

The innervation of muscle spindles in the Australian opossum, *Trichosurus vulpecula*, with special reference to the motor nerve endings

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INTRODUCTION

A considerable controversy has arisen following Boyd's (1962*a, b*) suggestion that the two types of mammalian intrafusal muscle fibre have an entirely separate motor innervation. In the cat, for example, the nuclear bag and nuclear chain type intrafusal fibres were described by Boyd (1962*a, b*) as receiving different and specific motor nerve endings. He found that typical motor end plates occurred only on nuclear bag fibres, usually near the poles of the spindle, and that diffuse networks of fine fibres occurred only on nuclear chain fibres, usually near the equator. Boyd's observations seemed to confirm those of Hess (1961) who, in the spindles of mice and rabbits, found cholinesterase distributed both as polar end plates and as juxta-equatorial 'diffuse multiterminal endings'. Hess was unable to state, however, if the two types of ending lay on the same or different kinds of intrafusal fibre.

Barker (1962) disagreed with Boyd's thesis and maintained that both nuclear bag and nuclear chain fibres in the cat received motor end plates only. The recent observation of diffuse trailing motor endings near the equator of cat and rabbit spindles by Barker & Ip (1965*a*) does not entirely resolve the controversy, for they see in these 'trailing endings' some resemblances to configurations previously described by them (1965*b*) as 'plate ending fibres carrying out end plate replacement'.

Barker and his colleagues (Barker, 1962; Barker & Cope, 1962; Adal & Barker, 1965; Barker & Ip, 1965*a*) have also denied Boyd's (1962*a, b*) claim that nuclear bag end plates and nuclear chain networks are supplied by γ -efferent nerve fibres which are distinguished by specific differences in axon diameter.

In view of the contradictory accounts of the above authors, detailed studies of spindle innervation in other species are clearly desirable to further the understanding of mammalian muscle spindle innervation as a whole. Muscle spindles were first observed in a marsupial by Langworthy (1924), who saw them in the tongue of the (Virginian) opossum. The number of spindles was studied in the lumbrical muscles of the same animal by Voss (1937), but only Barker & Chin (1961) have made any comment about the innervation of the marsupial spindle. This was limited to the observation that in the opossum, as in many other mammals, γ -efferent nerve fibres never arise as branches of α -efferents when examined close to the spindle. The present paper, therefore, records the results of a detailed study made on the innervation of muscle spindles in an Australian marsupial, *Trichosurus vulpecula*, using teased whole preparations and sectioned material.

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METHOD

Twenty adult specimens of *T. vulpecula* were used. The muscle spindles were examined by means of teased whole specimens and by sections.

A total of 187 whole spindles were teased chiefly from the small muscles of the manus and pes, but also from the tibialis anterior, medial head of gastrocnemius, rectus femoris and flexor carpi ulnaris. For teased preparations, two staining methods were used. The most successful was the supravital methylene blue technique of Boyd (1958) in which the dye, dissolved in Krebs's solution, is perfused at constant temperature and pH whilst being continually oxygenated. After perfusion, whole muscles were removed, immersed in oxygenated Krebs's solution for half an hour and finally fixed in ammonium molybdate. The muscles were then teased in glycerine under a dissecting microscope. Other muscles were stained with various modifications of the Ranvier-Loewit gold chloride technique and whole spindles teased from them under the dissecting microscope. Whilst the gold chloride technique gave good preparations of the primary and secondary sensory nerve endings in the spindles, it was on the whole unsatisfactory for demonstrating the finer details of the motor endings.

Longitudinal frozen sections at 50 μm were made from five manus lumbrical muscles and stained with Schofield's (1960) silver stain. A further lumbrical muscle from the manus was serially sectioned longitudinally at 12 μm and stained with Bodian's (1936) stain.

Serial transverse sections of a number of small muscles from the manus stained with haematoxylin and eosin or with Lillie's (1948) modification of the van Gieson stain were found useful for confirming observations on the intrafusal fibres.

The diameters of nerve fibres (to the nearest 0.5 μm) were measured at a constant distance (1 mm) from the spindles using an eyepiece micrometer. These measurements were made in methylene blue and gold chloride preparations only, as there is some shrinkage in preparations stained with silver. Sensory and motor fibres were identified on the basis of the morphology of their endings.

RESULTS

General structure of the muscle spindle

In all the spindles examined two types of intrafusal muscle fibre were seen. The first, of which each spindle contained at least two, were 12–18 μm in diameter when measured within the spindle capsule. These were longer than the second type, and were characterized by a large bulky aggregation of vesicular nuclei in the equatorial region. The second type, of which each spindle contained 4–12, were smaller fibres, each with an intracapsular diameter of 4–6 μm , and contained a single chain of centrally placed vesicular nuclei in the equatorial region. These were shorter, not always extending as far beyond the poles of the capsule as the first group (Figs. 25, 26). Following the terminology of Boyd (1962*a, b*), these two types of intrafusal fibre will be termed nuclear bag fibres and nuclear chain fibres respectively.

*The motor innervation**Structure and distribution of motor nerve endings*

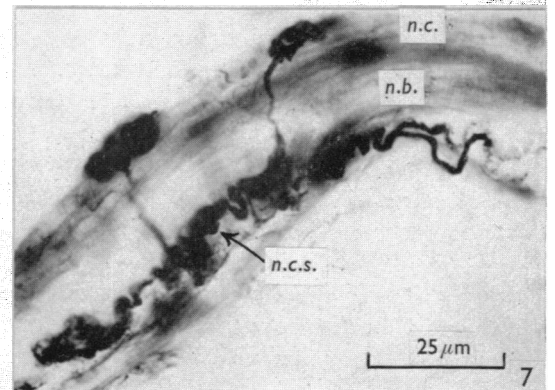
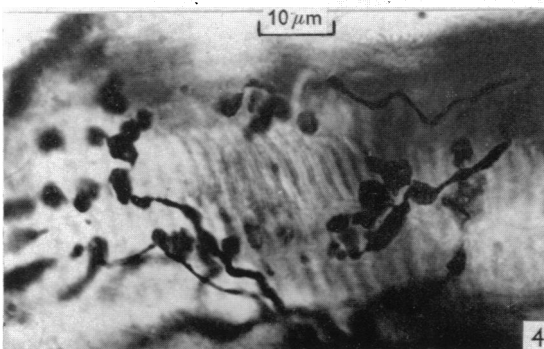
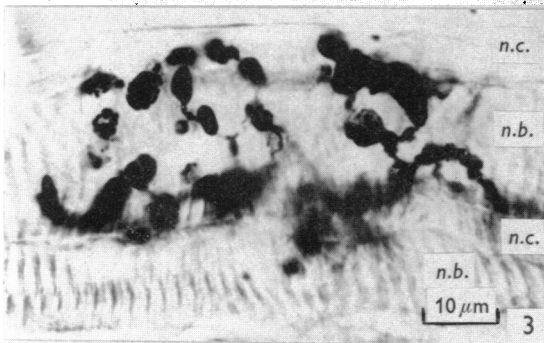
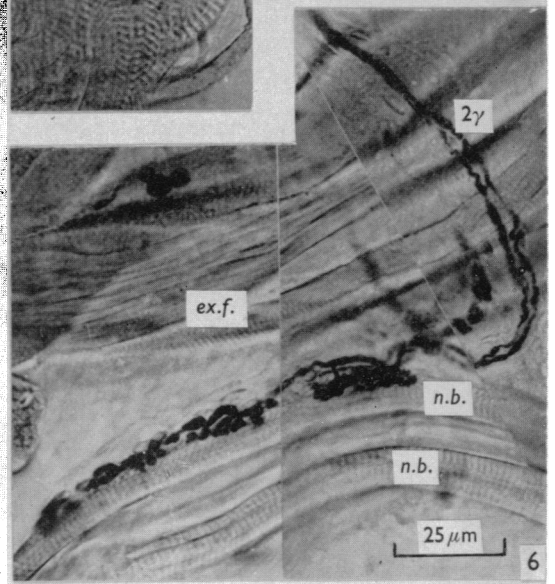
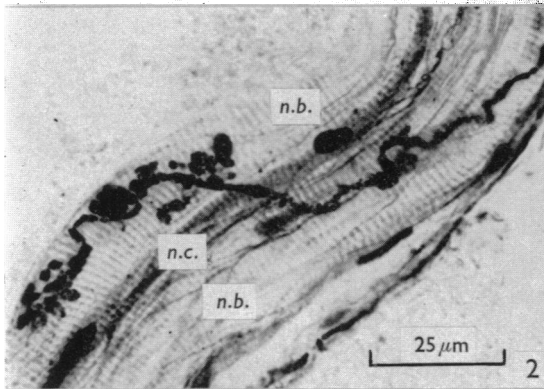
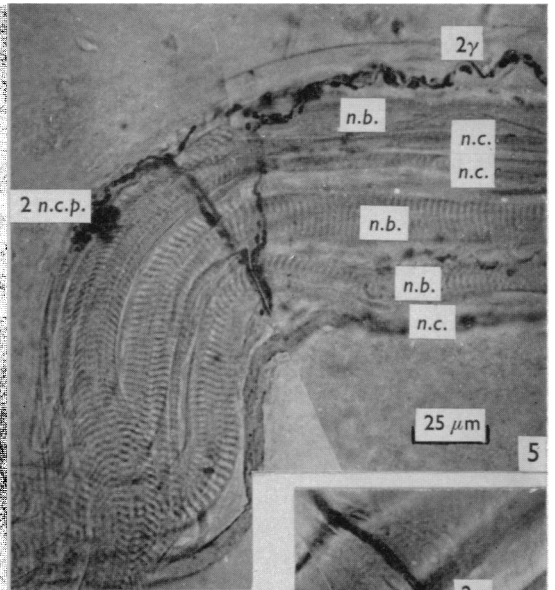
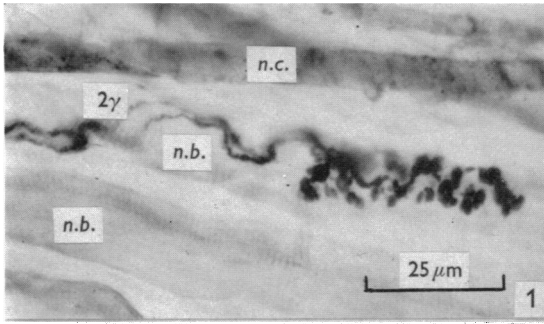
In the following account it is convenient to describe the end formations on nuclear bag and nuclear chain fibres separately. It should, however, be emphasized that, while the formations on nuclear bag fibres most commonly resembled the nuclear bag end plates described by Barker (1948, 1962) and by Boyd (1962*a, b*) and those on nuclear chain fibres more commonly resembled the diffuse multi-terminal endings of Hess (1961), the ' γ -2 network' of Boyd (1962*a, b*), and the 'trail endings' of Barker & Ip (1965*a*), a complete range of end formations from compact end plates to very diffuse sprays was seen on both types of intrafusal fibre.

