

THE RESPONSES OF MUSCLE SPINDLES IN SHEEP EXTRAOCULAR MUSCLES

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SUMMARY

1. Responses from de-efferented muscle spindles in sheep extraocular muscles have been recorded in the Gasserian ganglion using glass micro-electrodes.

2. The afferent fibre conduction velocities ranged from 32 to 106 m/sec and most were intermediate. The distribution was unimodal.

3. The afferent responses to ramp stretches and longitudinal vibration of the muscle could not be divided into two groups, but both the dynamic indices and vibration sensitivities of the afferents increased with their conduction velocities.

4. Injection of suxamethonium did not help to classify afferents with intermediate conduction velocity.

5. It is concluded that the afferents from sheep extraocular muscle spindles form a single population whose properties are correlated with their nerve fibre diameters.

INTRODUCTION

Sheep extraocular muscles contain large numbers of muscle spindles (Cilimbaris, 1910). The afferent fibres from these spindles run in small nerve bundles, which are mostly separate from the motor nerves, to join the ophthalmic division of the trigeminal nerve (Winkler, 1937; Whitteridge, 1955). Their cell bodies lie in the Gasserian ganglion (Manni, Bartolami & Desole, 1966).

Afferent impulses from sheep extraocular muscle spindles were first recorded by Cooper, Daniel & Whitteridge (1951, 1955), Cooper & Daniel (1957), and Whitteridge (1955, 1959). They described the responses to stretch and to contraction of the muscle as similar to those of cat hind-limb muscle spindles; however, at that time the responses of primary and secondary endings had not been distinguished.

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Sheep extraocular muscle spindles have both nuclear bag and nuclear chain intrafusal fibres and typical primary and secondary sensory endings (Harker, 1972). The purpose of the present study was to investigate quantitatively the responses of de-efferented muscle spindles and, if possible, to distinguish the behaviour of primary and secondary endings. A preliminary account of some of these results has appeared (Browne, 1974).

Since the present experiments were performed, Bach-y-Rita & Lennerstrand (1974) have reported primary and secondary responses from extraocular muscle spindles of the pig.

METHODS

Experiments were performed on thirty-two sheep. They were anaesthetized with *i.v.* pentobarbitone sodium (Nembutal) 30 mg/kg, and then decerebrated. The roof of the orbit was removed and the dura overlying the Gasserian ganglion stripped off. The trochlear nerve was cut and placed on stimulating electrodes. Extracellular recordings from single cells in the Gasserian ganglion were obtained using glass micro-electrodes. The ganglion was sometimes covered in tough connective tissue which was difficult to remove without damaging the underlying cells. In these animals the connective tissue was softened using a 2% solution of pronase (BDH), applied for 5 min.

The main afferent nerve bundle was stimulated close to the muscle with pulses of 50 μ sec duration to allow measurement of spindle-afferent conduction velocities. The conduction distance was found at the conclusion of the experiment by measuring the length of the nerve with a piece of fine thread.

Stability of recording in the ganglion was often poor due to the close proximity of the internal carotid artery and the cavernous sinus. Therefore in experiments when suxamethonium was used, more stable conditions were obtained by recording from strands of the afferent nerve split within the orbit. In these cases conduction velocity measurements could not be obtained.

Most experiments were performed on the superior oblique muscle, but in three the superior rectus was used. The results did not differ and were pooled. The muscle tendon was detached from the globe together with a small piece of sclera. The distal portion of the muscle was covered in a mixture of paraffin and petroleum jelly and the temperature maintained at 37–39°C by a feed-back controlled heating lamp. The interior of the skull was filled with warm paraffin. The muscle was attached to a servo-controlled electromagnetic stretcher via a tension transducer made from silicon strain gauges bonded to a beryllium copper strip. The length of the muscle was kept within the physiological range. The timing of muscle stretches and electrical stimuli was controlled by a Digitimer (Devices). The control signal to the stretcher was derived from either a ramp generator or a sine wave generator (Feedback Ltd). The maximum amplitude of vibration available at 100 Hz was 1.4 mm. Ramp stretches were usually 3 mm in amplitude at velocities from 4 to 60 mm/sec. The average length of the superior oblique muscle was 55 mm and the eye-ball diameter was 32 mm. Thus a 3 mm stretch represents an angular rotation of 11° and the angular velocities of eyeball movement equivalent to the ramp stretches were from 14 to 215°/sec.

