

**Fibre analysis of the nerve to the inferior oblique
muscle in monkeys**

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INTRODUCTION

Tozer & Sherrington (1910) claimed that afferent nerve fibres from extra-ocular muscles pass to the brainstem in their motor nerves, based on evidence obtained from degeneration studies in monkeys, cats and rabbits, and Sherrington maintained this view in later years. Despite some support (Tarkhan, 1934; Sunderland & Hughes, 1946; Fukuda, 1958) this opinion has been challenged by most subsequent workers, who have used various methods which showed that such afferents reach the brainstem in the trigeminal rather than the ocular motor nerves. Firstly, filaments passing from muscle motor nerves to branches of the trigeminal nerve in the orbit or cavernous sinus were described in various species, and, in some, these passed directly from muscles to trigeminal branches (Stibbe, 1930; Kiss, 1935; Winckler, 1937, 1956; Cooper, Daniel & Whitteridge, 1955; Ruskell, 1964). Secondly, many fibres in oculomotor branches survived intracranial division of the oculomotor nerve in cats (Gay, Joffe & Barnet, 1964; Buisseret-Delmas, 1976), and many fibres degenerated in distal but not in central parts of ocular motor nerves after intracranial ophthalmic neurectomy (Batini, Buisseret & Buisseret-Delmas, 1975). Thirdly, responses to muscle stretch were recorded from filaments joining motor with trigeminal branches in ungulates and cats (Cooper *et al.* 1955; Whitteridge, 1955, 1959); similar electrophysiological results were obtained directly from the trigeminal nerve or ganglion (Manni, Bortolami & Desole, 1968).

The evidence from several varied studies in cats denies Tozer & Sherrington's claim, except with regard to the abducent nerve in which some or all of the muscle afferents pass to the brainstem (Bach-y-Rita & Murata, 1964; Batini & Buisseret, 1974; Batini *et al.* 1975). Of other animals used by Tozer & Sherrington, the rabbit has been studied little and monkeys not at all; both require re-assessment.

Nerve endings in extra-ocular muscles of primates are under study in this laboratory and knowledge of the composition of nerves serving these muscles is obviously required. The present report provides information for the nerve to the inferior oblique muscle. Sherrington's views on afferent paths were tested, fibre diameter spectra were produced, unmyelinated fibres were counted, and their sources were determined.

MATERIALS AND METHODS

Eleven young adult monkeys of both sexes were used, four rhesus (*Macaca mulatta*) and seven cynomolgus (*Macaca fascicularis*). They were sedated parenterally by 2–3 mg/kg Sernylan (phencyclidine hydrochloride) and anaesthetised by 15–25 mg/kg Nembutal (pentobarbital sodium) given via the saphenous vein or

