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AFFERENT IMPULSES IN THE OCULOMOTOR NERVE, FROM THE EXTRINSIC EYE MUSCLES

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The fact that large numbers of muscle spindles are present in the extrinsic eye muscles of the goat and sheep led us to attempt to record the afferent impulses from these organs in a branch of the oculomotor nerve.

It is widely believed that mammalian eye muscles are devoid of muscle spindles, but Cooper & Daniel (1949) reported the finding of upwards of forty-seven muscle spindles in a single human extrinsic eye muscle and comparable numbers in all the other five extra-ocular muscles*. They reviewed some of the literature, both histological and physiological, on the extrinsic eye muscles of mammals, and in the course of comparative studies, they confirmed the finding of Cilimbaris (1910) that muscle spindles are present in the extrinsic eye muscles of the sheep and also the goat.

A number of workers have studied the histology of the extrinsic eye muscles of the common laboratory animals but muscle spindles have not been found in them. Cooper & Daniel (1949) confirmed that spindles are not present in the eye muscles of the rabbit, cat, dog and rhesus monkey. However, Sherrington (1897) had demonstrated reflex effects from pulling gently on the inferior oblique muscle of monkeys and cats, and Tozer & Sherrington (1910) showed that many endings of tendon organ type are present in the eye muscles of these animals. These observations have been overlooked by many investigators; de Maré (1928) failed to elicit reflex effects from the eye muscles of rabbits, McCouch & Adler (1932) from those of the cat and Irvine & Ludvigh (1936) from human eye muscles. Corbin & Harrison (1940) state that stretching the eye muscles of the cat gave no sensory potentials in the appropriate nerves, and McIntyre (1941) failed to record afferent impulses in the oculomotor nerves of the cat and monkey.

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* These findings were demonstrated at the XVIIth International Physiological Congress in Oxford in 1947.

It is known from previous work on the cat (Denny-Brown, 1929; Cooper & Eccles, 1930; Brown & Harvey, 1941) that the extrinsic eye muscles have very brief time relations, the rising phase of the twitch, or contraction time, lasting 7–15 msec. and a stimulus frequency of about 350 shocks/sec. being needed for a fused tetanus. During reflex contractions of the extrinsic eye muscles, initiated by neck movements, a rate of motor discharge in individual motor units much higher than that found in limb muscles has been recorded by Reid (1949). The mechanical responses of the cat's eye muscles are also very small and not easy to record. All these features make work on cat's eye muscles peculiarly difficult.

Goats and sheep not only provide us with eye muscles that are rich in muscle spindles, which might be expected to behave as do the muscle spindles of other somatic muscles as recorded by Matthews (1931*a*, *b*, 1933), but these animals also have muscles and nerves which are much larger than those of the ordinary laboratory animals and they thus present a less difficult experimental problem.

METHODS

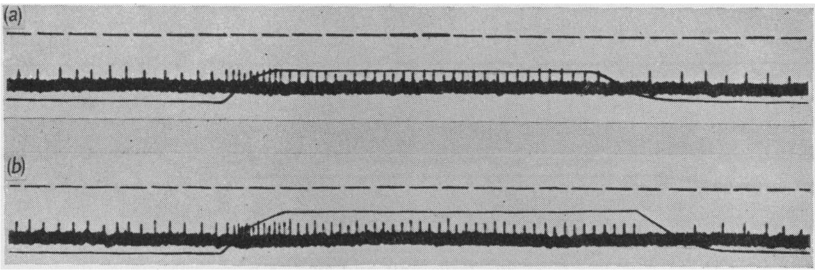
Young goats and sheep weighing between 10 and 20 kg. were anaesthetized with intra-peritoneal pentobarbitone in a dosage of 7 mg./kg. A venous cannula was inserted and further doses were given about every half-hour. A tracheal cannula was also inserted. (Profuse salivation in goats and sheep is a troublesome complication.) An infero-lateral approach to the orbit was used, which involved removing the zygoma and much of the inferior wall of the orbit. The coronoid process of the mandible was also removed. The nerve to the inferior oblique muscle was found as it ran on the lateral edge of the inferior rectus muscle. It was followed, as far as possible, towards the apex of the orbit and cut where it wound over the inferior rectus on to its superior surface. This gave a length of about 2 cm. of nerve with which to work. The nerve enters the inferior oblique muscle on its posterior edge at the junction of its middle and distal thirds. At this point many blood vessels also enter the muscle and therefore no attempt was made to clean the nerve in this region. The muscle was detached from the sclera at its insertion and the eye was usually eviscerated in order to give more room in the orbit. A myograph was attached to a semicircular aluminium band whose ends gripped the upper margins of both orbits. The myograph consisted of flat spring leaves of Perspex or celluloid clamped at one end and with the free end attached to the tendon of the inferior oblique muscle by stout thread or wire. The flat spring leaves were painted with aquadag in acetone and varnished with Perspex solution, thus making semiquantitative strain gauges, with a natural period of 130 cyc./sec. A small aneroid capsule was fixed beneath the strain gauge near the clamped end. Inflation of the capsule rapidly stretched the muscle about 2·0 mm. With stiff strain gauges there was a nearly linear relationship between the pressure in the capsule and the stretch applied to the muscle. In later experiments, movement was signalled by the change in capacity between a fixed plate and a plate carried on the muscle lever, and recorded by the oscillator and amplifier described by Dickinson (1950). Stimulating electrodes were applied to the nerve close to the muscle, whilst leading electrodes were applied to a slip of the nerve cut from the side of its proximal end and then cut down until a recognizable number of units were present, or sometimes until a single unit only was present.