After conventional a.c. amplification, the afferent discharges triggered an instantaneous frequency meter whose output was displayed on a storage oscilloscope

(Tektronix 564). Records of afferent discharge, muscle length and tension, and trigger pulses were made on a Hewlett Packard 3960 instrumentation tape recorder.

In some experiments suxamethonium chloride (BDH) was administered intravenously. The dose was 200 $\mu\text{g}/\text{kg}$ in a dilution of 1 mg/ml. Recovery from this injection took approximately ten minutes but successive doses were not given at an interval shorter than 30 min. Ventilation was normally maintained by a Palmer respirator pump and the end-tidal CO_2 was monitored on an infra-red CO_2 meter and kept at 4.5%.

Histological preparations of the afferent nerve were made by fixation in osmic acid (2%), dehydration and embedding in paraffin wax. Sections 5 μm thick were cut and measurements of total nerve fibre diameter including the sheath were made directly from a photomicrograph of the preparation at a magnification of 1000 times.

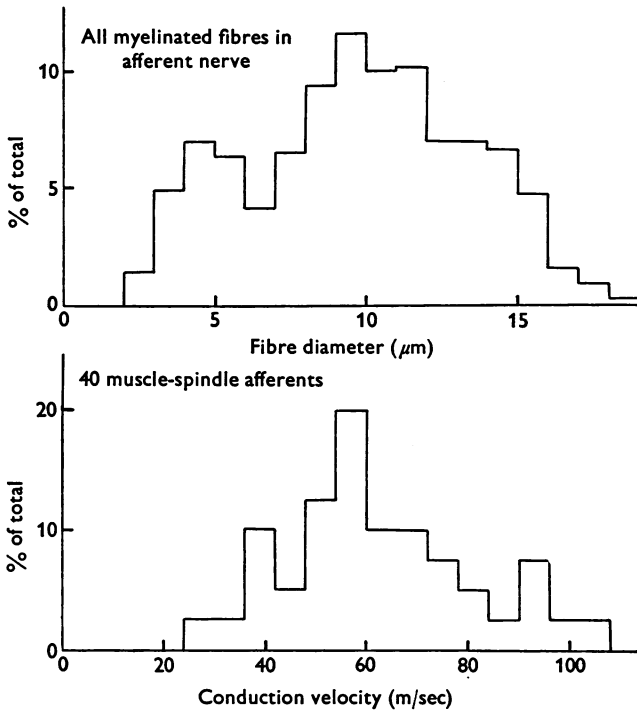


Fig. 1. The upper histogram is the fibre diameter distribution of the afferent nerve from the superior oblique muscle. The lower histogram gives the conduction velocities of forty muscle spindle afferents recorded in the Gasserian ganglion.

RESULTS

Identification of muscle spindle afferents

Responses from muscle spindles were identified by their low threshold to muscle stretch and by their responses to tetanic stimulation of the motor nerve. The intrafusal muscle fibres of sheep extraocular muscles are

frequently innervated by collaterals of the extrafusal motor innervation (Cilimbaris, 1910; Harker, 1972). Thus, although some afferent discharges paused during an extrafusal contraction, most showed a more complicated response which varied with the strength of the extrafusal contraction. During minimal extrafusal contractions they were excited, at slightly higher strengths unloaded, and during maximal contractions they were again excited. Some afferents were not unloaded during extrafusal contraction, but these were also classified as spindle afferents if they gave a prominent burst of action potentials during the relaxation phase of muscle tension.