(a) *Motor nerve endings on nuclear bag fibres.* Typical motor end plates were always found on nuclear bag fibres at or beyond both poles of the spindle capsule. Throughout this paper these will be termed 'nuclear bag end plates'. In methylene blue and gold chloride preparations these nuclear bag end plates appeared as elongated structures consisting of bulbous interconnected strands some what radially arranged (Figs. 1, 2, 6, 21, 22). They were similar in structure to extrafusal motor end plates (Fig. 30), but were usually rather longer. A typical extrafusal motor end plate measured 25 μm by 45 μm and was 15 μm thick; the usual nuclear bag end plate was 20 μm wide, 50–65 μm long and 10 μm thick and it covered most of the width of the nuclear bag fibre. In silver preparations the nuclear bag end plates consisted of a typical Doyère eminence with finely branched nerve terminals and several sole nuclei (Fig. 16).

In the polar region, each nuclear bag fibre had one or two nuclear bag end plates which could overlap considerably (Figs. 1, 6, 21). In addition, each nuclear bag fibre often had another motor end plate well within the spindle capsule in the region of the nuclear chain endings. This additional end plate, while similar in structure to that described above, was commonly more irregular or diffuse (Figs. 19, 22).

(b) *Motor nerve endings on nuclear chain fibres.* (i) *Diffuse nuclear chain sprays.* In all muscle spindles all or most of the nuclear chain fibres possessed a common motor nerve ending. In methylene blue preparations, this took the form of a diffuse, elongated, often grapelike spray 75–150 μm long which spread irregularly over a bundle of nuclear chain fibres (Figs. 4, 8–11, 22, 23). Throughout this paper, this is termed a 'diffuse nuclear chain spray'. The preterminal and terminal expansions of the spray made contact with one or more nuclear chain fibres so that a single nuclear chain fibre commonly received more than one short branch of the spray. In silver preparations the constituent terminal portions of the spray appeared as fine, short filaments, occasionally branched, ending in relation to one or two sole nuclei (Figs. 17, 18).

In many spindles a single diffuse nuclear chain spray was present but frequently there were, instead, several short sprays on the same or different bundles of nuclear chain fibres. The diffuse nuclear chain spray lay nearer the equator than the pole of the muscle spindle and if a secondary sensory ending was present the spray lay near it but never overlapped nor mingled with it. The spray was frequently mingled in such a manner with the more irregular type of nuclear bag end plate that it was



impossible to decide on which intrafusal fibre they each lay. When the intrafusal fibres were satisfactorily separated, however, there was no doubt that the diffuse spray lay on nuclear chain fibres as the cytoplasm and nuclear chains of these fibres stain palely with methylene blue, whereas the nuclear bag fibres remain colourless unless damaged in teasing, when the distribution of the dye indicates that damage has occurred. On two separate occasions a diffuse spray was actually seen on a nuclear bag fibre (Fig. 3).

(ii) *Nuclear chain end plates*. In about one-third of the spindles there were nuclear chain fibres which did not have a diffuse nuclear chain spray lying on them. While some of these nuclear chain fibres had all the characteristics of typical nuclear chain fibres, others lay solitarily outside the nuclear bag fibres, were not collected into bundles and often passed through the equatorial region without the reduction in diameter that was characteristic of most nuclear chain fibres (Figs. 25, 26). They frequently stained quite intensely with methylene blue (Fig. 29). Motor nerve endings on this type of nuclear chain fibre took the form of a single (rarely two) small, compact end plate which often encircled the muscle fibre (Figs. 5, 7, 15). Throughout this paper these endings are termed 'nuclear chain end plates'. Nuclear chain end plates always lay on the same side of the equator as a diffuse nuclear chain spray.

Motor nerve fibres ending within the spindle

(a) *Diameters and numbers of spindle motor nerves*. Spindle motor nerve fibres were measured and counted 1 mm from individual spindles in methylene blue and gold

LIST OF ABBREVIATIONS

<i>ex.f.</i>	Extrafusal muscle fibre	<i>P</i>	Primary sensory nerve ending
<i>n.b.</i>	Nuclear bag intrafusal fibre	<i>S</i>	Secondary sensory nerve ending
<i>n.b.p.</i>	Nuclear bag end plate	<i>Ia</i>	Group Ia afferent nerve fibre
<i>n.c.</i>	Nuclear chain intrafusal fibre	<i>Ib</i>	Group Ib afferent nerve fibre
<i>n.c.p.</i>	Nuclear chain end plate	<i>II</i>	Group II afferent nerve fibre
<i>n.c.s.</i>	Diffuse nuclear chain spray	γ	Small motor axon

All muscles were fixed in a relaxed state unless otherwise indicated.

Fig. 1. Two overlapping nuclear bag end plates supplied by separate small motor axons and lying on the same nuclear bag fibre in the polar region of a spindle from a manus lumbrical. Methylene blue.

Fig. 2. Elongated nuclear bag end plate in the polar region of a spindle from a pes lumbrical. Methylene blue.

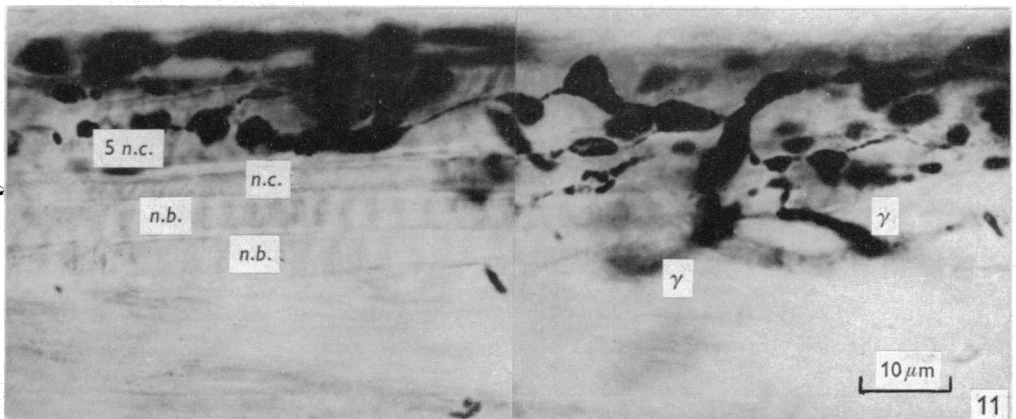
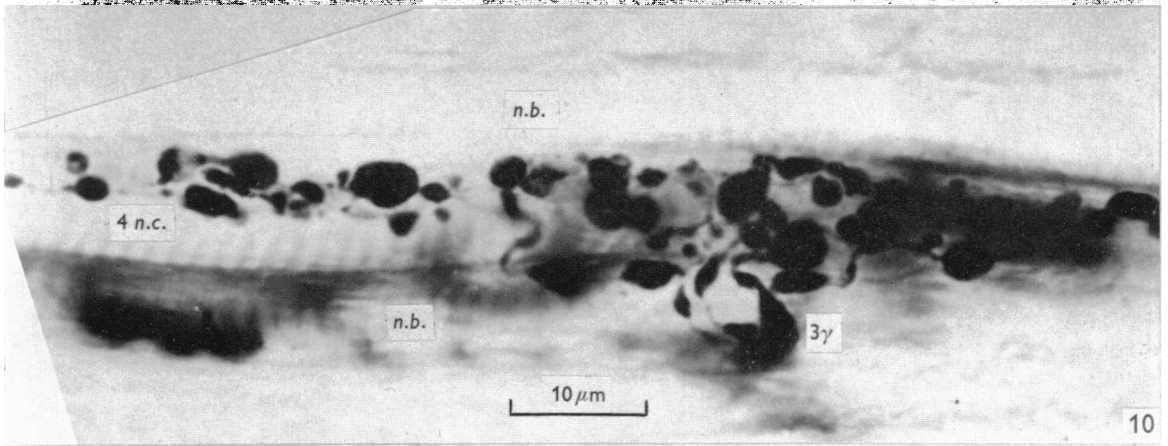
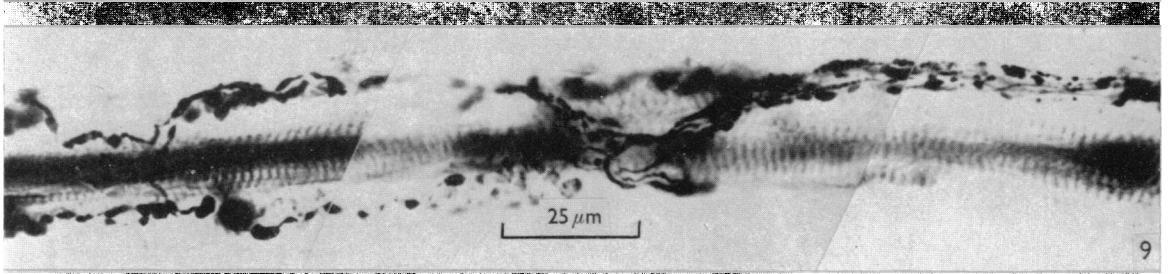
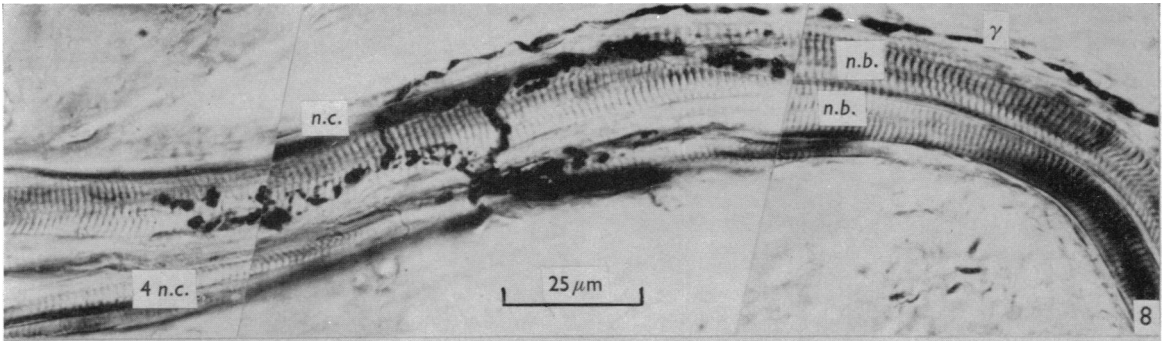
Fig. 3. A diffuse spray of the type frequently seen on nuclear chain fibres, in this case lying on a nuclear bag fibre in a spindle from a manus lumbrical (cf. Fig. 4). Methylene blue.