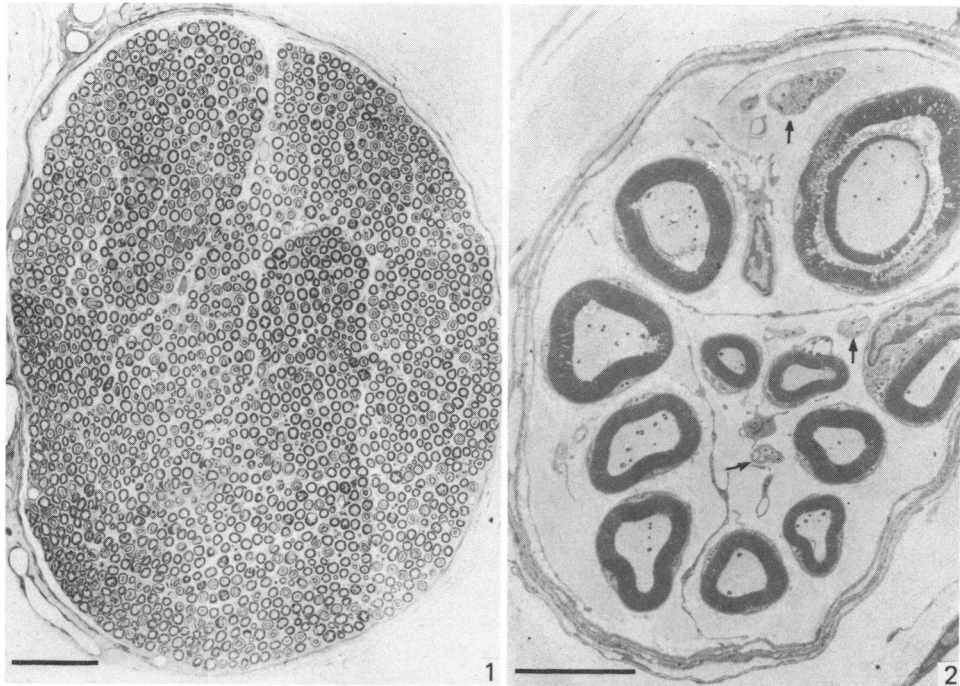


Fig. 1. Light micrograph montage of a transverse section through a nerve to the inferior oblique muscle. Cynomolgus. Marker indicates 100 μ m.

Fig. 2. Electron micrograph of a transverse section through a small division of the nerve to the inferior oblique muscle to show variety of myelinated fibre size and unmyelinated fibres (arrows). Rhesus. Marker indicates 5 μ m.

intraperitoneally. All animal operations were on the left side. The superior cervical ganglion was removed from five cynomolgus monkeys and three were killed 3, 7 and 15 days later. A short length of oculomotor nerve was removed intracranially from the other two, 14 and 16 days after the first operation, and from a sixth cynomolgus monkey.

The superior cervical ganglion was excised with little difficulty by the usual neck approach in cynomolgus monkeys; excision of the ganglion in rhesus was not attempted because it is partly lodged in the carotid foramen and therefore is not fully accessible. The calvarium was removed in preparation for oculomotor neurectomy and the dura was reflected. The oculomotor nerve was exposed by elevation of the cerebrum when it was divided, and a short length of it was removed. By dividing the isolated nerve close to the brainstem before it enters the cavernous sinus, damage to neighbouring structures was avoided and complete division was facilitated. The dura was then sutured, and the calvarium was replaced and secured by strong bridging sutures connecting the temporalis muscles, when the skin wound was closed. Survival times after oculomotor neurectomy were 10, 10 and 12 days.

A short length of ophthalmic nerve was removed intracranially from one cynomolgus and four rhesus monkeys, as was a short length of the maxillary nerve in two of the rhesus monkeys by the same operative approach. To minimise the risk of damage to adjacent nerves and the cavernous sinus, the ophthalmic nerve sheath was cut longitudinally close to the trigeminal ganglion, the nerve was freed from sheath

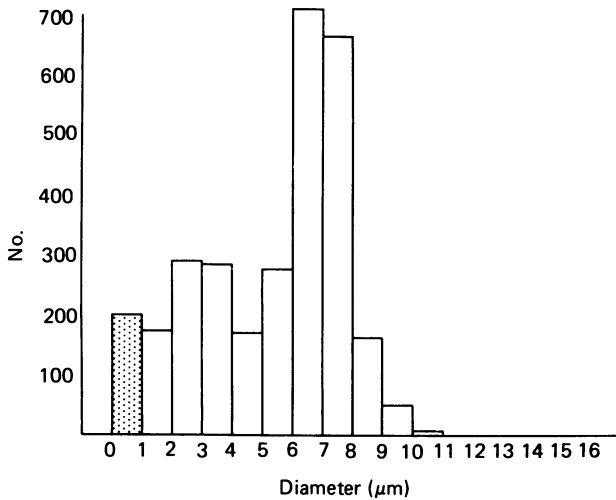
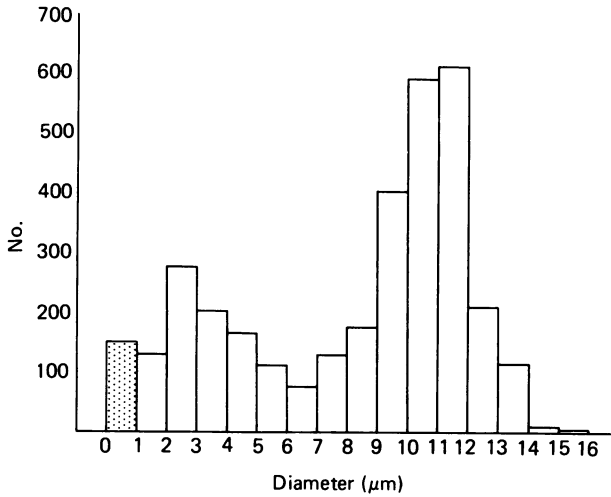


Fig. 3. Nerve fibre diameter spectra for two rhesus monkeys. The unmyelinated nerve fibre bin is shaded.

attachments, then divided and reflected, and a piece was removed. The maxillary nerve was similarly treated.