When an active contraction was evoked the stimulus escape from electrodes a few mm. from the leading electrodes was considerable. In addition, a maximal nerve volley was set up. To shorten the effect of the stimulus escape 0·005 μF. coupling condensers were used throughout the amplifier (cf. Matthews, 1933), and occasionally the balanced-bridge method described by Blair & Erlanger (1933) was found to be very valuable. Owing to the short twitch duration it was necessary for the amplifier to have recovered from the stimulus in from 1·0 to 2·0 msec. Stimuli of approximately

100 μsec. duration were derived from the condenser discharges set up by a Schmitt trigger working from the time base. The arrangement used was designed by Dr G. Dawson. Recording was by a double-beam cathode-ray oscillograph and camera in the usual way. The strain gauge had a resistance of about 100,000 Ω. Its resistance changes were converted to voltage fluctuations by putting a 40 V. source and $\frac{1}{2}$ MΩ. resistance in series with it. The voltage fluctuations across the $\frac{1}{2}$ MΩ. resistance were amplified by a resistance capacity coupled amplifier, of time constant 2·0 sec., and only rapid changes therefore could be measured. No appreciable error was introduced into the records of the time relations of these twitches.

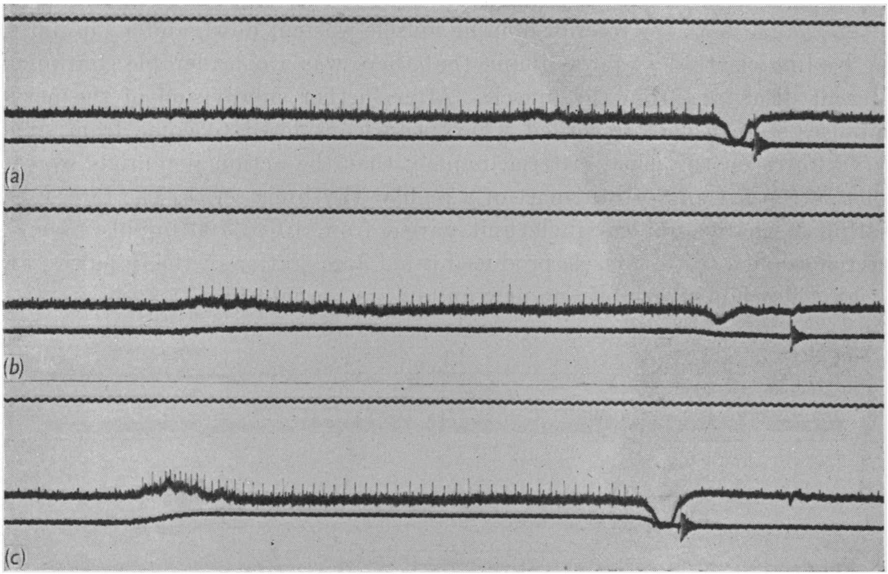
RESULTS

When the nerve to the inferior oblique muscle was cut down and a slip put on the leading electrodes, it was found that there was a considerable continuous afferent discharge from the muscle. After further subdivision of the nerve, impulses were usually recorded which were considered to come from single nerve fibres on the usual criteria, namely that the action potentials were of constant height and formed part of a regular rhythmic series. The rate of the resting discharge from a single unit varied from 10 to 100 impulses/sec. A stretch applied to the muscle produced rapid acceleration of the impulses, and usually, but not invariably, no new units were brought in.