Fig. 4. The terminal portions of a diffuse nuclear chain spray lying on a bundle of nuclear chain fibres in a spindle from the tibialis anterior. Methylene blue.

Fig. 5. The polar region of a spindle from the tibialis anterior showing two small motor axons ending in small end plates on two nuclear chain fibres. Because of the alteration in the plane of focus, the two nuclear chain fibres receiving the end plates are only faintly visible in the left half of the photograph but come into prominence in the right half. Methylene blue.

Fig. 6. Two small motor axons ending in end plates on the same nuclear bag fibre in the polar region of a spindle from a manus lumbrical. Methylene blue.

Fig. 7. Two small motor end plates on the same nuclear chain fibre receiving branches of the diffuse nuclear chain spray seen in the lower part of the photograph. Spindle from a pes lumbrical. Methylene blue.



chloride preparations. A histogram of the axon diameters of such fibres has two peaks (Fig. 12). All spindles received motor axons which lay in the 1–2 μm range, the commonest single diameter being 1.5 μm . Throughout this paper, these are

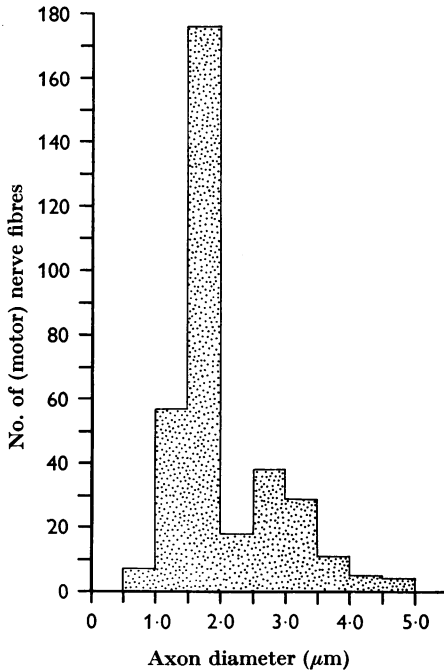


Fig. 12

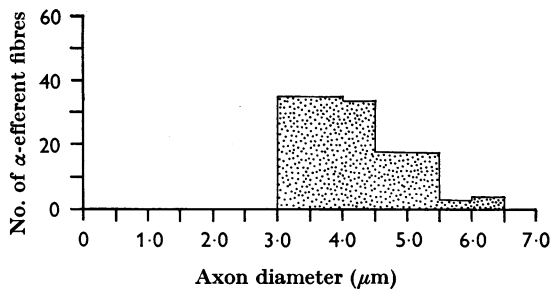


Fig. 13

Fig. 12. A histogram of axon diameters of spindle motor nerve fibres. The measurements were made 1 mm from isolated spindles stained with methylene blue or gold chloride. Axons in the 0.5–2 μm range are 'small motor axons' and are present in all spindles; axons in the 2.5–5 μm range are 'large motor axons' and are only present in about one-third of spindles.

Fig. 13. A histogram of axon diameters of 160 α -efferent nerve fibres. The measurements were made 1 mm from end plates on extrafusal fibres, irrespective of branching, in methylene blue and gold chloride preparations. The diameter range overlaps the second peak of the histogram of spindle motor axon diameters.

Fig. 8. Polar region of a spindle from the short flexor of the hallux. A very irregular diffuse spray, supplied by a single small motor axon is present. In the lower part of the photograph the spray lies on nuclear chain fibres but, elsewhere, appears to spread on to the two nuclear bag fibres. Methylene blue.

Fig. 9. An elongated diffuse nuclear chain spray in a spindle from a manus lumbrical fixed stretched. The distinction between nuclear bag and nuclear chain fibres is not clear in the photograph. Methylene blue.

Fig. 10. High-power view of a diffuse nuclear chain spray in a spindle from a manus lumbrical, fixed stretched. The branches of the spray clearly lie on the bundle of four nuclear chain fibres lying between the two nuclear bag fibres. Three small motor axons enter the spray. Methylene blue.

Fig. 11. High-power view of a diffuse nuclear chain spray in a spindle from a pes lumbrical, fixed stretched. Two small motor axons are seen; one of these ends in a diffuse nuclear chain spray while the other passes out of the plane of focus. The latter ended as a nuclear bag end plate. Methylene blue.

referred to as 'small motor axons'. One-third of the spindles examined received, in addition to small motor axons, one or more motor axons which lay in the 2.5–4.5 μm range, the commonest single diameter being between 2.5 and 3 μm . Throughout this paper, these are referred to as 'large motor axons'. Large motor axons possessed myelin sheaths which were both absolutely and relatively thicker than the myelin sheaths of small motor axons. Large motor axons with their sheaths had a total diameter of 4.5–6.5 μm , the commonest single diameter being 6.5 μm , while small motor axons never had a total diameter exceeding 2.5 μm .

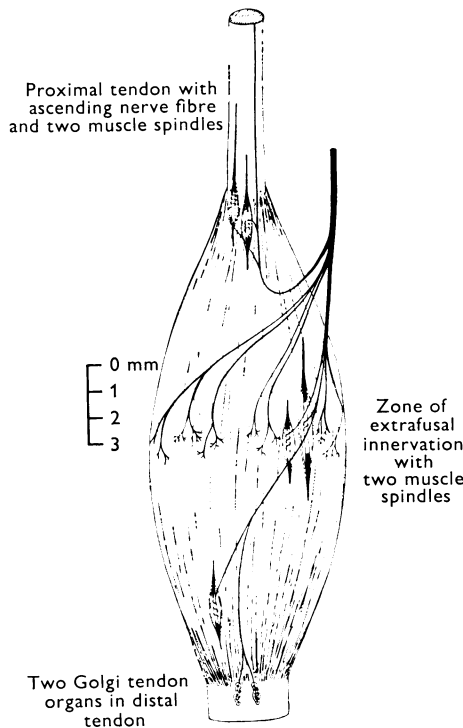


Fig. 14. A semi-diagrammatic representation of the distribution of receptor organs in a typical lumbrical muscle of the pes. Partially embedded in the proximal tendon of the muscle are two muscle spindles which were never seen to have motor innervation at their proximal ends. The ascending nerve fibre usually ended in the tendon but was sometimes a group *Ib* afferent.

Motor nerve fibres most frequently entered the spindle at the equator with the sensory nerve fibres and passed towards one or both poles parallel to the intrafusal bundle. Sometimes a group of motor fibres entered at a pole. All the motor nerve fibres, no matter what their point of entry, were ultimately derived from the same small intramuscular nerve trunk which commonly contained α -efferents as well. However, within 1 mm of the spindle, spindle motor axons were not seen to arise as branches of α -efferents. Each polar region of a spindle received an average of three spindle motor nerve fibres but the number seen could vary from two to eight.

In two-thirds of spindles all the motor axons belonged to the small group. In one third a large motor axon was present; in some of these spindles it accompanied one or more small motor axons to one pole, while in others, one (rarely two) large motor axon was the sole motor supply to one pole (Fig. 29). Large motor axons never passed to both poles of the same spindle.

(b) *Mode of termination of spindle motor nerve fibres.* In the two-thirds of spindles innervated by small motor axons only, branching of these axons was common, although not every small motor axon in a spindle did so. Nuclear bag and nuclear chain motor endings always received different small motor axons.

Small motor axons ending in nuclear bag end plates usually branched to supply more than one ending, not necessarily on the same intrafusal fibre. The irregular nuclear bag end plates within the capsule received branches of the small motor axons passing to the poles. Sometimes a small motor axon terminated in one end plate only.

Large diffuse nuclear chain sprays received one or more small motor axons which, when close to the spindle, might or might not branch several times. Where branching occurred, all branches ended in the spray. When several small nuclear chain sprays were present they were supplied individually, either by separate small motor axons or by branches of the same small motor axon (Figs. 22, 23).

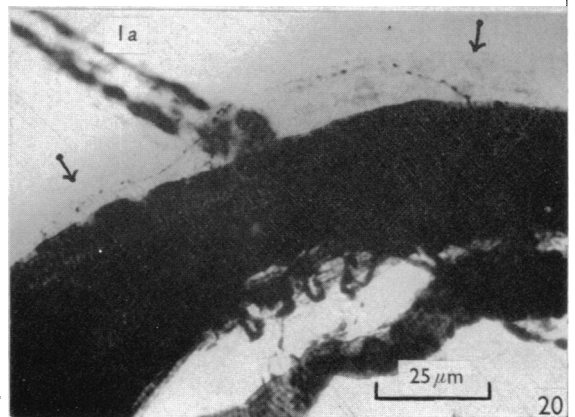
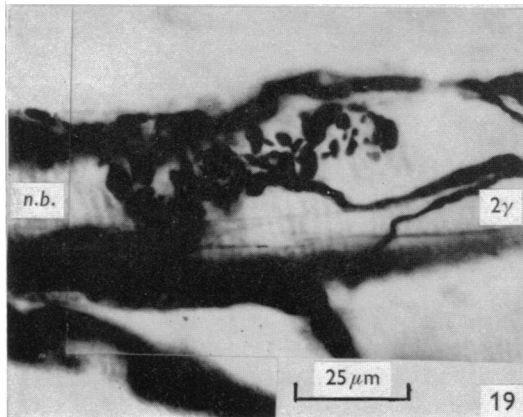
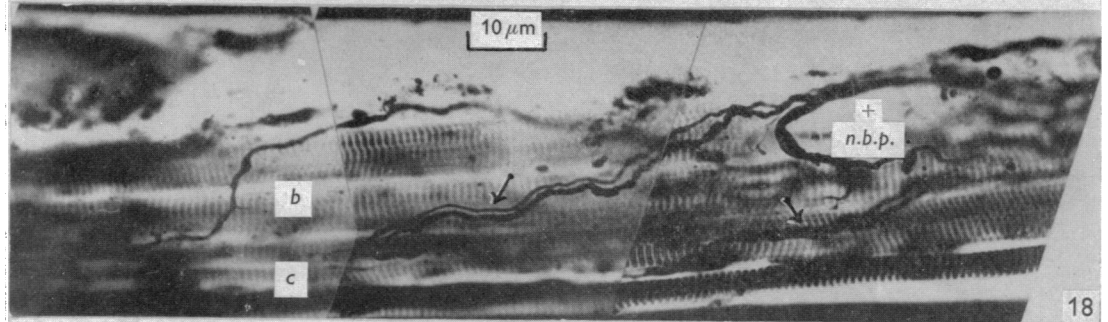
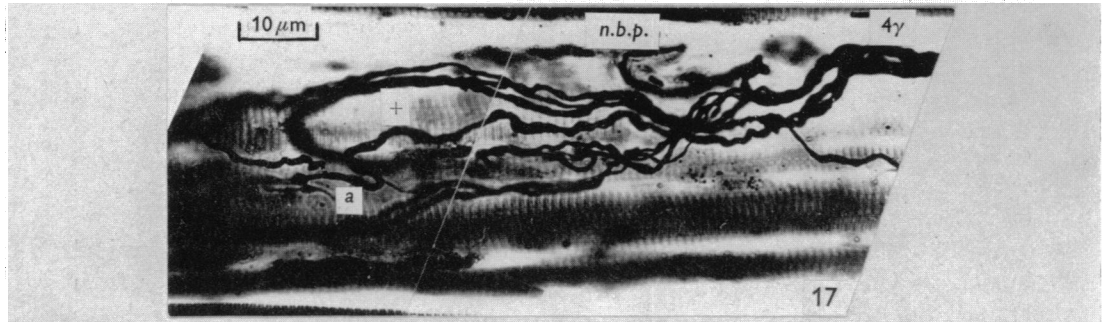
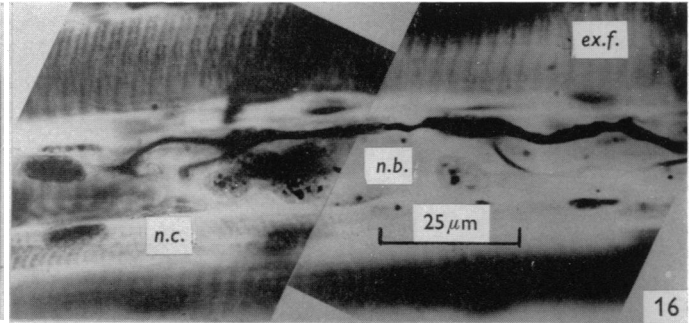
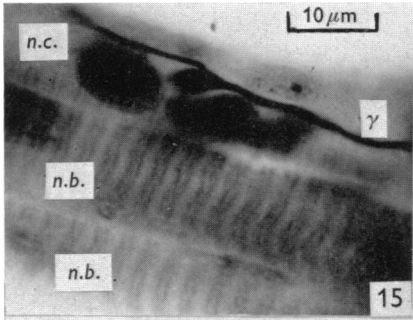
The small nuclear chain end plates, when present, were derived from preterminal branches of small motor axons entering a diffuse nuclear chain spray or from branches of the spray itself (Fig. 7). Rarely, a small motor axon entered the spindle and, without branching, terminated as a single nuclear chain end plate (Figs. 5, 15).