The operations were designed to induce Wallerian degeneration, so that fibres from the divided nerves passing to the nerve to the inferior oblique muscle could be traced.

Following sedation, anaesthesia and injection of the anticoagulant heparin sodium (1500 units), all animals were perfused with 1% sodium nitrate (for vasodilation) in physiological saline, followed by 5.5% cacodylate-buffered glutaraldehyde, through both common carotid arteries or the heart, with the external jugular veins cut. The heads were stored in fixative at approximately 4 °C and dissected while immersed in buffered sucrose, using a dissection microscope.

On both sides, the whole nerve to the inferior oblique muscle, from the ciliary

Table 1. *Nerve to the inferior oblique muscle fibre analysis (operated sides)*

Species	Neurectomy and post-operative survival (days)	Normal myelinated fibres	Normal unmyelinated fibres	Degenerated myelinated fibres	Degenerated unmyelinated fibres
R	Ophthalmic 6	3214	116	7	33
R	Ophthalmic 7*	2854	247	4	25
C	Ophthalmic 7	2167	140	12	29
R	Ophthalmic 16	2765	285	21	63
R	Ophthalmic 28*	3094	77	24	57
C	Oculomotor 10	27	98	Most	Most
C	Oculomotor (SCG) 10	17	49	Most	Most
C	Oculomotor (SCG) 12	27	10	Most	Most
C	SCG 3	1976	261	0	18
C	SCG 7	2081	74	0	29
C	SCG 15	2450	320	0	141

C, cynomolgus; R, rhesus; SCG, superior cervical ganglionectomy. *Also maxillary neurectomy. Control nerves contained an average of two Schwann cells without enclosed axons: otherwise, no fibre meeting the criteria for degeneration were present.

ganglion to its muscle, was isolated and cut into proximal and distal halves. Tissues were post-fixed in 1% unbuffered osmium tetroxide, dehydrated, and then embedded in Araldite and transversely sectioned. Mounted sections were immersed in a saturated solution of uranyl acetate in 30–70% ethanol for about 20 minutes, washed, immersed in 0.4% lead citrate in 0.1 N sodium hydroxide for about 10 minutes, and examined by electron microscopy. Thicker sections were cut for light microscopy, and stained with 1% toluidine blue in an equal amount of 2.5% sodium carbonate. Large montages made from light micrographs of some of the nerves were used for measuring myelinated fibre diameters. Unmyelinated and all degenerated fibres were counted using electron microscopy, and the number of fibres covered by grid bars was estimated; after oculomotor neurectomy, the normal fibres were similarly counted.

RESULTS

Nerve fibre content

The nerve contained myelinated fibres of widely varying diameter, and, at higher magnifications, scattered small unmyelinated nerve fibre bundles could be made out (Figs. 1, 2). Myelinated fibre counts produced a mean of 3107 in rhesus monkeys (range 2613–3613), and in cynomolgus monkeys a mean of 2251 (range 1976–2523). The spectrum of myelinated nerve fibre diameters showed a bimodal distribution in both species. One peak occurred between 2.5 and 3.0 μm (varying with the individual animals) and the second between 7 and 11 μm . The marked variation of the second peak applied equally to rhesus and cynomolgus monkeys, and the histograms of Figure 3 have been selected to show the extremes. Small myelinated fibres (less than 5 μm) amounted to 16–30% of the total, with a mean of 24%.

Unmyelinated fibres were sparsely scattered throughout the nerves. From 134 to 348 were found in rhesus monkeys, with a mean of 245, or 7.3% of all nerve fibres. A greater variation was found in cynomolgus monkeys (103–657), with a mean of 297, or 10.4% of the total. Most of the bundles contained one or two axons.