Text-fig. 1. Records of afferent impulses from a unit during passive stretch of the inferior oblique muscle of a goat. The initial tension of the muscle was low, but the unit showed a resting discharge. Stretching the muscle produced a short burst of impulses at a high frequency; the discharge then settled to a slower steady rate whilst the stretch was maintained. On relaxation there was a pause in the discharge followed by a return to the resting rate. (*a*) weak stretch, 0·6 mm.; (*b*) slightly greater stretch, 0·85 mm. Above: time $\frac{1}{10}$ sec.; below: stretch signalled by pressure in aneroid capsule.

Impulses at a regular rate continued whilst the stretch was maintained. Adaptation occurred very slowly; e.g. in one case the rate of discharge during a stretch continued at a rate of 65 impulses/sec. over a period of 5·5 sec. The rate of discharge diminished as soon as the tension was released, and dropped to the original resting level almost at once when the muscle had been under moderate resting tension, or it might drop below the resting level for 0·1 to 0·2 sec. if the resting tension had been very low. Records of impulses from a single unit in the goat are shown in Text-fig. 1*a*, *b*. The sensory ending was giving a regular resting discharge of about 20 impulses/sec. When a weak stretch was applied, Text-fig. 1*a*, the rate rose at once to about 60 impulses/sec. After a short burst at this speed the rate of discharge settled to approximately 35 per sec. This rate was maintained throughout the period of stretching, but showed a slight falling off due to slow adaptation. When the stretch was released impulses stopped immediately for 0·1 sec. and then built up again to the resting discharge. Text-fig. 1*b* shows a similar general picture when the muscle was more strongly stretched.

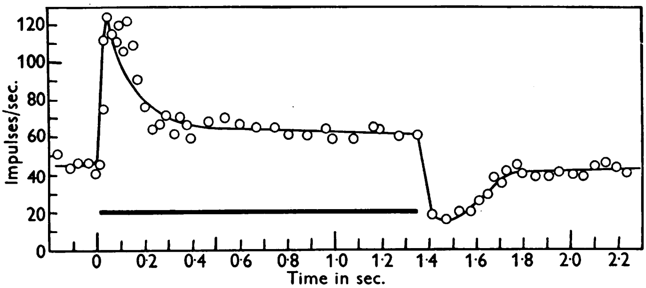


Text-fig. 2. Afferent impulses from one large unit and two or more small units during passive stretch of the inferior oblique muscle of a lamb. The initial tension of the muscle was low. Note that small impulses were present at rest. The large unit gave no resting discharge, but discharged on the application of a stretch. (*a*) weak stretch, 1·5 mm.; (*b*) moderate stretch, 2·0 mm.; (*c*) strong stretch, 2·5 mm. Above: time, 50 cyc./sec.; below: stretch signalled by condenser system.

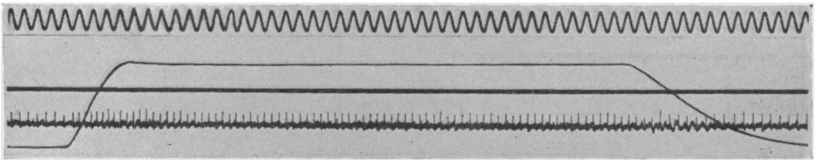
In the case of a lamb, whose records are illustrated in Text-fig. 2, two units were giving small impulses during the resting phase, but as soon as a stretch was applied a single unit began to give large impulses. The maximum rate of discharge was reached during the application of the stretch, a slightly lower rate was maintained during the stretch and the discharge ceased at once on release of the stretch. With increasing degrees of stretch the maximum initial rates of discharge were 40, 50 and 100 impulses/sec.; the subsequent steady rates were 25, 35 and 45 impulses/sec.

Some indications of the variations in the rate of discharge whilst a slack muscle was being stretched are shown in the form of a graph in Text-fig. 3.

The results described above were obtained from experiments in which the resting tension of the muscle was low. The record shown in Text-fig. 4 shows the response obtained from stretching a muscle with a high resting tension. The rate of discharge during rest was 80 impulses/sec., and this increased during the application of the stretch to 140 impulses/sec., settling to 100 impulses/sec. during the maintained stretch. The rate fell off at once on the release of the stretch and returned to the resting rate without the pause which is seen in the case of a slack muscle. The maximum rates of discharge which have been recorded in experiments of this nature have been 300 impulses/sec. during the application of a stretch, whilst maintained rates of 150–250 impulses/sec. have been recorded.