At 1 mm from the spindle there was little difference in diameter between small motor axons destined for nuclear bag end plates and those destined for nuclear chain motor endings. Within the spindle, those passing to diffuse nuclear chain sprays or to nuclear chain end plates became narrower towards their terminations, each branch varying from 0.5 to 1.0 μm , whereas those passing to nuclear bag end plates changed little in diameter.

In about one-third of the spindles a large, more heavily myelinated motor axon was present, which provided the entire motor innervation to one pole (Fig. 29) or was accompanied by one or more small motor axons. These small axons provided all or only a proportion of the diffuse nuclear chain sprays. In the latter case the other nuclear chain sprays or end plates received branches of the large motor axon. Branches of large motor axons whether destined for nuclear bag or nuclear chain endings always arose within the spindle, were short and varied considerably in diameter (0.5–2.0 μm).

Spindles lacking motor innervation at one end

Trichosurus has only two lumbrical muscles in the pes. In each of these, there were constantly present two or three muscle spindles deeply embedded in the long thin proximal tendon of each muscle to such an extent that even the equatorial regions were surrounded by tendon rather than by muscle. These spindles, although they were long and in most cases had one or even two secondary sensory endings, did not have motor nerve endings at their proximal pole (Figs. 14, 31). The distal



pole, embedded in the muscle, received a normal spindle motor innervation provided by small or large motor axons. Other muscle spindles wholly within the belly of the pes lumbrical had motor endings at both poles. Two or three Golgi tendon organs were constantly seen at the distal musculo-tendinous junction of the muscle.

The sensory innervation

The primary ending and its nerve

The group Ia afferent nerve fibre, whose total diameter 1 mm from the spindle varied from 9 to 15 μm (average 12.5 μm) in gold chloride and methylene blue preparations (Fig. 24), entered the capsule more or less at right angles, dividing once or twice dichotomously as it did so. There was some slight preterminal increase in diameter. Within the capsular space, each branch divided once or twice more. Many of these branches ended in a spray of unmyelinated branches each about 0.5 μm in diameter, others lost their myelin sheath and passed directly without further branching to their terminations. One or more of the fine unmyelinated terminal branches passed to each intrafusal muscle fibre in the region of its central nuclear aggregation. These fine branches became continuous with the primary sensory nerve ending which usually took the form of a series of tightly wound regular spirals (Fig. 28). A frequent variation occurred in which the terminal non-myelinated branches became wider, aligning themselves along the long axis of the intrafusal fibre, and from them a series of rings encircled the muscle fibre (Fig. 27). The rings were usually complete and disposed at right angles to the muscle fibre but they were sometimes incomplete, in which case they were frequently obliquely disposed. In methylene blue preparations the constituent fibres forming the spirals or ring formations were each 3 μm in diameter; in gold chloride 2.5 μm . In silver preparations a spiral ribbon of variable diameter and with a markedly neurofibrillar appearance was seen.

The primary ending occupied the equatorial region only. The portions of the ending on adjacent fibres usually lay side by side, but in spindles fixed in a stretched state they could be arranged in step fashion. Usually every nuclear bag and nuclear chain fibre received a separate spiral or ring formation, but the rings or spirals on the nuclear chain fibres were rather more tightly wound and had fewer turns (6-8), so that these endings were rarely more than about one-quarter to one-third as

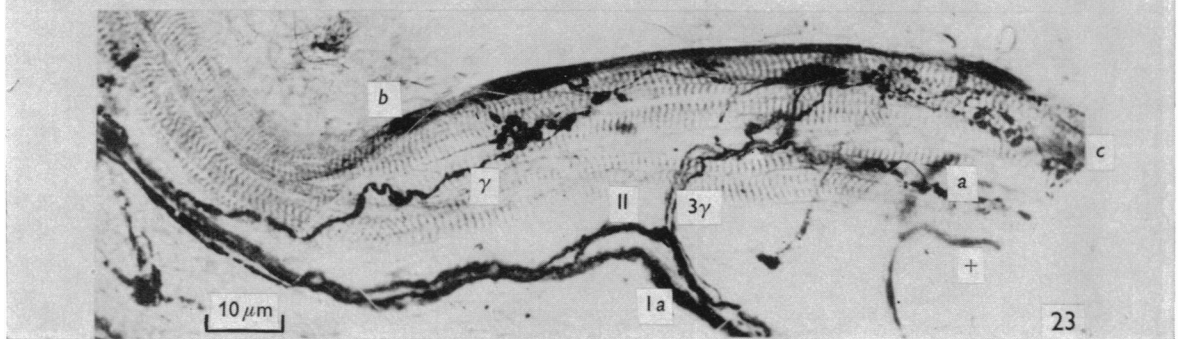
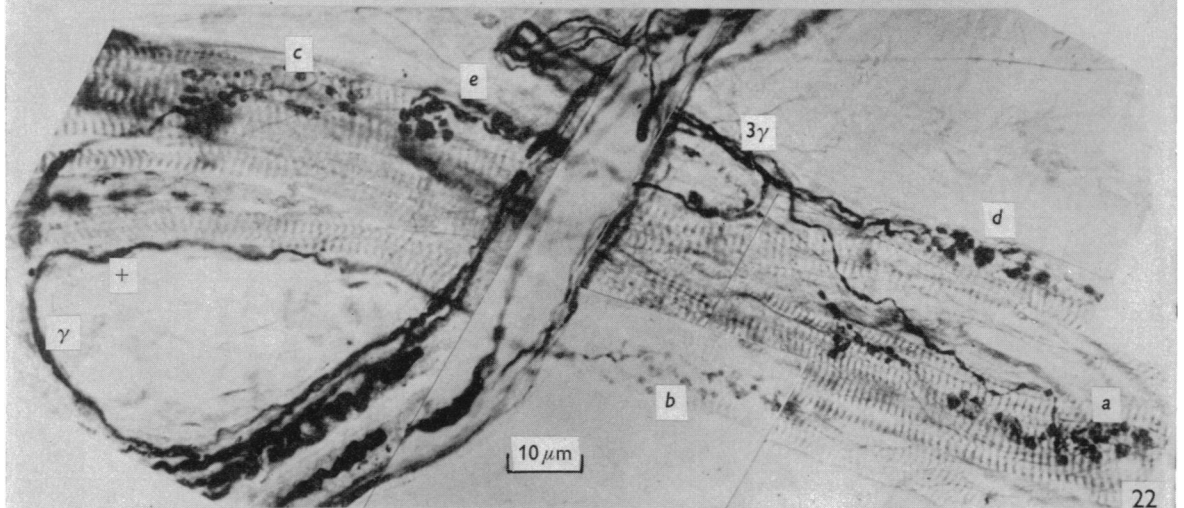
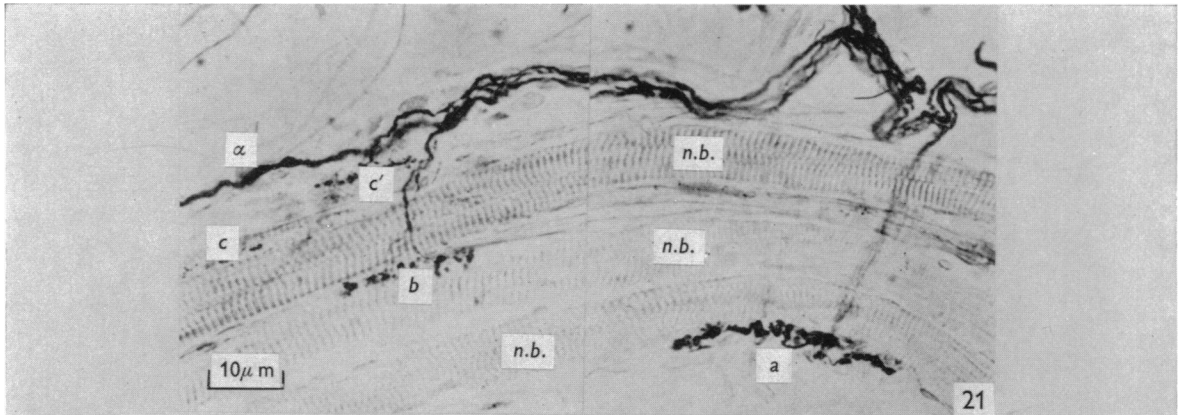
Fig. 15. A small motor end plate on a nuclear chain fibre in a spindle from a manus lumbrical. Schofield's stain.