Cell bodies were found at intervals in the nerves from each side of one rhesus and two cynomolgus monkeys. There were seldom more than four cells in a single

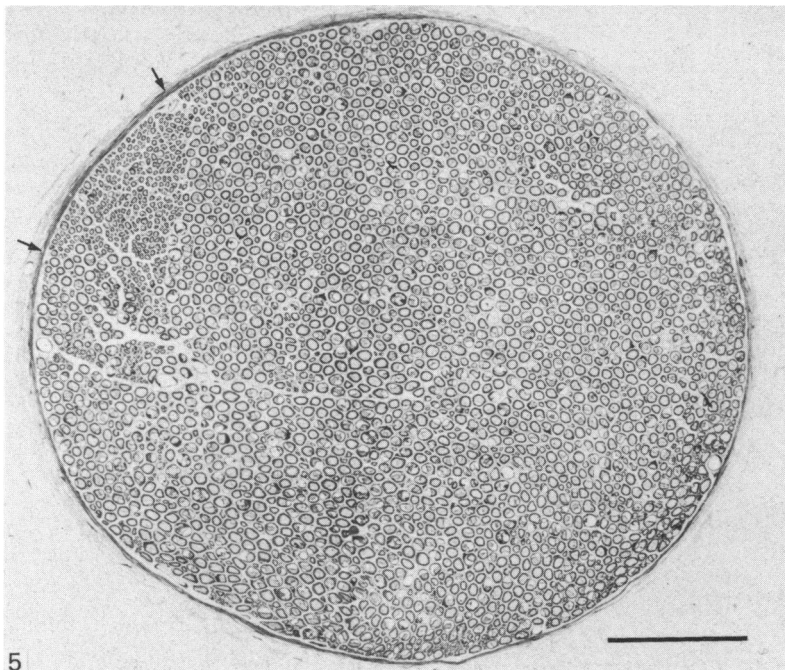
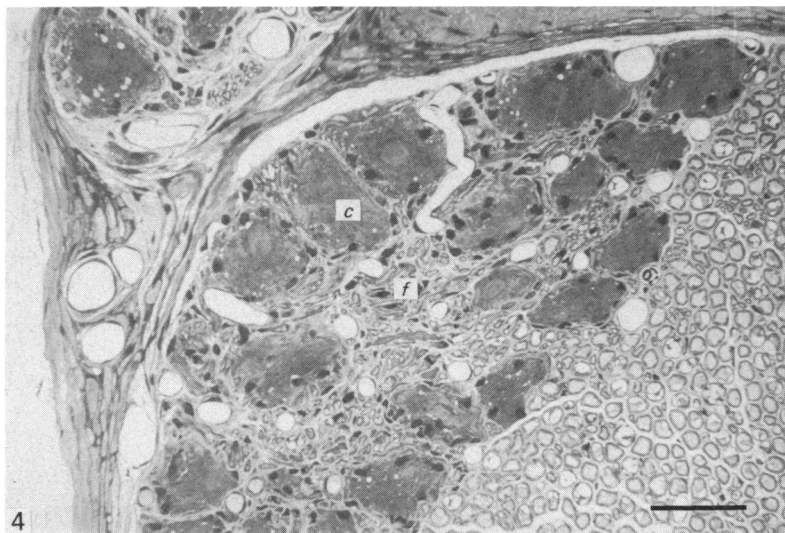


Fig. 4. Cell bodies (*c*) aggregated at the surface of the nerve among a group of small myelinated fibres (*f*) of similar diameter. Rhesus. Marker indicates $50\ \mu\text{m}$.

Fig. 5. Light micrograph montage showing a group of small myelinated fibres at the surface of the nerve (between the arrows). Rhesus. Marker indicates $100\ \mu\text{m}$.

section but in one pair of nerves groups of up to 15 cells were occasionally seen (Fig. 4). They were large (mean diameter $32\ \mu\text{m}$), dendritic, and with synapses, and were aggregated at the nerve surface together with substantial groups of small myelinated fibres. In many sections, only the aggregated small fibres could be seen (Fig. 5) but, in contrast to the other nerve fibres, they were of uniform diameter (mean $3.5\ \mu\text{m}$) and so were easily distinguished. Numerous capillaries infiltrated the