Text-fig. 3. Graph of the response of a single unit during passive stretch. Recorded from the nerve to the inferior oblique muscle of a goat, with the muscle under no initial tension. The heavy black line indicates the duration of the stretch.



Text-fig. 4. Records of afferent discharges from a single unit during passive stretch of the inferior oblique muscle of a goat. The initial tension of the muscle was high. There was a high resting rate of discharge. This increased during the application of the stretch, settling to a steady rate with practically no adaptation during the period of stretching. There was no pause on relaxation, but the rate of discharge immediately fell to the resting level. Above: time, 50 cyc./sec.; below: stretch, of 1·4 mm., signalled by optical system.

The variations in the rate of discharge of a taut muscle during the application of a stretch are shown in the form of a graph in Text-fig. 5.

The apparatus used was inadequate for producing extensions of the same amount at different rates, but the discharge during the period of extension was related to the rate at which the stretch was applied.

Further experiments were performed in which active contraction of the muscle was induced by stimulating the nerve, near its point of entry into the muscle, by a condenser discharge. The afferent impulses were recorded from leading electrodes placed on a cut-down slip of the nerve farther from the muscle. A twitch in the inferior oblique muscle of the goat, induced in this way, gives at most a tension in the muscle of 50 g. This tension is reached in a rising phase or contraction time (Cooper & Eccles, 1930) of 10–20 msec. In nearly all the units investigated there was a silent period during the rising phase of the contraction. This silent period was followed by a brief burst of impulses whose frequency might rise to a rate of 300–500 impulses/sec. (Text-fig. 6). In muscles which were under tension at the onset of the twitch the impulses, after this brief burst at a high rate, fell smoothly back to the initial frequency as shown in the graph in Text-fig. 7. In muscles under low initial tension there was a further pause, after the rapid burst, before the initial rate of discharge was attained, as is shown in the graphs in Fig. 8. With an increase in the initial tension the contraction time was hardly altered but the silent period was shortened (Text-fig. 8). Sometimes an impulse or two appeared at the end of the rising phase of the contraction. The maximum rate of discharge of the burst of impulses was in some cases low, whilst in others it rose to nearly 500 impulses/sec.

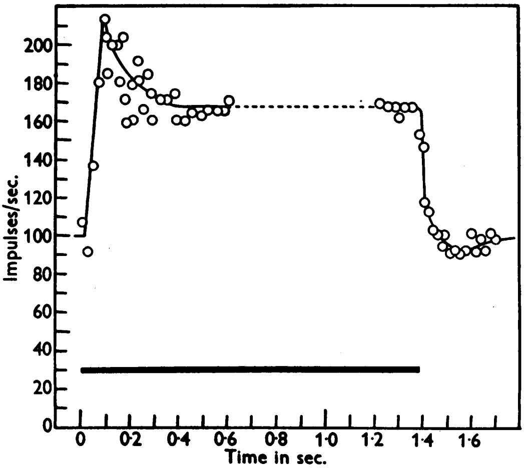


Fig. 5.

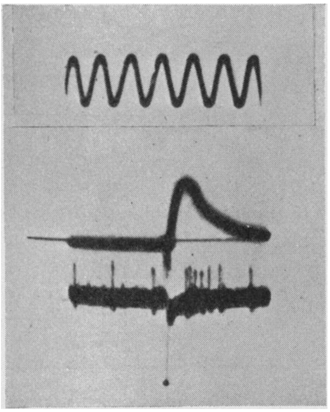
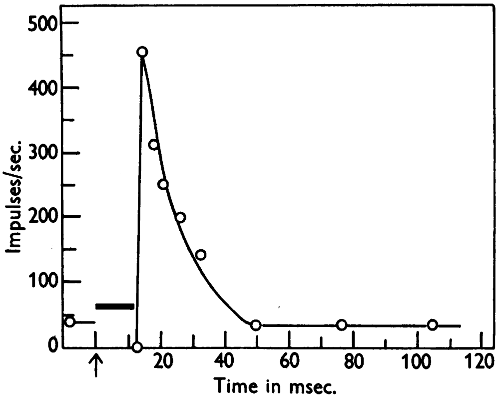