Fig. 16. A typical elongated nuclear bag end plate in the polar region of a spindle from a manus lumbrical. Schofield's stain.

Figs. 17, 18. These are photographs of the same field at different planes of focus; overlapping points in each photograph are marked by a cross. Four small motor axons enter from the right; two of these end as large motor end plates apparently on nuclear bag fibres; the other two break up into an irregular spray of branches some of which (arrows) double back on themselves. The branches of the spray terminate variably, but in relation to sole nuclei (*a, b, c*). Spindle from a manus lumbrical. Schofield's stain.

Fig. 19. A large irregular nuclear bag end plate within the capsule of a spindle from the first interosseous muscle of the manus. Methylene blue.

Fig. 20. A fine beaded nerve fibre ramifying in the capsular region of a spindle from a pes lumbrical. The edge of the capsule is marked by the arrows. Gold chloride stain.



long as those on the nuclear bag fibres. The average total length of the primary ending was 150–250 μm but they were occasionally as short as 100 μm or as long as 350 μm , the length chiefly depending on the degree to which the muscle was stretched in fixation. The rings or spirals on the nuclear bag fibres lay on the nuclear bag region and could extend on to the myotube region where they ended as a bleb or sometimes as a small but coarse spray. The rings or spirals on the nuclear chain fibres tended to occupy the junctional region between myotube and narrowed nuclear chain region.

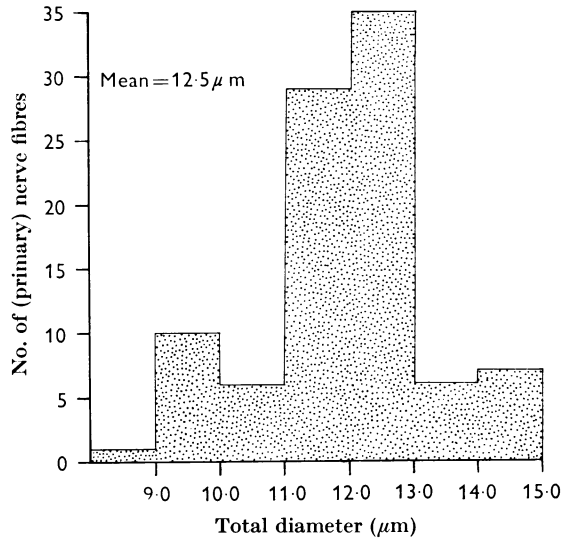
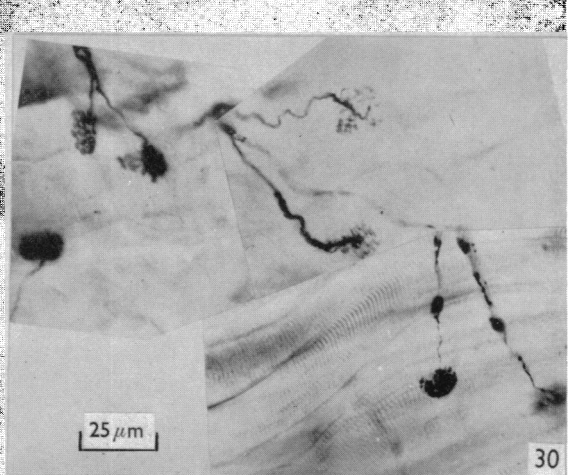
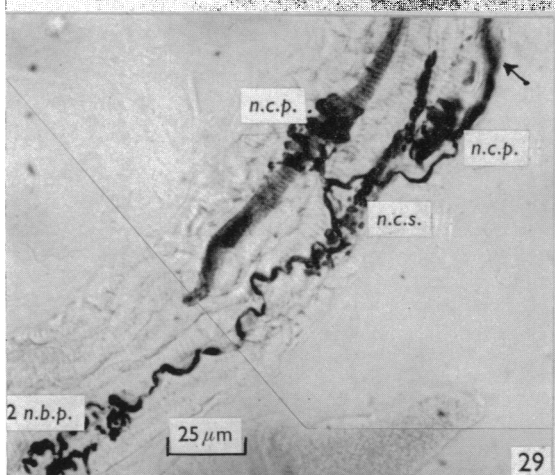
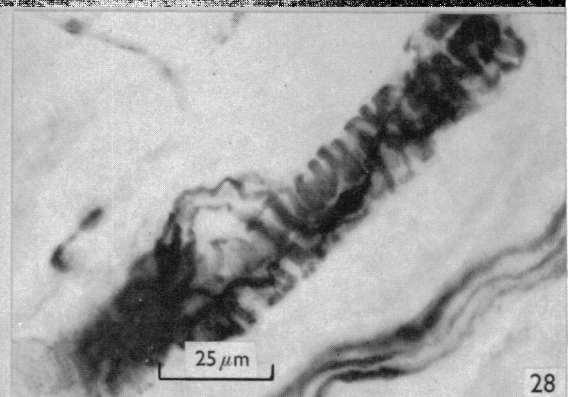
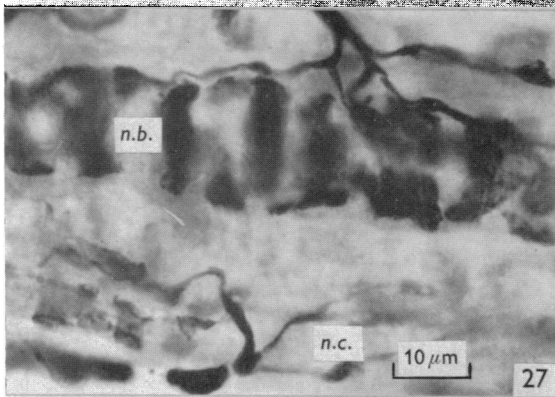
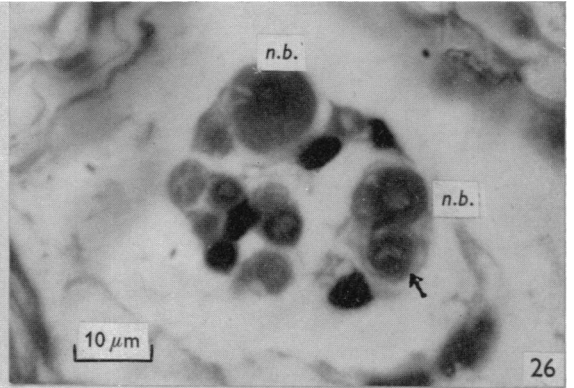
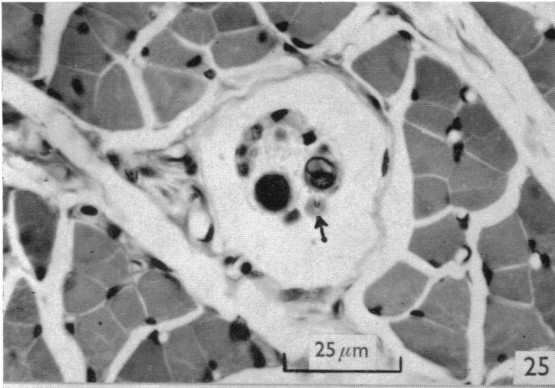


Fig. 24. A histogram of the total diameters of nerve fibres ending in primary sensory nerve endings in isolated spindles stained with methylene blue or gold chloride. The measurements were made 1 mm from the spindles. The diameters range from 8 to 15 μm with a peak at 11–13 μm and thus fall within the range usually given for group I afferents.

On three occasions, in spindles from the tibialis anterior of two animals, fixed relaxed, the primary ending occurred on the two nuclear bag fibres only and did not extend on to the four to six nuclear chain fibres. This did not seem to be a teasing artefact as no broken branches of the primary nerve fibre could be seen. In all three

Figs. 21–23. These are from the same end of a large spindle teased from a lumbrical muscle of the pes. The spindle contained three nuclear bag fibres and seven or eight nuclear chain fibres and the complete motor innervation at one end is demonstrated. Fig. 21 is from the polar region and shows the three nuclear bag fibres, each of which has a nuclear bag end plate (*a*, *b*, *c*). The end plate at *c* was apparently separated from *c* in teasing. α is an α -efferent fibre which terminated in an extrafusal motor end plate close to the spindle. The fields shown in Figs. 22 and 23 overlap one another slightly (crosses) and are separated from that of Fig. 21 by approximately 600 μ . In Fig. 22 at *a*, four nuclear chain fibres overlap a single nuclear bag fibre and the irregular spray seen at this point seemed to lie on the nuclear chain fibres. *b* and *c* were nuclear bag end plates each supplied by the same small motor axon. *d* was a nuclear bag end plate and *e* also appeared to be a nuclear bag end plate lying on the same nuclear bag fibre that was overlapped by the four nuclear chain fibres at *a*. In Fig. 23 *a* was a nuclear bag end plate. All the other endings lay on nuclear chain fibres and constituted a diffuse nuclear chain spray stretching from *b* to *c*; in this spray four small motor axons can be seen to terminate. Methylene blue.



spindles, a secondary sensory ending was present and lay on both nuclear bag and nuclear chain fibres (Fig. 32).

No spindles contained more than one primary ending; within 1 mm of its termination, no group I afferent fibre supplied more than one spindle nor a spindle and a Golgi tendon organ.

The secondary ending and its nerve

A secondary sensory ending was present in about 50% of spindles. Its presence was fairly constant in even the smaller spindles from lumbrical muscles of the pes, but was more variable in spindles from other muscles. The group II afferent nerve fibre which terminated in these endings, had a total diameter which varied from 4 to 10 μm (average 8 μm , Fig. 34). It might or might not approach the spindle capsule in company with the nerve to the primary sensory ending, although they were ultimately derived from the same small intramuscular nerve trunk. If the group II nerve fibre approached independently from the group Ia nerve fibre, it usually did so very obliquely, winding around the intrafusal bundle from one pole; this was the common arrangement in those muscle spindles embedded in the proximal tendon of the pes lumbrical.