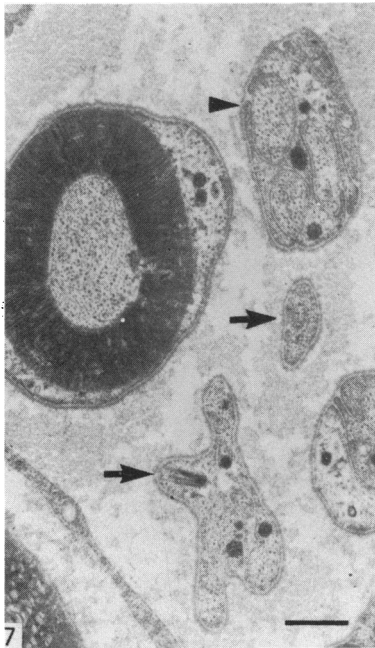
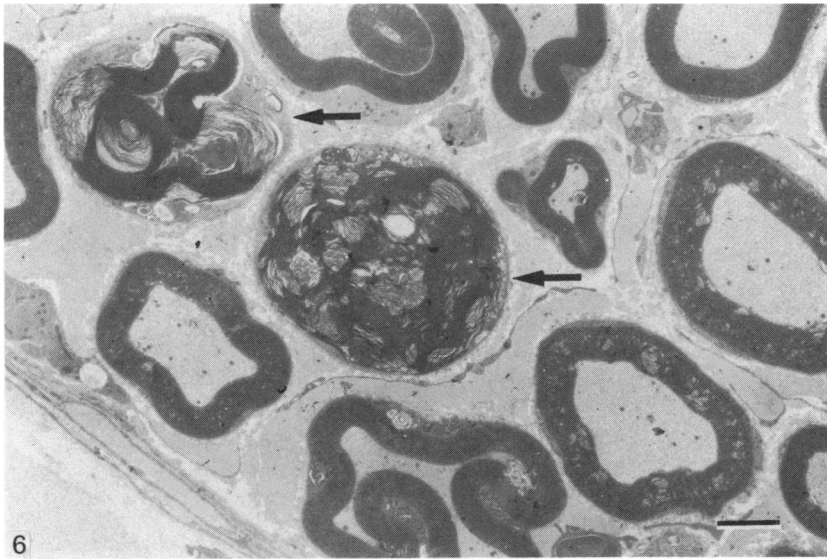


Fig. 6. Two degenerated myelinated fibres (arrows) among fibres of normal appearance. Rhesus, fixed 7 days after ophthalmic neurectomy. Marker indicates $2 \mu\text{m}$.

Fig. 7. Two Schwann cell bundles without enclosed axons (arrows). The larger bundle of irregular shape contains several processes within the basal lamina. The uppermost bundle (arrowhead) has a normal appearance and contains three axons. Rhesus, fixed 16 days after ophthalmic neurectomy. Marker indicates $0.5 \mu\text{m}$.

Fig. 8. A Schwann cell bundle with several processes but without axons. Cytoplasm is unusually substantial and the basal lamina undulates. Rhesus, fixed 16 days after ophthalmic neurectomy. Marker indicates $1 \mu\text{m}$.