Fibre diameters and conduction velocities

The upper histogram of Fig. 1 shows the fibre diameter distribution of the afferent nerve from a single superior oblique muscle. The portion of nerve studied was taken from its orbital course and all its branches entered the superior oblique muscle. Contamination of the nerve by extraneous afferents is unlikely since, when split into filaments, only muscle afferents were found, and during recording in the Gasserian ganglion, all the cells isolated which could be activated by a stimulus to the nerve proved to be superior oblique muscle afferents. It is clear from Fig. 1 that there is no separation into Groups I and II with a boundary near its conventional position at 8–10 μm .

The lower histogram shows the conduction velocities of forty spindle afferents. The average conduction distance was 25 mm and the conduction delays ranged from 370 μsec to 1 msec. 150 μsec was subtracted from the conduction delays to allow for the utilization time and the slow conduction of the action potential along the glomerular segment of the axon within the Gasserian ganglion. For cat cutaneous afferents, the sum of the utilization time and conduction time along the monopolar segment has been found to range from 130 to 540 μsec with a mean of 330 μsec (Darian-Smith, Mutton & Proctor, 1965). The precise value was independent of the conduction velocity of the peripheral axon segment. For sheep extraocular afferents an allowance larger than 150 μsec would give impossibly high conduction velocities for the fastest conducting axons and it is clear from the work of Darian-Smith *et al.* that a smaller figure would be unlikely. The best evidence that the resulting calculations of conduction velocity were reasonably reliable comes from plots such as Fig. 5 where a relationship between spindle afferent vibration sensitivity and conduction velocity is clearly demonstrable.

The spindle afferents recorded had a wide range of conduction velocities, from 30 to 110 m/sec, but the majority had intermediate conduction velocities and it was not possible therefore to decide which responses were

from primary endings and which from secondary endings on the basis of their conduction velocities.

Responses to ramp stretches

In Fig. 2 the muscle was stretched 3 mm at 10 mm/sec and the two traces are from an instantaneous frequency meter. The upper afferent has a response similar to the responses of primary endings in cat soleus muscle spindles. There is an abrupt increase in firing rate at the beginning of the stretch and a sudden fall on completion of the stretch. This unit had a conduction velocity of 77 m/sec. The lower afferent had a conduction

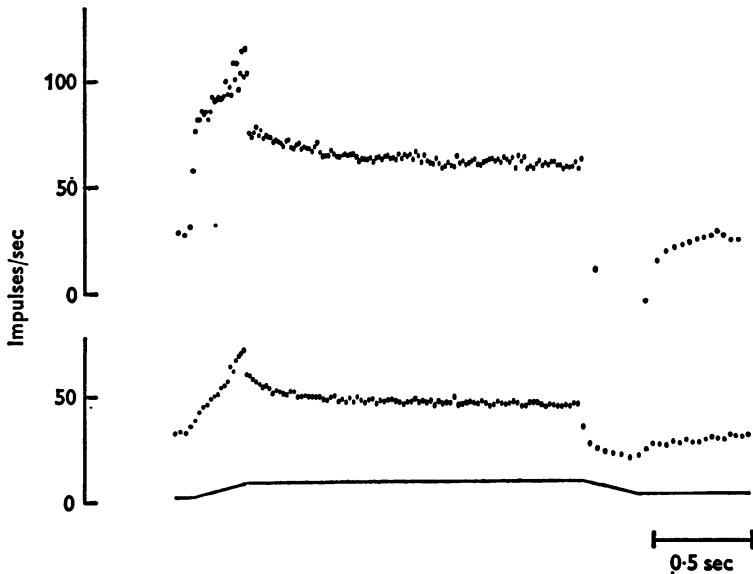


Fig. 2. The response of two muscle spindle afferents to a 3 mm ramp stretch of the superior oblique muscle at a velocity of 10 mm/sec. The records are from an instantaneous frequency meter. Each spot represents an action potential and its vertical displacement is proportional to the reciprocal of the time interval since the immediately preceding spike. The condition velocity of the upper afferent was 77 m/sec and of the lower afferent, 56 m/sec.