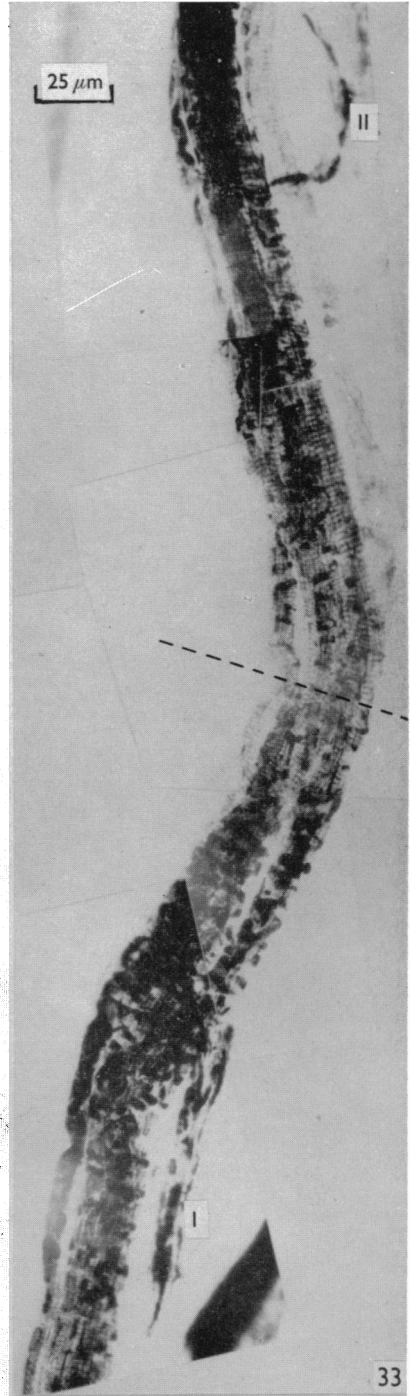
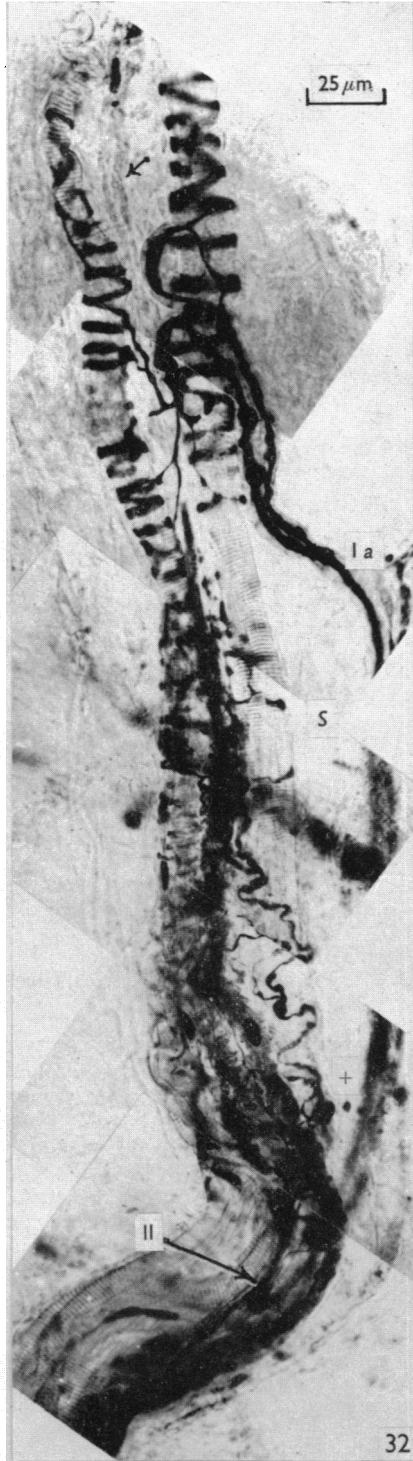
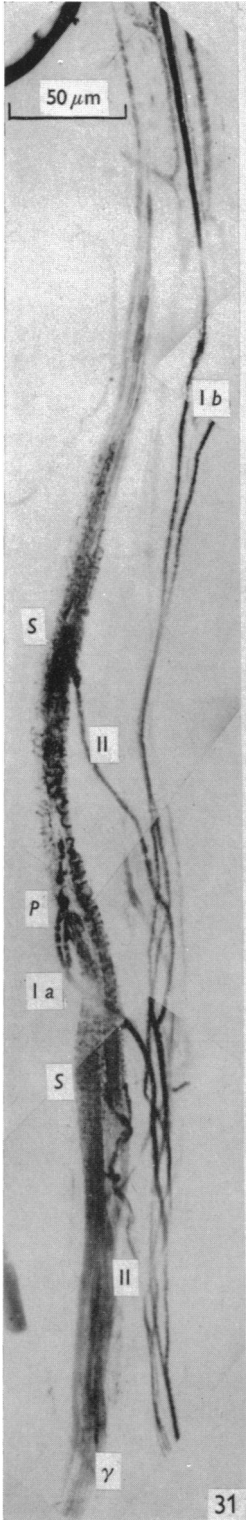
The initial division of the group II fibres, usually dichotomous but occasionally more spraylike, occurred some 300–500 μm from the capsule. One of the branches so formed might re-divide dichotomously and the other not. The two or more branches so formed had a diameter similar to that of the parent fibre. They entered the capsule and tended to clasp the intrafusal bundle where they each broke up into sprays of short unmyelinated branches of 0.5 μm or less in diameter (Fig. 32). The endings of these fine branches occupied chiefly the juxta-equatorial portions of all the nuclear chain fibres. A small part of the secondary ending did, however, lie on the myotube region of the nuclear bag fibres. On the nuclear chain fibres the ending took the form of a series of tightly wound spirals which were often less regularly disposed than the rings or spirals of the primary ending. The components of the spirals were from 1 to 1.5 μm in diameter. On the nuclear bag fibres, the secondary endings were short clasp-like arrangements consisting of two to four half- or quarter-turns. The average total length of the secondary ending was 200–300 μm (Figs. 31–33).

Figs. 25, 26. Transverse sections through the equatorial regions of spindles in lumbrical muscles of the manus. In each, a large, solitary nuclear chain fibre is present (arrows) and lies independent of the remaining smaller nuclear chain fibres. In teased preparations, similar fibres tended to possess nuclear chain end plates rather than diffuse nuclear chain sprays. Haematoxylin and eosin.

Figs. 27, 28. Primary sensory endings in spindles from manus lumbricals. In Fig. 27 the ending has a more annular form and the different diameters of the ring formations on a nuclear bag and a nuclear chain fibre are demonstrated. In Fig. 28, a more spiral configuration is shown on two nuclear bag fibres. Methylene blue.

Fig. 29. A single large motor axon (arrow) supplying all the motor endings at one end of a pes lumbrical. The intense staining of one of the nuclear chain fibres is shown. Methylene blue.

Fig. 30. A group of extrafusal motor end plates teased from a manus lumbrical. Their form is rather more compact and regular than nuclear bag end plates in the muscle spindles. Methylene blue.



The number of secondary endings per spindle varied from 0 to 2, 0-1 being the commonest (Table 1). If two were present they almost invariably lay on different sides of the primary ending; only on one occasion, in a spindle from the adductor pollicis, were two secondary endings seen on the same side of the primary. If two secondary endings were present in a spindle they were usually supplied by nerve fibres that were separate as far back as they could be traced. Infrequently, one of the preterminal branches of a group II afferent nerve fibre destined for one side of a spindle passed by the primary ending to provide a second secondary ending on the other side. This 'accessory' secondary ending was usually short (not more than $100\ \mu\text{m}$) and ended on nuclear bag fibres only. No single group II afferent fibre supplied secondary sensory endings in more than one muscle spindle.

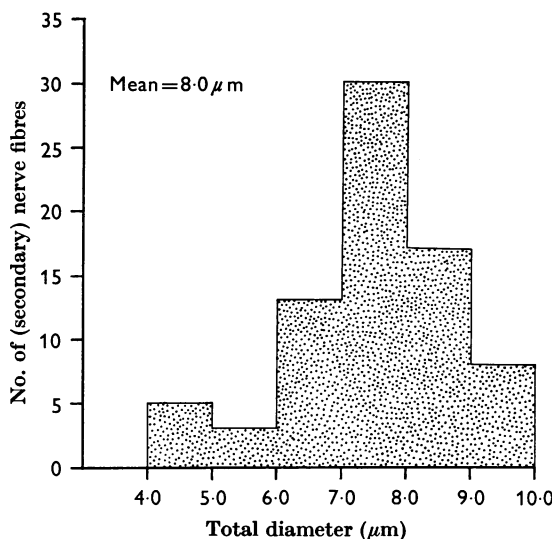


Fig. 34. A histogram of the total diameters of nerve fibres ending in secondary sensory nerve endings in isolated spindles stained with methylene blue or gold chloride. The measurements were made 1 mm from the spindles. The diameters range from 4 to $10\ \mu\text{m}$, with a peak at 7-8 μm and thus fall within the range usually given for group II afferents.

Fig. 31. A whole muscle spindle teased from the proximal part of a pes lumbrical, fixed stretched. The spindle lacks motor endings at its upper (proximal) end; a few motor endings are faintly seen at the lower (distal) end. In the equatorial region is a single primary sensory ending, on each side of which is a secondary sensory ending with a spiral appearance. Gold chloride stain.

Fig. 32. The equatorial region of a spindle from the tibialis anterior. Two nuclear bag fibres are clearly seen and five nuclear chain fibres were also present. The latter appear as a narrow bundle (upper arrow) lying between the nuclear bag fibres. In this spindle, the primary sensory ending occupied the nuclear bag fibres only. At the cross, a group II afferent nerve fibre breaks up into a number of unmyelinated branches whose short endings on the nuclear bag fibres are demonstrated at S. The parts of the secondary ending on the nuclear chain fibres are not clearly seen in this photograph. Methylene blue.

Fig. 33. The equatorial region of a spindle from a pes lumbrical. The secondary sensory ending lies above the broken line and has a spiral configuration. The primary sensory ending lies below the broken line. Gold chloride stain.

Distribution of sensory nerve endings in 180 non-tandem spindles are given in Table 1 and of motor nerve endings in Table 2. It can be seen that the commonest type of muscle spindle was one which had a single primary sensory ending, no secondary sensory ending, a diffuse nuclear chain spray at one end and nuclear bag end plates at both ends, the number at one end outnumbering those at the other.

Other nerve fibres in the spindle

Infrequently, very fine (*c.* 0.5 μm), beaded, unmyelinated nerve fibres were seen ramifying quite widely on the inner surface of the muscle spindle capsule. Their distribution could never be clearly ascertained and, while they crossed the equatorial sensory endings, they never came in contact with the intrafusal muscle fibres (Fig. 20).