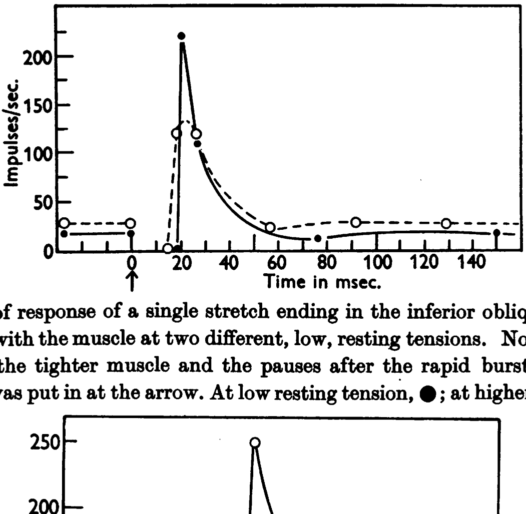
Fig. 6.

Text-fig. 5. Graph of the response of a single unit during a passive stretch of 2·6 mm. Recorded from the nerve to the inferior oblique muscle of a goat, with the muscle under some degree of initial tension. The heavy black line indicates the duration of the stretch.

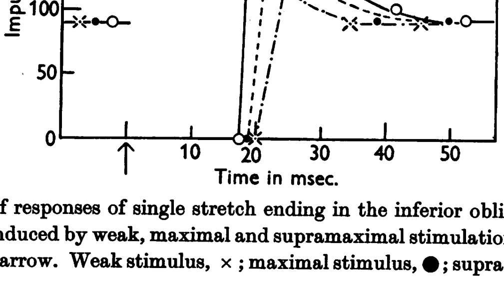
Text-fig. 6. Records of the response of a single afferent unit in the inferior oblique muscle of a goat during a motor twitch. Note that the afferent discharge ceased completely during the contraction of the muscle, beginning again at the onset of relaxation. Above: time, 50 cyc. /sec.; mechanical response of muscle; below: response of afferent unit.



Text-fig. 7. Graph of the response of a stretch ending in the inferior oblique muscle of a goat during a motor twitch. The muscle was under a high initial tension. Note that after the twitch the rate of discharge of the impulses does not fall below the resting rate. The motor stimulus was put in at the arrow. Contraction time marked by heavy line.



Text-fig. 8. Graphs of response of a single stretch ending in the inferior oblique muscle of a goat during twitches with the muscle at two different, low, resting tensions. Note shortening of the silent period in the tighter muscle and the pauses after the rapid bursts of impulses. The motor stimulus was put in at the arrow. At low resting tension, ●; at higher resting tension, ○.



Text-fig. 9. Graphs of responses of single stretch ending in the inferior oblique muscle of a goat, during twitches induced by weak, maximal and supramaximal stimulation. The motor stimulus was put in at the arrow. Weak stimulus, × ; maximal stimulus, ●; supramaximal stimulus, ○.

Text-fig. 9 shows graphically the effect of increasing the strength of the stimulus with a tight muscle.

The effect of supra-maximal stimuli was also investigated, but these did not produce the outburst of impulses during the rising phase of the contraction which was described by Matthews (1933) in limb muscles, and attributed by him to his A_2 endings. In a few experiments in which submaximal stimuli were used the afferent discharge was increased during the whole of the rising phase of the contraction, but when the strength of the stimulus was increased the usual silent period was seen. It will thus be seen that the silent period was usually present whether the muscle was slack or tight. It must be made clear that during the work no serious attempt was made to obtain truly isometric contractions.

No other recognized patterns of discharge in the oculomotor nerve were seen during these experiments. However, tendon organ impulses probably have a high threshold, and the failure to obtain records of such impulses must not be taken as evidence against tendon organ afferents.

Histological investigation of the inferior oblique muscle of the goat and sheep shows that it is profusely supplied with muscle spindles (Pl. 1, figs. 1–6). In human eye muscles the various types of nerve endings tend to be segregated in specific regions of the muscle (Cooper & Daniel, 1949) but in these ungulates this segregation is less marked, and both motor nerve endings and muscle spindles are more widely scattered throughout the muscle. The muscle spindles, which are more numerous in the proximal than in the distal half of the muscle, tend to lie in small groups and are found more frequently near the periphery than in the central core of the muscle. An idea of the profusion of these organs can be gained from the fact that fourteen muscle spindles were counted on one low-power field of a longitudinal (frozen) section of an extrinsic eye muscle of a goat. Five muscle spindles are shown in Pl. 1, fig. 3. In some experiments, when an afferent unit was discharging, the inferior oblique muscle was prodded with a glass rod until a point was found at which prodding gave a marked increase in the discharges. This point on the muscle was marked with methylene blue and the small block so marked was cut out, sectioned and stained. In all cases groups of muscle spindles were found in this piece of muscle.