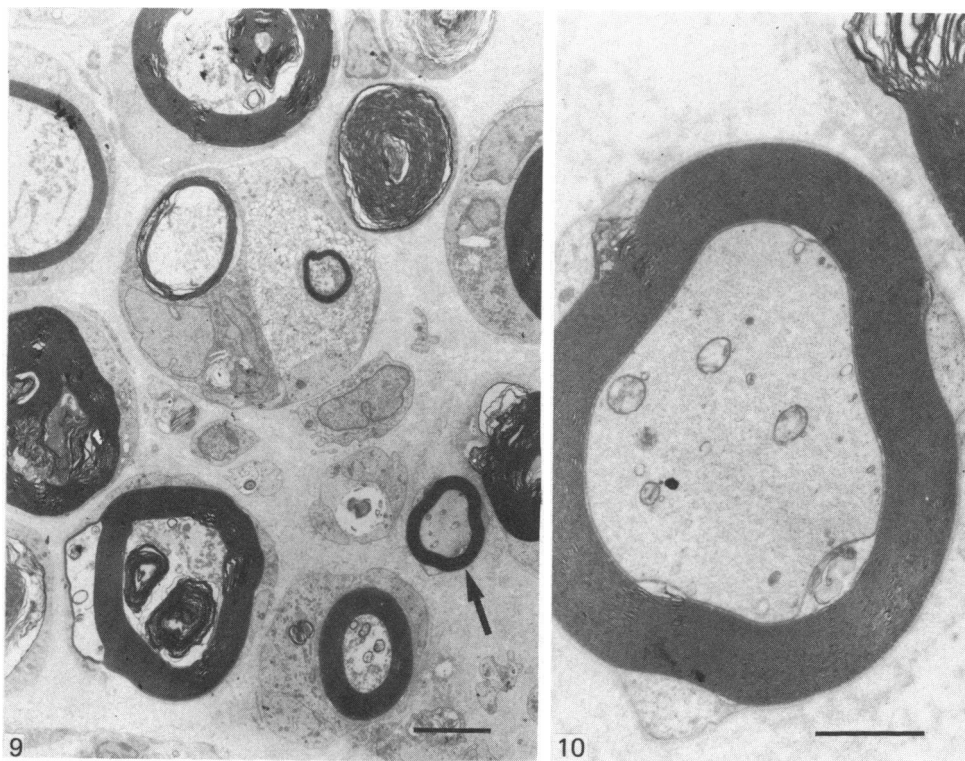


Fig. 9. Degenerated myelinated and unmyelinated fibres. One small myelinated fibre (arrow) has a normal appearance. Cynomolgus, fixed 36 days after superior cervical ganglionectomy and 10 days after oculomotor neurectomy. Marker indicates $4\ \mu\text{m}$.

Fig. 10. Detail of Fig. 9 showing the normal organelles of the surviving nerve fibre. Marker indicates $1\ \mu\text{m}$.

nerves at loci containing cell bodies. The colonies of cell bodies and small fibres were present only in the proximal part of four nerves, but in one pair they extended forward nearly as far as the muscle. These fibres were excluded from the counts shown in Table 1.

Ophthalmic nerve fibres

A few scattered, degenerated fibres were present in the nerve to the inferior oblique muscle in each of five monkeys after ophthalmic neurectomy (see Table 1). Infrequent myelinated fibres of intermediate size were included among the degenerated fibres (Fig. 6) but most were small or unmyelinated. The main criterion for identifying degeneration of myelinated fibres was the absence of axoplasm or of normal axoplasmic organelles as determined by electron microscopy; normal axoplasm was invariably present in fibres of control nerves. Schwann cells without enclosed axons were considered to represent degenerated unmyelinated fibres (Fig. 7) but this was a slightly less secure criterion because from one to four empty Schwann cells were found in the control nerves; these were considered too few to warrant use of a correction factor in calculating proportions of degenerated fibres. Other features of degeneration not seen in controls are shown in Figures 7 and 8. The number of degenerated fibres in the motor nerves was similar whether or not the maxillary nerve had also been cut (Table 1).

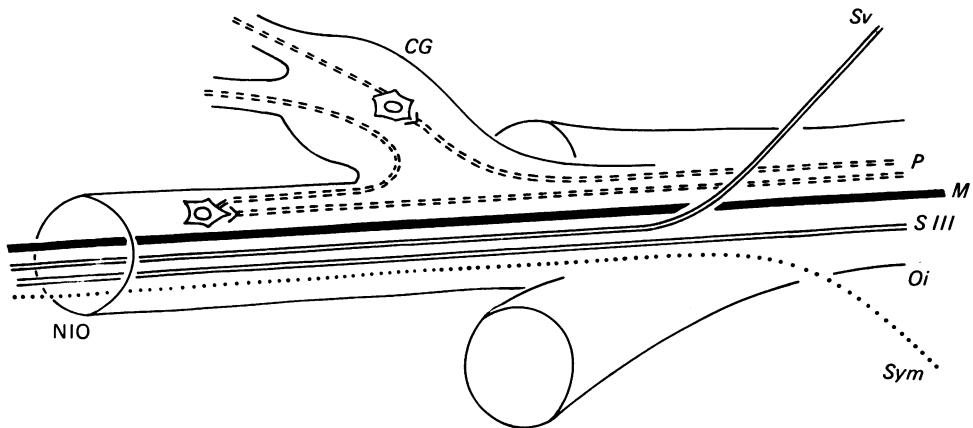


Fig. 11. Scheme of the nerve-fibre pathways through the nerve to the inferior oblique muscle (NIO). The positions where sensory (*Sv*) and sympathetic (*Sym*) fibres leave the oculomotor nerve (*Oi*) is uncertain and the recurrent parasympathetic (*P*) pathway is inconstant. The majority of sensory fibres (*S III*) enter the brainstem in the oculomotor nerve. *CG*, ciliary ganglion; *M*, somatic motor fibres.