Table 1. *Distribution of sensory nerve endings in 180 non-tandem muscle spindles stained with methylene blue or gold chloride*

Spindles with a primary sensory nerve ending only	101
Spindles with one primary and one secondary sensory nerve ending	67
Spindles with one primary and two secondary sensory nerve endings	
(i) On different sides of the primary	11
(ii) On the same side of the primary	1
Spindles with more than two secondary sensory nerve endings	0
Total	180

Table 2. *Distribution of motor nerve endings in 139 non-tandem muscle spindles stained with methylene blue*

Spindles in which nuclear bag end plates at one pole outnumbered those at the other	97
Spindles with diffuse nuclear chain sprays on one side of the equator only	108
Spindles with diffuse nuclear chain sprays on both sides of the equator	31
Spindles with diffuse nuclear chain sprays and nuclear chain end plates	44
Spindles with nuclear chain end plates only	0
Total	139

Tandem muscle spindles

Tandem muscle spindles were quite common, even the small first lumbrical muscle of the manus usually containing one. They were, however, difficult to tease out intact and only seven whole preparations were obtained. Each capsular unit of the tandem had a single primary sensory nerve ending supplied by different group Ia afferent fibres. At least one, and often both, units had a secondary sensory ending which could lie on either side of the respective primary. The secondary sensory endings were always supplied by different group II afferent fibres, one of which might be very small (4–5 μm). At the free poles of the tandem were typical spindle motor end plates, one or two lying on each nuclear bag fibre. In addition, one only of the free ends had one or more diffuse sprays on nuclear chain fibres. These sprays were identical to those present in non-tandem spindles. The junctional region joining the two tandem units also had motor nerve endings: there was always a single

motor end plate on each nuclear bag fibre and a large diffuse spray, supplied by three to five small motor axons, spreading over all the nuclear chain fibres. The nuclear bag end plates were supplied by one or two small motor axons or by a single large one.

Other receptor end organs

Typical Golgi tendon organs were common in the vicinity of musculo-tendinous junctions. They were supplied by large myelinated nerve fibres of average total diameter $12\ \mu\text{m}$ when measured 1 mm from the organ. Frequently, a single fibre branched to terminate in two or three Golgi tendon organs. Where a Golgi tendon organ was in series with a muscle spindle, it was never seen to be supplied by a branch of the group I afferent to that muscle spindle.

DISCUSSION

The structure of the muscle spindle in *Trichosurus vulpecula* was similar to that described by Barker (1948) for the rabbit, Boyd (1962*b*) for the cat, and Cooper & Daniel (1963) for man. It has not, therefore, been considered necessary to give a detailed account of features other than the innervation. The number of intrafusal fibres approached that described in man by Cooper & Daniel, who state that there are three to four nuclear bag and nought to ten nuclear chain fibres in each human spindle and that nuclear chain fibres usually outnumber nuclear bag fibres. In *Trichosurus*, two nuclear bag fibres were commonly present and four to twelve nuclear chain fibres, even in the smallest spindles. Although these spindles contained more intrafusal fibres than those of the cat, which Boyd describes as commonly having two nuclear bag and four nuclear chain fibres per spindle, the greater numbers in *Trichosurus* did not result in a more complex innervation. The nuclear chain fibres which at the equator of some spindles lay solitarily outside the nuclear bag fibres, instead of being collected into bundles lying between the nuclear bag fibres, are of uncertain significance. While they did not undergo the reduction in size at the equator that was characteristic of most nuclear chain fibres, they never contained nuclear bags and, at present, it would be premature to classify them with the intermediate fibres which Barker & Gidumal (1961) observed in one-third of cat spindles.

The innervation. It should be emphasized that the conclusions in this study are based on appearances seen in normal material. While to decide conclusively that certain nerve fibres and their endings are motor and others sensory would require a further investigation using de-afferented and de-efferented material, for the following reasons, it seems likely that the interpretations given have been valid: (1) The diameters of fibres interpreted as motor in this study are of the same order ($1.5\text{--}4.5\ \mu\text{m}$) as those which Boyd (1962*a, b*) and Barker & Ip (1965*a*) have shown by appropriate degeneration studies to be motor in the cat and rabbit; (2) the endings interpreted as motor in this study are situated in similar positions to those described by the same investigators in the cat and rabbit; (3) the endings described as sensory in this study, and the diameters of the nerve fibres supplying them, were in almost every way similar to those described by Barker (1948) in the rabbit and by

Barker & Cope (1962) and Boyd (1962*a, b*) in the cat; (4) the general structure of the *Trichosurus* spindle is so similar to that of Eutherian mammals that there seems little reason for assuming that the innervation should be fundamentally different.

It is also necessary to emphasize that this investigation is based entirely on observations made within 1 mm of individual spindles. While certain conclusions can be drawn from such a study, the degree of branching of nerve fibres before entering the field of observation, remains unknown.

The motor innervation. Physiological evidence indicates that the muscle spindles of the cat have dynamic and static properties, which are each influenced by different γ -efferent nerve fibres (Jansen & Mathews, 1962*a, b*). Morphological studies have clearly shown that most muscle spindles in most mammals possess two clearly distinct types of intrafusal muscle fibre. The important question, therefore, is whether there is any specificity in the innervation of these two types by the two types of γ -efferent demonstrable physiologically. Several studies have been devoted to the elucidation of this problem but there is little agreement on whether nuclear bag and nuclear chain fibres are specifically innervated; nor is there agreement that the visible differences between their motor endings have in themselves a functional significance. Boyd (1962*a, b*) and Boyd & Davey (1962) felt that, in the cat, nuclear bag and nuclear chain fibres each received γ -efferents which were distinguished by differences in diameter at the spindle and in the muscle nerves, and also, that the larger type ended specifically as end plates on nuclear bag fibres and that the smaller type ended specifically as diffuse networks on nuclear chain fibres. Barker and his colleagues, while admitting the presence of γ -efferents of different diameters, have always denied (Barker, 1962; Barker & Cope, 1962; Barker & Ip, 1965*a*; Adal & Barker, 1965) that there is any specificity in their distribution to nuclear bag or nuclear chain fibres. Initially, they also denied (Barker, 1962; Barker & Cope, 1962) the existence of a diffuse nuclear chain ending, claiming both nuclear bag and nuclear chain fibres always receive plate endings only. Subsequently, Barker & Ip (1965*a*) have demonstrated diffuse 'trail endings' in the cat, which seem to be equivalent to the diffuse network of Boyd but they have shown that these endings occur indiscriminately on both bag and chain fibres. Moreover, they demonstrated that some nuclear chain fibres received plate endings as well as trail endings and, also, that trail endings occur in the rabbit, whose spindles, they say, contain only nuclear bag fibres (Barker & Hunt, 1964).

The present investigation indicates that, while in two-thirds of spindles, nuclear bag and nuclear chain fibres were supplied respectively by axons that remained separate as far back as they could be traced, in one third, at least some bag and chain endings arose from a single axon. It should be noted, also, that even when nuclear bag and nuclear chain fibres were supplied by separate axons, such axons could not be differentiated by their diameters. In addition, it has been shown that, while nuclear chain fibres commonly received diffuse spray-like endings and nuclear bag fibres had end plates, nevertheless, chain fibres often had end plates and bag fibres often had diffuse end plates and, in two cases, sprays. It thus seems likely that neither the morphology of the motor endings nor the diameters of γ -efferents close to the spindle are, alone, sufficient criteria for a functional separation of intrafusal fibres and their motor supply.

The motor nerve endings. The morphology of the motor endings in *Trichosurus* resembled that previously described by several authors in a variety of mammals, but there were a few important differences. The nuclear bag end plates were somewhat longer than extrafusar end plates; this is the reverse of the situation in man (Cooper & Daniel, 1963). There was frequently a considerable inequality in the number of nuclear bag end plates situated at different poles of the same spindle, in contrast to the rabbit and cat where the numbers are approximately equal (Barker, 1948; Boyd, 1962*b*).

There is now good evidence that diffuse, juxta-equatorial motor endings occur in the muscle spindles of many mammals (Hess, 1961, mouse and rabbit; Boyd, 1962*a, b*, cat; Coërs, 1962, cat, rat and man; Cooper & Daniel, 1963, man; Barker & Ip, 1965*a*, cat and rabbit). The descriptions of these diffuse endings, however, vary: Boyd described a fine 'γ-2 network' lying on nuclear chain fibres and insisted that this was the only motor innervation received by these fibres; Cooper and Daniel were unable to distinguish details of the terminations of the sprays of fine branches which they observed near the equator, and Coërs, who described complex motor arborizations, did not distinguish on which fibres the arborizations were situated. The 'trail endings' of Barker & Ip seem to be equivalent to the endings described by Boyd and by Coërs but they lack the specificity described by Boyd in that they occur on both nuclear bag and nuclear chain fibres. Moreover, Barker & Ip's comment that they have interpreted similar formations as plate endings undergoing replacement, implies a different interpretation from that of Boyd. With two exceptions the diffuse nuclear chain sprays in *Trichosurus* tended to have the same specificity as the 'γ-2 network' described by Boyd in the cat, although the branches of the sprays never formed an intercommunicating net. In silver preparations, the branches of the spray appeared to end in relation to sole nuclei so the whole spray may merely constitute a diffuse type of motor end plate which causes the bundle of nuclear chain fibres on which it lies to contract as a whole. The presence of small motor end plates on some nuclear chain fibres does not detract from this suggestion as they were commonly derived from preterminal branches of axons entering a spray, or even from the spray itself. Barker & Ip (1965*a*) also observe that, in the cat, some nuclear chain fibres may receive 'trail endings' only, while others receive plate endings as well.

In the two cases where a diffuse spray was seen on a nuclear bag fibre, there was an additional spray on the nuclear chain fibres. The nuclear bag fibres possessing a spray had polar end plates as well. Boyd (1962*b*) observed a similar type of arrangement in the cat and considered it 'an anatomical peculiarity without physiological significance'. It seems likely that such an arrangement represents an unusually diffuse end plate. The finding of more irregular end plates and even diffuse sprays on nuclear bag fibres is in accord with the work of Kupfer (1960) who, in spindles in human extra-ocular muscles, found thin intrafusar fibres with numerous discrete loci of cholinesterase activity and thicker intrafusar fibres with both typical end plates and discrete loci. Histochemical studies such as the above, the present evidence that branches of diffuse nuclear chain sprays end in relation to sole nuclei, and Merrillees's (1960) electron microscopic studies in which all the motor endings he saw were similar, seem to indicate that the fundamental structure of the motor

terminals is probably the same on both nuclear bag and nuclear chain fibres, despite apparent differences in gross morphology.

The motor nerves. There were generally fewer motor nerve fibres entering the spindles of *Trichosurus* (4–16) than the number quoted by Boyd (1962*b*) for the cat (7–23), in both cases counted 1 mm from the spindle. The number of motor nerve endings was correspondingly fewer in *Trichosurus*.

Boyd (1962*a, b*) was of the opinion that nuclear bag end plates and nuclear chain networks in the cat were innervated by two different kinds of γ -efferents. These he called ' γ -1' (2.5–4 μm) and ' γ -2' (1.5–2 μm) on the basis of their axon diameters 1 mm from the spindle in gold chloride preparations. Whilst the range of diameters of γ -efferent fibres was similar in *Trichosurus*, there was no specificity of termination on nuclear bag or nuclear chain fibres, the only distinction being that fibres destined to end as diffuse nuclear chain sprays narrowed more markedly within the spindle capsule than those destined for nuclear bag end plates.