Serial transverse sections of the inferior oblique muscle of a goat were prepared by the method described by Cooper & Daniel (1949). An attempt was made to identify every spindle in the muscle. In all, one hundred and twenty muscle spindles were counted, and this is probably a minimum figure. This number is greater than that given by Cilimbaris (1910) for the total number of muscle spindles in the inferior oblique muscle of the sheep, and it is also greater than the number of muscle spindles found in the human extrinsic eye muscles by Cooper & Daniel. No published figures of the number of muscle spindles in other somatic muscles give anything like so high a count (Gregor, 1904; Voss, 1937).

Double and treble muscle spindles are fairly often seen in these muscles. Such spindles do not usually have their equatorial regions exactly side by side, since they are often arranged with some degree of overlap. Pl. 1, figs. 4, 6, show paired muscle spindles in transverse section. Each muscle spindle has from two to twelve intrafusal muscle fibres of small diameter. The disparity in size between intrafusal and extrafusal muscle fibres in these ungulate eye muscles is greater than is that seen in the human. Bags of nuclei in the intrafusal muscle fibres are a prominent feature of the equatorial region of these muscle spindles (Pl. 1, fig. 4, upper spindle). The many nerve fibres observed within the capsule make an extremely complicated pattern, and are often seen to make spiral turns around one or several intrafusal muscle fibres. A spiral arrangement of an intrafusal nerve fibre is shown in Pl. 1, fig. 1. Motor nerve endings are seen on intrafusal muscle fibres at the poles of each spindle.

In addition to muscle spindles, examples of tendon endings have been found both at the origin and at the insertion ends of the muscle. It is also believed that there are other, unrecognized, sensory endings in these muscles, supplied by some of the abundant nerve fibres which are present.

Afferent impulses from the muscle spindles in eye muscles have been recorded, by means of needle electrodes, in various regions of the mid-brain (Cooper, Daniel & Whitteridge, 1950). Details of the distribution of afferent impulses in the mid-brain will be published later.

DISCUSSION

These experiments show conclusively that there are proprioceptive nerve endings in the extrinsic eye muscles of the goat and sheep and that these endings send afferent discharges up the oculomotor nerve. Histological study of these muscles shows that large numbers of muscle spindles are present in them. The afferent discharges from single units generally behaved as did the discharges from A_1 endings in muscle spindles which were studied in the frog and cat by Matthews (1931*a*, *b*, 1933). We therefore conclude that the afferent discharges which we recorded in the oculomotor nerve were coming from muscle spindles in the extrinsic eye muscles.

The shortness of duration of the twitch of extrinsic eye muscles and the inaccessibility of their nerves makes work on the muscle spindles and analysis of their response, such as that carried out by Matthews (1931*a*, *b*, 1933), Leksell (1945) and Katz (1949) on limb muscle spindles, extremely difficult. Our aim therefore was to establish the presence or absence of afferent discharges from these muscles rather than to provide a detailed quantitative account of their activity.

We have shown that these eye muscle spindles are organs exquisitely sensitive to stretch. Any passive stretch of the muscle is immediately signalled by an increase of the discharge rate, and if the stretch is sharply applied this increased rate may reach a high figure. The muscle spindle is equally sensitive to a decrease in tension, for as soon as the stretch is released the rate of discharge falls. This behaviour is strictly comparable with the behaviour of the A_1 endings of Matthews in response to stretch.

The responses of these muscle spindles in eye muscles to an active twitch is of considerable interest. During the rising phase of the contraction the unit is silent, but immediately relaxation starts a very rapid burst of impulses occurs. This is suggestive of a very brief stretch. Matthews (1933) shows in his fig. 10B a comparable burst of impulses from an A_1 ending at the onset of relaxation after a tetanic contraction. This, he suggests, is similar to the behaviour of the ending during a sudden stretch. Impulses are seen in fig. 9 of Matthews's (1933) paper during relaxation after a twitch, but these are a much less conspicuous feature of the behaviour of these limb muscle nerve endings than are the striking bursts of impulses which are seen at this phase in the twitch of eye muscles.

Outbursts of impulses during relaxation after a twitch very similar to those reported in the present paper have been seen by Hunt & Kuffler (1951).

Whether the arrangement of the muscle fibres in the types of muscle preparation used could be the cause of this difference in behaviour is not known. It is, however, of some interest that the limb muscles used by Matthews were penniform, while the extrinsic eye muscles have parallel fibres.