velocity of 56 m/sec and gave a response similar to that of secondary afferents in cat soleus. There is no abrupt increase in firing at the beginning of the stretch and only a small fall on its completion. The difference in dynamic sensitivity of the two afferents is also shown during release of the muscle when the upper afferent stops firing altogether while the lower afferent continues to fire, although at a slower rate. In cat soleus, primary afferents fire less regularly than secondary afferents (Matthews & Stein,

1969). This can also be seen in Fig. 2 where the upper afferent has a more variable discharge than the lower.

The responses of different afferents to ramp stretches were compared by measuring their dynamic indices, defined by Crowe & Matthews (1964) as the difference between the firing rate at the peak of discharge and the rate 0.5 sec later. Fig. 3 shows the relationship of dynamic index to velocity of stretch for four afferents from the same experiment. The dynamic index increases more or less linearly with the velocity of stretch and the primary-type afferents *A* and *B* have a higher dynamic index than the secondary-type afferent *D* at all stretch velocities. The conduction velocities of

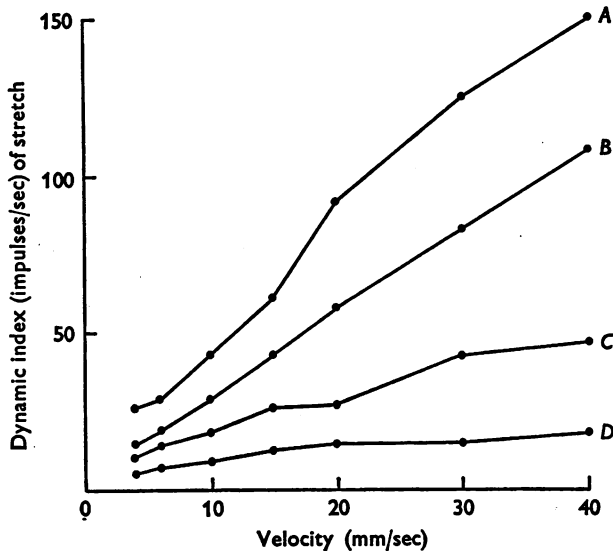


Fig. 3. The relation between dynamic index and the velocity of stretching for four spindle afferents from the same superior oblique muscle. The stretch was 3 mm with a ramp wave form as in Fig. 2. The conduction velocities of *A*, *B*, *C* and *D* were 92, 83, 53 and 30 m/sec respectively.

A and *B* were 92 and 83 m/sec and that of *D*, 30 m/sec. The conduction velocity of *C* was intermediate, 53 m/sec, and its dynamic indices were between those of *B* and *D*. In fact there was a continuous distribution of dynamic indices as shown in Fig. 4. Here the stretch velocity was 40 mm/sec and the dynamic indices of 28 different afferents are plotted against their conduction velocities. The responses do not form two groups, but the size of the dynamic indices increases with the conduction velocity of the afferents from 18 impulses/sec for the slowest conducting afferent to over 200 impulses/sec for the fastest conducting afferents.

Sensitivity to vibration

Brown, Engberg & Matthews (1967) showed that primary afferents in cat soleus are much more sensitive to longitudinal vibration of the muscle than secondary afferents and can be driven to fire 1 impulse per cycle of vibration at smaller amplitudes. The threshold for driving different extraocular spindle afferents was measured at 100 Hz. As the length of the