Boyd & Davey (1962) suggested that γ -1 and γ -2 efferents were represented in the muscle nerves of the cat by fibres with diameters of 6–7 μm and 3–4 μm respectively. Adal & Barker (1965) seem to have disproved this by showing that, in the lumbrical muscles of the cat, both types of γ stem fibre terminate as branches which enter muscle spindles as fibres of γ -1, γ -2, or both γ -1 and γ -2 calibre. Similarly, Bianconi, Granit & Reis (1964*a, b*) failed to find any conclusive evidence for selective γ -2 stimulation affecting the late (i.e. secondary) afferent discharge from cat spindles. An effect should have occurred if γ -2 fibres ended solely on nuclear chain fibres as it is on this group of intrafusal fibres that the secondary sensory endings are concentrated (Barker & Cope, 1962; Boyd, 1962*a, b*). The present study shows that nuclear bag and nuclear chain endings can not only be derived from branches of the same axon, but also that, when they are derived from separate axons, such axons are not separable on the basis of their diameters. Boyd's hypothesis for functionally distinct γ -1-nuclear bag and γ -2-nuclear chain systems must, therefore, be considered unsubstantiated.

If γ -efferent nerve fibres are similar to α -efferents, then they probably branch many times over the long distance from spinal cord to spindle. The apparent specificity in their distribution in two-thirds of spindles may, thus, not be reflected in the ventral horn cells. If this is so, then some, or even all, of the motor fibres ending in a muscle spindle could conceivably be branches of a single stem axon. The large motor axons which supplied some or all of the motor endings, both spray and plate, at one pole of some *Trichosurus* spindles might be examples of such stem axons which had not branched as frequently, or at all, before entering the muscle. The observations of Jansen & Matthews (1962*a, b*) and of Appelberg, Bessou & Laporte (1965) on static and dynamic γ -efferents render such a supposition unlikely, but observations made close to the spindle cannot elucidate the problem.

Large motor axons which supplied all or some of the motor endings at one end of some spindles were also observed by Barker (1948) in the rabbit. Mathews (1964) notes that these could belong to a special α -efferent group which innervates only muscle spindles. However, as pointed out by Barker (1959), fibres of this diameter are not too large to lie within the range usually given for γ -efferents.

The question of innervation of muscle spindles by branches of α -efferent nerve

fibres has been raised at intervals and recent physiological evidence indicates that it occurs in at least some muscles of the cat (Granit, Pompeiano & Waltman, 1959 *a, b*; Bessou, Emonet-Dénand & Laporte, 1963) and possibly in the rat (Steg, 1962, 1964). Adal & Barker (1965), who followed motor nerve fibres from the muscle nerves to their terminations in deep lumbrical muscles of the cat, reported five instances of such branching. Again, observations made close to the spindle, as in the present study and in those of Barker & Chin (1961) and Boyd (1962 *b*), cannot demonstrate this point.

The spindles in the lumbrical muscles of the pes

The two or three spindles which were constantly present partially embedded in the long, thin proximal tendon of the pes lumbricals, appear to be special in lacking a motor innervation at their proximal ends. Having their proximal portions embedded in relatively inextensible tendon, it seems likely that only their distal portions would be subjected to much stretch and it is they that are under the influence of motor nerves. It is conceivable that these two or three spindles could monitor changing tensions in the long flexor tendons during flexion of the digits against resistance. Such an explanation may be of some relevance in an animal which uses the claws of its lateral four pedal digits as simple suspensory hooks. None of the spindles in the lumbrical muscles of the manus had the same arrangement of motor nerve endings; these muscles are, however, very different from their counterparts in the pes, lacking the long proximal tendon and being attached by fleshy fibres directly to the common deep flexor tendon, proximal to the point at which it gives rise to its digital tendons.

Primary and secondary sensory nerve endings. Each spindle had only one primary sensory ending which was composed of a series of regular spirals or rings and was similar to that described in the cat by Ruffini (1898), Barker & Ip (1960) and Boyd (1962 *a, b*), and in the rabbit by Barker (1948). It was rather more regular than that described by Cooper & Daniel (1963) in man. Each intrafusal fibre had only one set of rings or spirals on it and even though many of the nuclear chain fibres were collected into bundles at the equator, they had separate rather than common portions of the primary ending. The ring formations on the nuclear chain fibres were usually much shorter than those on the nuclear bag fibres but the overall length of the primary ending (150–200 μm) was similar to that given by Barker (1948), Boyd (1962 *b*) and Cooper & Daniel (1963).

Secondary sensory endings were present in about one-half of all spindles, one being the commonest number, and even large tandem spindles rarely had more than one in each unit. Barker (1948) gave 0–2 as the commonest number in the rabbit and Boyd (1962 *b*) 0–5 in the cat. The secondary endings lay to one side of the primary ending and could mingle with it. A long, regular, tightly wound spiral encircled each nuclear chain fibre and a small number of thin half or quarter rings lay on adjacent nuclear bag fibres. Again, the form of the secondary ending was similar to that described by Barker (1948) in the rabbit and by Barker & Ip (1960) and Boyd (1962 *a, b*) in the cat. These authors, however, give the portion of the ending lying on nuclear bag fibres a spray-like form. Cooper & Daniel (1963) agree that in man the secondary ending lies predominantly on nuclear chain fibres. The overall length of

the secondary ending in *Trichosurus* was 200–300 μm which is a little shorter than that described by Barker (1948) (500 μm , rabbit) and Boyd (1962*a, b*) (300–500 μm , cat), but is about the same as that described by Cooper & Daniel (1963) for man.

Afferent nerve fibres. The mean diameter of group Ia and group II afferent fibres to muscle spindles in *T. vulpecula* when measured 1 mm from the spindle was 12.5 and 8 μm respectively. These diameters are similar to those given by Barker (1948) for the rabbit (8–12 and 6–9 μm) and by Boyd (1962*a, b*) for the cat (12 and 6 μm). Group Ib afferents to Golgi tendon organs had an average diameter of 12 μm and branched frequently, a single Ib nerve fibre often supplying two or three end organs. Within 1 mm of their terminations, group Ia afferents never supplied more than one spindle and never supplied a spindle and a Golgi tendon organ in series with it as suggested by Hines & Tower (1928) and others but denied by Barker & Chin (1961).

Group II afferents occasionally divided near a spindle and supplied two secondary endings in that spindle. Boyd (1962*b*) claims that secondary endings in adjacent spindles may be supplied by branches of the same group II afferent fibre and Swett & Eldred (1959) gave physiological evidence for such an occurrence but it was never observed in the present study.

Other nerve fibres in the spindle. The very small (0.5 μm), beaded, non-myelinated nerve fibres occasionally seen in the capsular region had little relation to the intrafusal fibres. They were quite distinct from other nerve fibres in the spindle and cannot be classed as ' γ -2 efferents' as Boyd (1962*b*) suggested was the case with similar fibres seen passing to the poles by Barker (1948) or those in the capsular region described by Hines & Tower (1928). It was not possible to say if the small nerve fibres observed in this study innervated the capsule or merely blood vessels. If they are autonomic in nature then they may only supply blood vessels as stated by Boyd (1962*b*). On the other hand, Cooper & Daniel (1963) described fine fibres in relation to both the capsule and blood vessels, and Eldred, Schnitzlein & Buchwald (1960) and Hunt (1960) have shown that stimulation of the sympathetic trunk in the cat will affect the afferent discharge from a muscle as recorded from dorsal root filaments.

The findings of this investigation closely resemble those of Barker and his colleagues (Barker, 1962; Barker & Cope, 1962; Adal & Barker, 1965; Barker & Ip, 1965*a*) and clearly indicate that in at least one-third of the spindles examined in this animal, nuclear bag and nuclear chain intrafusal fibres can be innervated by the same γ -efferent nerve fibre. Furthermore, it has been shown that there is a complete range of motor nerve endings from compact end plates to very diffuse sprays which can and do lie on both types of intrafusal fibre. It is, however, noteworthy that diffuse endings more frequently occurred on nuclear chain fibres and end plates more frequently on nuclear bag fibres. In this, the findings resemble those of Boyd (1962*a, b*) but, unlike his findings, there was definitely no specificity in the supply of bag or chain fibres by motor axons of different diameter.

SUMMARY

1. The innervation of muscle spindles was studied in the Australian opossum, *Trichosurus vulpecula*, by means of teased whole spindles stained with methylene blue or gold chloride and by sections stained with silver.

2. Two types of spindle motor nerve endings were described: The first was a diffuse spray, supplied by one or more axons, lying on bundles of nuclear chain intrafusal fibres within the capsule and near the secondary sensory ending if present. Solitary nuclear chain fibres often had small compact motor end plates derived from preterminal branches of axons entering a spray or from the spray itself. Rarely, they were supplied by a solitary axon.

The second type consisted of one or more typical motor end plates lying on each nuclear bag fibre, commonly near the poles of the capsule, but additional nuclear bag end plates were often present within the capsule among the nuclear chain motor endings. These additional nuclear bag end plates were often more irregular or diffuse.

3. While nuclear chain sprays more commonly occurred at one end only of a spindle they were frequently seen at both ends. Nuclear chain end plates were never present in the absence of nuclear chain sprays. Nuclear bag end plates were usually concentrated at one end of a spindle, while at the other end there was often only one end plate per nuclear bag fibre.

4. Two types of spindle motor axons were described: (a) small (1–2 μm) axons supplied nuclear bag end plates or nuclear chain sprays and end plates. Those entering nuclear chain sprays narrowed more markedly within the spindle. (b) In about one third of spindles, one or two large (2.5–3.5 μm), more heavily myelinated motor axons supplied some or all of the motor endings, both sprays and end plates, at one end of the spindle. Their total diameter, including the myelin sheath, was usually 6.5 μm .

5. It was concluded that the fundamental structure of motor nerve terminals on nuclear bag and nuclear chain fibres is probably essentially similar, and that differences in the gross morphology of the motor endings do not of themselves provide criteria for a functional separation of the two types of intrafusal muscle fibre. Evidence against functional specificity based on the diameter of γ -efferents was that, when nuclear bag and nuclear chain fibres were supplied by separate motor axons, such axons were not separable on the basis of their diameters. Furthermore, in at least one third of spindles, both nuclear bag and nuclear chain endings at one pole were supplied by the same motor axon.

6. Two or three spindles lacking a motor innervation at their proximal ends were constantly present partially embedded in the long proximal tendons of the pes lumbricals.

7. Sensory nerve endings in the spindles and their nerves were similar to those described in other mammals.

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