More unmyelinated than myelinated nerves were degenerated in each of the five nerves and together they amounted to a mean of 1.8% of all fibres (range 0.9–2.7%).

Because these results indicated that some fibres pass to the ophthalmic nerve from the nerve to the inferior oblique muscle, they should survive intracranial oculomotor neurectomy, and so it proved. Amid the mass of degenerated fibres induced by this manoeuvre a fibre of normal appearance was occasionally observed (Figs. 9, 10). In fact, the numbers of myelinated fibres surviving oculomotor neurectomy compared with those that were degenerated after ophthalmic neurectomy. Most of the survivors had a diameter of 1–3 μm . Comparability of unmyelinated fibre numbers in the two experiments occurred only when the superior cervical ganglion had also been removed (Table 1). The nerve to the inferior oblique muscle of the one animal in which this was not done contained many more normal unmyelinated fibres than the others, presumably because normal sympathetic fibres were present.

Sympathetic fibres

Evidence of degeneration was found in the nerve to the inferior oblique muscle after cervical ganglionectomy in three animals, but only unmyelinated fibres were affected. The number of degenerated nerve fibre bundles was 18, 29 and 141, representing 6.4, 28 and 31%, respectively, of all unmyelinated fibres.

DISCUSSION

Bimodality of extra-ocular muscle nerve fibre diameters is a feature of all mammals so far examined, and one of the numerous earlier reports dealt with monkeys; Häggvist (1962) produced histograms for the trochlear and abducent nerves of cynomolgus monkeys showing bimodality with peaks corresponding well with those of this study.

The claim in most of the older literature that ocular motor nerves in man and animals contain only myelinated fibres is no longer tenable. Earlier tentative and

largely disregarded claims for the presence of unmyelinated fibres have been vindicated by recent electron microscopical studies in man (Kerns, Smith, Jannotta & Alper, 1979), rats (Kerns, 1980), Peking ducks (Weidman & Sohal, 1977), and now in monkeys. Although the degeneration experiments showed that unmyelinated fibres pass into the nerve to the inferior oblique muscle in ophthalmic and sympathetic connecting branches, the mean proportions of unmyelinated fibres acquired from these sources are only 22 % and 21 %, so that, if no further peripheral junctions occur, then the majority are presumably present in the oculomotor nerve at brainstem level.

The mean proportion of degenerated fibres in the nerve to the inferior oblique muscle after ophthalmic neurectomy is 1.8 %. The mean proportion of fibres surviving oculomotor neurectomy combined with superior cervical ganglionectomy, and therefore probably representing fibres from the ophthalmic nerve, is also 1.8 % (this figure was calculated as a percentage of fibres in control nerves because the widespread disruption on the operated sides prevented accurate counting of degenerated fibres). Hence, 1.8 % of fibres serving the inferior oblique muscle are derived from the ophthalmic nerve, and there is no reason to doubt that they are sensory. Despite their claim that extra-ocular muscle afferents pass to the brainstem in motor nerves, Tozer & Sherrington (1910) recognised that a few join the ophthalmic nerve. Could these represent all afferents of the muscle, or is Tozer & Sherrington's view correct? The mean proportion of 1.8 % represents a mere 54 fibres, and there are several reasons for believing that many more and a greater variety of fibres serve a sensory function in the muscle. For example, muscle receptors are very numerous in monkeys; they are served by fibres which are often larger than those that pass to the ophthalmic nerve, and they are a small fraction of the afferents identified in cat extra-ocular muscles. These three points will be considered in turn.