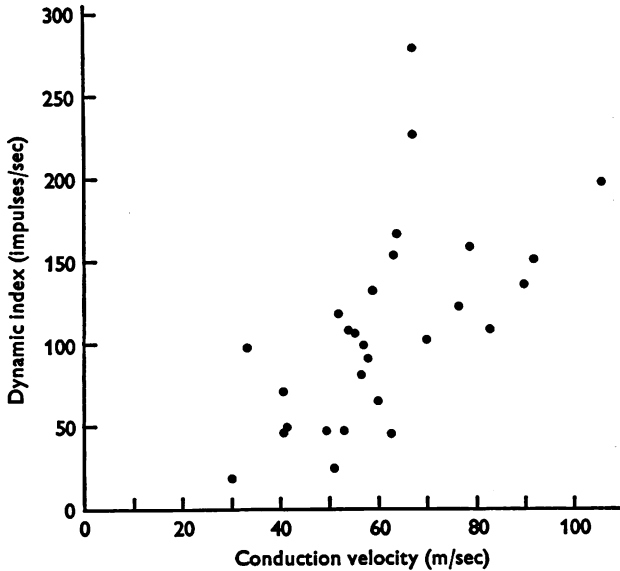


Fig. 4. The relation between the dynamic indices of twenty-eight spindle afferents and their conduction velocities. In all cases the velocity of stretch was 40 mm/sec and the amplitude 3 mm.

muscle was increased, the threshold for driving fell, generally to a more or less steady value. The lowest value reached within the physiological length range was taken as the vibration threshold for that afferent. All the afferents isolated could be driven at this frequency, but the slowly conducting afferents required much larger amplitudes, up to 700 μ m (Fig. 5). The most sensitive afferents could be driven at 40 μ m. However, there were also a large number of afferents with intermediate thresholds. It can be seen in Fig. 5 that the sensitivity to vibration of the afferents increases with their conduction velocity.

Responses to suxamethonium

Suxamethonium (succinyl choline or Sch) emphasizes the differences between primary and secondary afferents in response to dynamic stretching and it has enabled other workers to classify intermediate responses (Rack & Westbury, 1966; Cody, Lee & Taylor, 1972). Fig. 6 shows the effect of Sch 200 $\mu\text{g}/\text{kg}$ i.v. on two different afferents from the same muscle. The upper afferent had a dynamic index of 52 impulses/sec which was increased to a maximum of 171 impulses/sec by Sch while the lower unit had a dynamic index of 20 impulses/sec which was only increased to

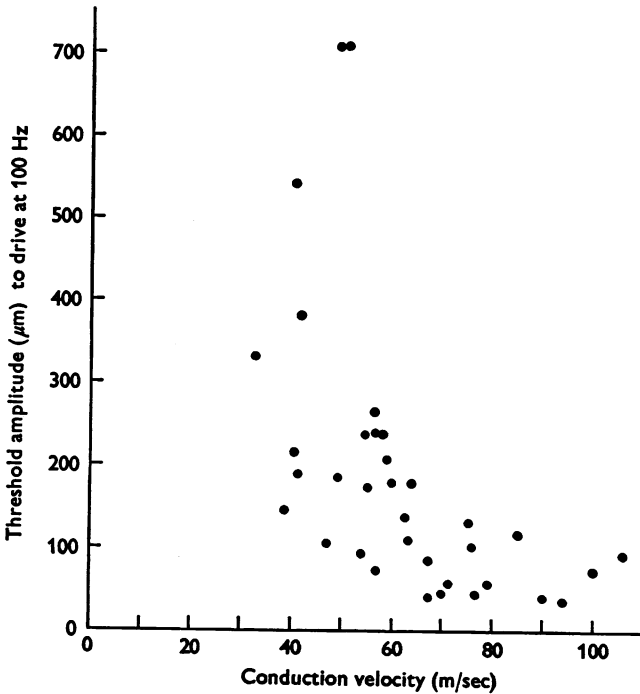


Fig. 5. The relation between the threshold amplitude of vibration required to drive each afferent to give 1 impulse per cycle at 100 Hz and their conduction velocities. The total number of afferents is thirty-five.

