupled with an often grossly disparate distribution and a delayed develop-

ment, their fidelity as monitors of muscle contraction is open to question.

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