Muscle spindles (Greene & Jampel, 1966) and Golgi tendon organs (Ruskell, 1979) are rare or absent from monkey extra-ocular muscles but, as Tozer & Sherrington (1910) recognised, many afferent terminals are present in the distal tendons. These are the *myotendinous cylinders*, of which 350 are estimated to be present in a single medial rectus muscle (Ruskell, 1978). They are innervated by myelinated fibres 2.5–6 μm in diameter measured at the distal tendon, whereas practically all the myelinated fibres passing from the nerve to the inferior oblique muscle into the ophthalmic nerve are 1–3 μm in diameter. Cats provide a suitable comparison with monkeys because they too possess many myotendinous cylinders (Alvarado-Mallart & Pinçon-Raymond, 1979) and lack muscle spindles, and one would not expect a substantial difference in the proportion of sensory fibres serving extra-ocular muscles in the two species. Yet up to 6 % of myelinated fibres of the abducent nerve and 10 % of those of the oculomotor and trochlear nerves (counted at orbital level) in the cat enter the brainstem in the trigeminal nerve, and these may represent the full sensory content of the motor nerves (Buisseret-Delmas, 1976). When the figures for monkeys are adjusted to include only myelinated fibres, for appropriate comparison with Buisseret-Delmas' data, only 0.5 % on average pass from the nerve to the inferior oblique muscle into the ophthalmic nerve. There is little room for doubt that these few fibres represent a minor pathway for muscle afferents to the brain, and that the main group of afferents enter the brainstem in the oculomotor nerve (Fig. 11).

The colonies of cell bodies found in some nerves are probably parasympathetic; they have the shape, size, fine structure, and synaptic arrangement of ciliary ganglion cells (Ruskell & Griffiths, 1979), and the small myelinated fibres associated with the cells are the size of parasympathetic pre- and postganglionic fibres of the ciliary

ganglion. Although trigeminal ganglion cells may be displaced as far forward as the orbit (Phillips, 1972; Bergmanson, 1977), they are unipolar and without peripheral synapses, unlike the cells under consideration. Their average diameter of $32\ \mu\text{m}$ is too large, and the variety of diameters too small, to belong to the sympathetic system. Neither cells nor associated fibres are found as far forward as the muscle, hence it appears likely that some preganglionic fibres of the oculomotor nerve fail to turn into the ciliary ganglion and proceed forward in the nerve to the inferior oblique muscle, terminating on the cells; postganglionic fibres retrace the same path and pass into the ciliary ganglion either by the main or a minor oculomotor root (Fig. 11).

The induction of fibre degeneration by superior cervical ganglionectomy demonstrates that the nerve to the inferior oblique muscle contains sympathetic fibres. All are unmyelinated and present in every section, so they must join the oculomotor nerve before the nerve to the inferior oblique muscle branches from it and they must enter the muscle. Their number varied eightfold in the three experiments, which is surely too great a variation to attribute to individual variation of sympathetic innervation of the muscle. Other pathways to the muscle for sympathetic fibres must be present if the notion of closer comparability between individuals is to be upheld. Because branches of the ophthalmic artery carry sympathetic nerves in their tunica adventitia (Ruskell, 1970), vessel-borne sympathetic fibres probably complement those reported here.

Allocation of separate functions to nerve fibres of different sizes is not attempted here; information on most varieties of nerve endings in primate extra-ocular muscles is sketchy, making such an exercise too speculative at present.

SUMMARY

The nerves to the inferior oblique muscles from both sides of four rhesus and seven cynomolgus monkeys were examined by light and electron microscopy. Myelinated fibres averaged slightly over 3000 in rhesus and 2000 in cynomolgus monkeys, with a bimodal distribution of diameters in both, the lower peak being $2.5\text{--}3.0\ \mu\text{m}$ and the upper $7\text{--}11\ \mu\text{m}$, the large variation of the latter applying to both species. Unmyelinated fibres were less than 10% of the total.

Following intracranial ophthalmic neurectomy in five monkeys, a few unmyelinated and small myelinated fibres were degenerated in the nerve to the inferior oblique muscle (1.8% of all fibres on average). A similar proportion of fibres *survived* oculomotor neurectomy in three cynomolgus monkeys when the superior cervical ganglion was additionally removed. A variable number of unmyelinated fibres were degenerated in the nerve after superior cervical ganglionectomy in three cynomolgus monkeys.

The experiments indicate that ophthalmic and sympathetic branches pass to the nerve to the inferior oblique muscle. The few ophthalmic nerve fibres entering the muscle appear inadequate to serve the large numbers of receptors present and therefore most of the sensory fibres probably enter the brainstem in the oculomotor nerve in both species. The sympathetic pathway to the muscle provided by its motor nerve may be augmented by others.

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