24 impulses/sec. Thus the afferent with a large initial dynamic index had a large increase in dynamic index. This pattern of response was found by Rack & Westbury (1966) to be typical of primary endings in cat soleus spindles. The lower afferent in Fig. 6, which had a small dynamic index, showed almost no increase following Sch and this is typical of secondary endings.

However, Sch also produces a prolonged contracture of slow extrafusals

muscle fibres in extraocular muscles (Bach-y-Rita & Ito, 1966) and it was necessary to show that this contracture was not responsible for the effect on the spindle by following the time course of its action on muscle tension, as shown in Fig. 7. The muscle was stretched 3 mm every 5 sec at a velocity of 10 mm/sec. Sch, 200 $\mu\text{g}/\text{kg}$, was injected at time 0 and the upper record shows the resultant extrafusal contraction, while the lower two records show the changes in dynamic index in two different afferent fibres. The contracture developed quickly to reach a maximum of 43.5 mN after

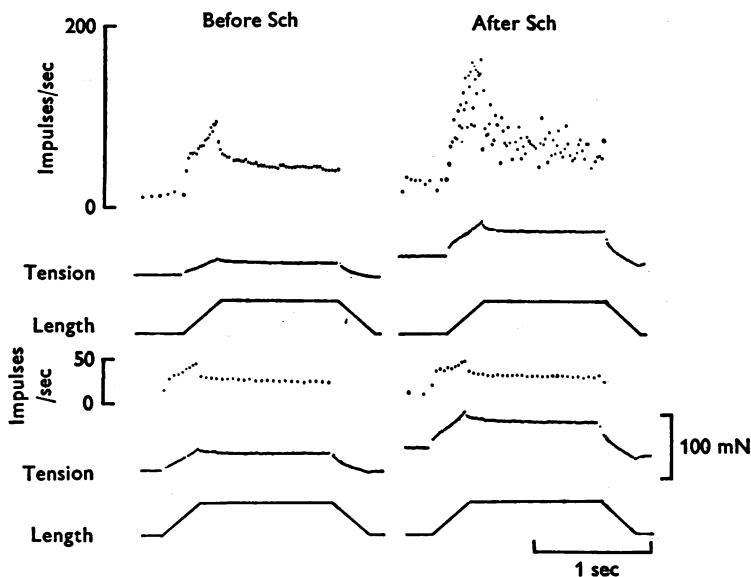


Fig. 6. The response of two spindle afferents to a 3 mm muscle stretch at 10 mm/sec before and 2 min 10 sec after an intravenous injection of Sch (200 $\mu\text{g}/\text{kg}$). The records of instantaneous frequency of firing are from a primary-like afferent above, and a secondary-like afferent below. The shift in the base line of the tension records illustrates the strength of the concomitant extrafusal contraction. The length records are diagrammatic.

30 sec while the increase in dynamic index of the upper afferent developed more slowly to a peak after 1 min 45 sec. This difference in timing was seen for all activated units and so it was concluded that the Sch-induced excitation was due to intrafusal rather than extrafusal contraction (cf. Brown, 1971).

The lower unit in Fig. 7 is from an afferent with an intermediate dynamic index of 29 impulses/sec to the 10 mm/sec stretch. There was hardly any late increase in dynamic index, only an early fall coincident with the peak of extrafusal contracture. Thus this afferent may be classified

as a secondary ending. However, most intermediate afferents did not show such a clear cut behaviour following Sch injection. Instead they tended to have increases in their dynamic index which were intermediate between the two extremes illustrated in Figs. 6 and 7. This is shown in Fig. 8. The abscissa of the graph gives the original dynamic index of each afferent to a standard 10 mm/sec stretch. Against this is plotted the peak increase in dynamic index following a standard injection of Sch. This peak increase