We are unable to make any useful contribution to the problem of the activation of intrafusal muscle fibres in mammals. Histological evidence on the diameter of motor nerve fibres to intrafusal muscle fibres is not available, and we have been unable to change the pattern of afferent discharge from the endings studied by using supramaximal stimuli. The muscles used in our experiments were not contracting under strictly isometric conditions, and the results therefore do not bear exact comparison with those of Leksell (1945) or Katz (1949). In view of the results obtained with a very elegant technique by Kuffler & Hunt (1949) the generally accepted views on the behaviour of muscle spindles probably need revision.

The simplest explanation of the findings recorded here is that some of the muscle spindles are in series with extrafusal muscle fibres. Study of a number of muscle spindles histologically shows that there is no uniform pattern of attachment of these organs, and that some are indeed arranged in series with extrafusal muscle fibres.

It is of interest to determine what angle of movement of the globe would be recorded by the proprioceptors in the eye muscles. The diameter of the eyeball of the young goat was found to be approximately 2·4 cm. The inferior oblique muscle is inserted near the equator, and a movement of its tendon of 2·0 mm. will therefore correspond to a rotation of the eye of about 11°. Records from one sensory ending show that there was an increase of 90 impulses/sec. in the steady discharge rate when the muscle was stretched by 2·0 mm. The relation of the increase of stretch to the increase of rate of discharge of impulses was approximately linear. The standard deviation of the resting discharge was 6·5 impulses/sec. An increase of the resting discharge of twice the standard deviation would therefore correspond to a rotation of 1·5°. These figures, however, relate to the steady discharge during a maintained stretch. During rotation the frequency of discharge may rise to twice or three times the resting value. The muscle proprioceptors, whether in the oblique muscles or in the recti, are therefore probably capable of detecting movements of less than 1·5°. As the macula in man subtends an angle of 1°, it seems that the sensitivity of this system is great enough to play some part in the control of eye movements.

SUMMARY

1. Impulses from single units coming from afferent nerve endings in muscle spindles in the inferior oblique muscle have been recorded from the branch of the oculomotor nerve to this muscle in goats and sheep.

2. These units showed a very rapid discharge, of up to 300 impulses/sec., during the onset of stretch, settling to a steady discharge with minimal adaptation during maintained stretch and falling off or ceasing abruptly on the release of the stretch.

3. During the rising phase of a twitch induced by stimulating the nerve all discharges ceased. The onset of relaxation was signalled by a striking burst of impulses, which might reach a rate of 450 or 500 per sec., before the resting rate of discharge was regained. The unit thus appeared to behave, during relaxation, as though the muscle had been stretched. Two units out of ten discharged during the rising phase of the twitch.

4. The absence of other recognized patterns of discharge should not be taken as evidence against the presence of other sensory endings in these muscles.

5. Histological examination shows that these muscles contain many muscle spindles essentially similar in type and distribution with those found in the extrinsic eye muscles of man.

The male goats used in these experiments were kindly given to us by Drs S. J. Folley and A. T. Cowie, of the National Institute for Research in Dairying. We are grateful to Mr W. T. S. Austin and Mr R. Beesley for much technical assistance.

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EXPLANATION OF PLATE 1

Fig. 1. Longitudinal section of a muscle spindle in the inferior oblique muscle of a goat. Note the well-defined spindle-shaped capsule and the spiral arrangement of one of the intrafusal nerve fibres. (Frozen section. Bielschowsky-Gros silver impregnation.)

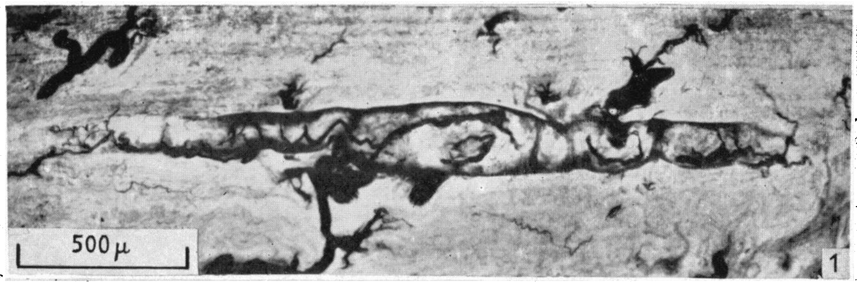
Fig. 2. Longitudinal section of a muscle spindle in the inferior oblique muscle of a goat. The capsule of this spindle is somewhat less thick than that of the spindle shown in fig. 1. One nerve trunk approaches the middle of the spindle, and smaller trunks enter each pole. Note that there are numbers of fine intrafusal nerve fibres. (Frozen section. Bielschowsky-Gros silver impregnation.)