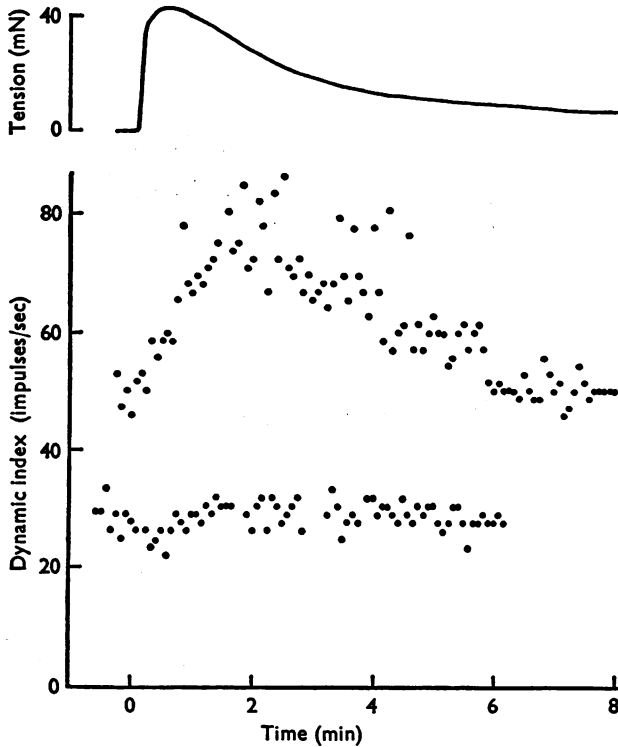


Fig. 7. The superior oblique muscle was stretched repetitively every 5 sec and Sch 200 $\mu\text{g}/\text{kg}$ was injected at time 0. The stretch was 3 mm at a velocity of 10 mm/sec. The upper curve shows the resultant change in muscle tension and the lower two curves the change in dynamic index of two different spindle afferents.

in dynamic index usually occurred 1 min after the peak extrafusal tension. The afferents with large dynamic indices have larger increases than the afferents with small dynamic indices but the intermediate afferents have retained their intermediate properties.

There were two exceptional units which had a large initial dynamic index but which showed no increase in dynamic index following Sch

injection. In fact they were strongly affected by the extrafusal contraction and showed a fall in dynamic index of 13–22 impulses/sec. Harker (1974) has observed incorporation of extrafusal fibres into sheep extraocular muscle spindles and this may provide an explanation for the anomalous behaviour of these two afferents.

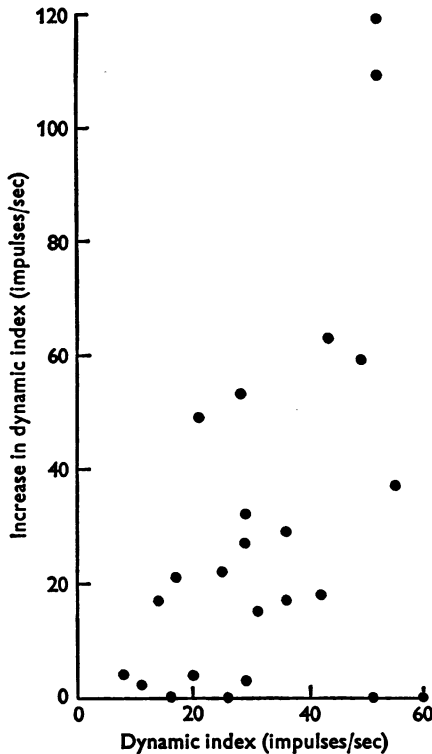


Fig. 8. The peak increase in dynamic index of twenty-four afferents following intravenous injection of Sch (200 $\mu\text{g}/\text{kg}$) plotted against their original dynamic index before the injection. The muscle stretch was 3 mm at 10 mm/sec.

DISCUSSION

Donaldson (1960) measured the nerve fibre diameters of branches of the ophthalmic nerve carrying afferents from the extraocular muscles of goat, and there was only one significant peak in the fibre diameter distribution. In five out of six nerves this peak was at 7–11 μm and in the sixth 12–15 μm while the range of fibre diameters was from 2 to 20 μm . There are many similarities between goat and sheep in the anatomy and physiology of their extraocular muscles (Winckler, 1937; Cooper *et al.* 1955) and Donaldson's

measurements are very similar to those for the sheep superior oblique (Fig. 1). This histogram suggests that the spindle afferents lie between 6 and 19 μm . Using the conversion factor of Boyd & Davey (1968) which is conduction velocity = $4.5 \times$ external fibre diameter, the slowest afferents recorded here would have fibre diameters of 6–7 μm . Therefore most of the population of spindle afferents have been investigated, although the number of slower afferents was not large enough to be certain that a distinct secondary group does not exist, particularly in view of the difficulty involved in measuring conduction velocity over a short length of nerve.

It is possible to make quantitative comparisons between cat soleus and sheep superior oblique muscles because both these muscles have similar lengths. It is then apparent that 25% of the responses to ramp stretch (Fig. 4) are within the secondary range described by Matthews (1963, Fig. 10) for soleus muscle spindles. Also 27% of the afferents had little or no increase in their dynamic index following Sch, and these also may be classified as secondary endings. Therefore the lack of distinction between primary and secondary afferents found here is more likely to be due to the large proportion of intermediate response than to a paucity of recordings from secondary afferents.

In the experiments of Brown *et al.* (1967) on cat soleus, only one secondary afferent could be driven by vibration at 100 Hz using amplitudes up to 250 μm , although in the present work all the afferents could be driven using amplitudes up to 700 μm . In this respect the extraocular muscle spindles are not unique, since secondary afferents from rat hind limb and tail muscle spindles could also be driven at 100 Hz by vibration of sufficient amplitude (Andrew, Leslie & Thompson, 1973). The sensitivities of the primary afferents also differ from those of cat soleus since the most sensitive was driven at 36 μm and only 14% of all the afferents by 50 μm while in cat the primary afferents had sensitivities down to less than 10 μm and nearly all could be driven by 50 μm (Brown *et al.* 1967).

The plot of dynamic index against conduction velocity shown in Fig. 4 is not greatly different from that of Matthews (1963, Fig. 12) for cat soleus and a relationship between conduction velocity and dynamic index is evident in his figure also. Renkin & Vallbo (1964) showed that the ability of an afferent to signal velocity varied directly with its conduction velocity in cat extensor muscles and Koeze (1973) in the baboon found a similar variation in dynamic index with conduction velocity. The vibration sensitivity of rat tail muscle spindles is positively correlated with conduction velocity (Andrew *et al.* 1973) and Brown *et al.* (1967) found afferents from cat soleus with intermediate conduction velocities which had intermediate sensitivities to vibration. Thus a continuous relationship between dynamic

sensitivity and conduction velocity is widespread in spindle afferents from a variety of species.

Suxamethonium produces a strong contraction in nuclear bag fibres (Smith, 1966) and thus is presumed to be the mechanism for its powerful action on the primary ending (Matthews, 1972). When the intrafusal fibres in cat soleus spindles are activated in this way, the responses from the afferents with intermediate conduction velocity fall into two groups which are similar to the response from primary and secondary afferents respectively (Rack & Westbury, 1966). Therefore it was unexpected that the intermediate afferents in sheep extraocular spindles should retain their intermediate character following Sch injection. It is possible that the action of Sch on these particular afferents was masked in some degree by the extrafusal contraction, since the measurements were made at the peak in spindle dynamic index when the extrafusal tension had not returned to zero from its earlier peak. However, Sch does produce small increases in the dynamic sensitivity of cat secondary endings (Rack & Westbury, 1966) and it also produces distinct increases in their static firing rates (Fehr, 1965), so Sch can produce effects other than through contraction of nuclear bag fibres. It is therefore possible that the increases in dynamic sensitivity of the intermediate afferents recorded here were produced by some similar mechanism.

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