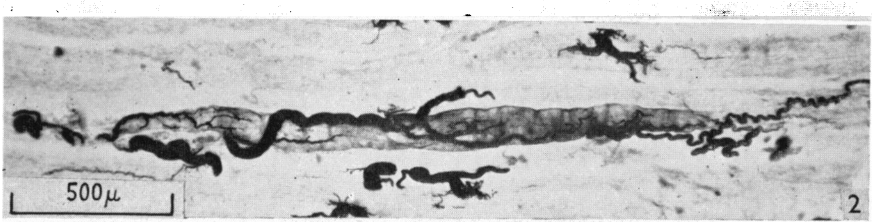
Fig. 3. Longitudinal section of rectus oculi muscle of a goat showing five muscle spindles. (Frozen section. Bielschowsky-Gros silver impregnation.)

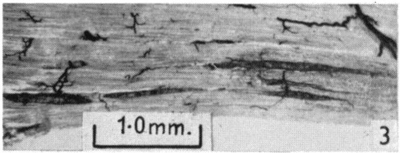
Fig. 4. Transverse section of twin muscle spindles in the inferior rectus oculi muscle of a goat. The upper spindle is cut through the equatorial region and the nuclear bags in the intrafusal muscle fibres are well seen. The intrafusal muscle fibres of the lower spindle are considerably smaller than the surrounding extrafusal muscle fibres. Note that these muscle spindles are in contact, on the right, with one of the fibrous septa of the muscle, a characteristic arrangement. (Paraffin section. H. and E.)

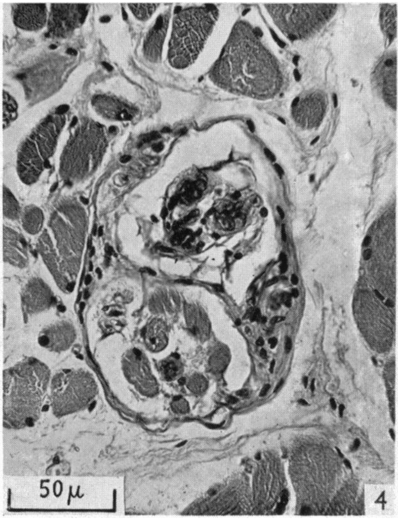
Fig. 5. Transverse section of a muscle spindle in the inferior oblique muscle of a goat. This spindle is cut through the equatorial region. Centrally placed nuclei are seen in the intrafusal muscle fibres. A fair-sized periaxial space is seen. (Paraffin section. H. and E.)

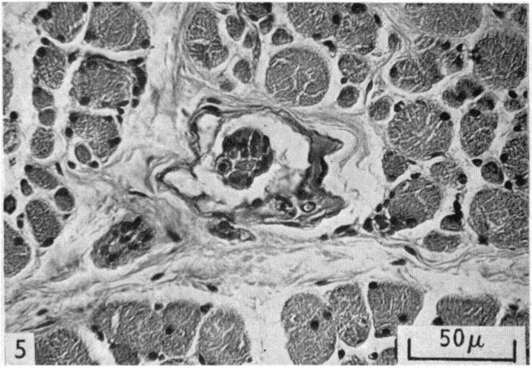
Fig. 6. Transverse section of twin muscle spindles in the inferior oblique muscle of a goat. The capsule in this case is considerably stouter than those seen in figs. 4 and 5. Central nuclei are again seen in the intrafusal muscle fibres. (Paraffin section. H. and E.)

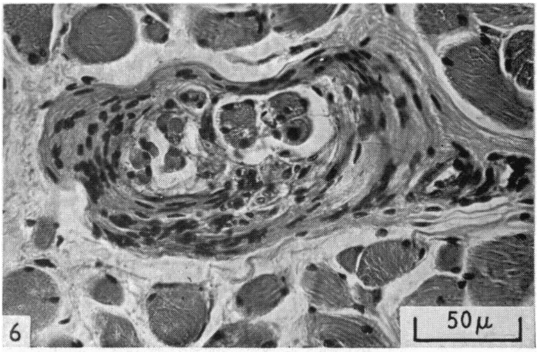

500 μ
1


500 μ
2


1·0 mm.
3


50 μ
4


5
50 μ


6
50 μ