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MUSCLE SPINDLE DISCHARGE IN NORMAL AND OBSTRUCTED MOVEMENTS

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SUMMARY

1. The discharge activity of muscle spindle endings located in tail and hind limb muscles was recorded during voluntary movements in the cat.

2. During active shortening of the receptor-bearing muscles, both primary and secondary endings tended to fall silent. This was more pronounced, the higher the rate of muscle shortening. We suggest that in unobstructed movements in which muscle velocities exceed 0·2 resting lengths per second (l_r/sec), the firing patterns of spindle afferents are dominated by their responses to the length variations. At velocities lower than 0·2 l_r/sec, fusimotor action may predominate.

3. When active muscle shortening was unexpectedly halted, both primary and secondary endings resumed firing, but the increases in discharge rate were not as abrupt as might have been expected had there been strong co-activation of fusimotor and skeletomotor neurones. Rather, for the types of movements studied, fusimotor action appears to have been quite modest.

INTRODUCTION

In the absence of fusimotor action, muscle spindle afferents fall silent during muscle shortening. Spindle primary endings fall silent even when the rate of extrafusal shortening is very low (of the order of 0·01 l_r/sec (Lennerstrand, 1968)). In acute studies, it has been shown that static fusimotor action can maintain and even accelerate the firing of primary and secondary endings during extrafusal shortening (Crowe & Matthews, 1964; Lennerstrand & Thoden, 1968). On this basis, it has been argued that co-activation of skeletomotor and fusimotor neurones in voluntary movements would ensure a continuity of spindle afferent feedback (Matthews, 1964).

This concept was formalized by Phillips (1969) in a schematic diagram showing the efferent and afferent activity likely to occur in active shortening of hand muscles, assuming graded co-activation of skeletomotor and fusimotor neurones. For simplicity, it was assumed that the fusimotor action would exactly balance the unloading effect on the spindle caused by extrafusal shortening, and so the spindle afferents would keep firing at a fixed rate. If an unexpected resistance to shortening occurred, the unloading effect would be reduced, but the fusimotor action would be

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unchanged, so spindle afferents would be expected to abruptly increase their discharge rate.

We have tested this hypothesis by studying the discharge trains of single identified muscle spindle afferents during normal and obstructed movements in cats (Eastman, Prochazka, Stephens & Wand, 1978). In all but the slowest tail and hind limb movements, there were considerable reductions in the firing rates of both primary and secondary endings during unobstructed muscle shortening. This further confirms the findings of Taylor & Cody (1974), Goodwin & Luschei (1975), Prochazka, Westerman & Ziccone (1976, 1977), and Loeb, Bak & Duysens (1977). When shortening was blocked mechanically, both primaries and secondaries generally showed resumptions in firing at rates which were only moderately larger than those seen when similar length variations were imposed during deep anaesthesia. Thus for the types of movements studied, fusimotor action does not appear to compensate for spindle unloading to the extent implied by the hypothesis.

METHODS

Detailed descriptions of the afferent recording technique have appeared elsewhere (Prochazka *et al.* 1976, 1977), and so only a summary is presented here.

Surgery

During one aseptic operation under halothane anaesthesia, pairs of fine (17 μm) wires insulated except for their tips were introduced into L6, L7 or S1 spinal roots through small slits in the dura mater. The wires were fixed to the dura using a drop of isobutylcyanoacrylate, and fine connecting cables were passed subcutaneously to a dental acrylic headpiece, along with a heparinized catheter from the jugular vein. In order to provide fixation points for externally attached length gauges, small (1 mm diam.), stainless-steel eyelets were attached subcutaneously to the ischium, the head of the tibia and the calcaneum. Flexible, Teflon-coated wires (250 μm diam., 25 mm long) looped through the eyelets, emerged through the skin at these three points. After recovery from the operation, the animals bore the implants with no apparent discomfort for up to 3 weeks.

Recording sessions

Starting 1 day post-operatively, a small capsule containing 2FM transmitters was clipped to the animal's head, and miniature plugs were mated with their appropriate sockets. If the implanted dorsal root electrodes happened to be favourably located, the discharge trains of single afferent fibres could now be recorded. In the four cats implanted for this study, stable recordings from twenty-six identified afferent fibres were obtained. Most afferents were held for between 6 and 10 hr, but seven could be recorded over a period of days. The most stable, a hair follicle afferent, was recorded on four consecutive days.

A given afferent was identified by mechanical, electrical and pharmacological tests (Prochazka *et al.* 1977) during a brief period (5–10 min) of anaesthesia (Epontol, Bayer). If the afferent was found to innervate a knee flexor or an ankle muscle, a mercury-in-rubber length gauge was tied to the appropriate percutaneous fixation wires so as to be in parallel with the muscle. In the case of tail muscles, the length gauge was attached at one end by adhesive tape to the tail, some 20 mm caudal to the ischium, and at the other end, to the skin overlying the head of the femur. A cable connecting the length gauge to the telemeter capsule was attached to the skin with adhesive tape. Fine electromyogram (e.m.g.) wires (250 μm diam.) were inserted into the appropriate muscle percutaneously, and also led to the telemeter capsule.

Subsequent recordings in the awake animal generally lasted about 1 hr. The movements studied depended on the afferent involved. An FM cassette recorder (Data Acquisition, type DA 1432-4) stored three transmitted signals: length, e.m.g. and neurogram, as well as a voice commentary. Segments of the record were later written onto paper using a Medelec fibre-optic recorder.

RESULTS

Of the twenty-six fully identified afferents in this study, fifteen proved to be cutaneous and one was a tendon organ afferent. Of the remaining ten afferents, seven were spindle primaries and three were spindle secondaries. The primaries were located in the following muscles: plantaris (one), biceps femoris (one), abductor femoris (two), abductor caudalis externis (three). The secondaries were located in: medical gastrocnemius (one), extensor digitorum longus (one), abductor caudalis externis (one).

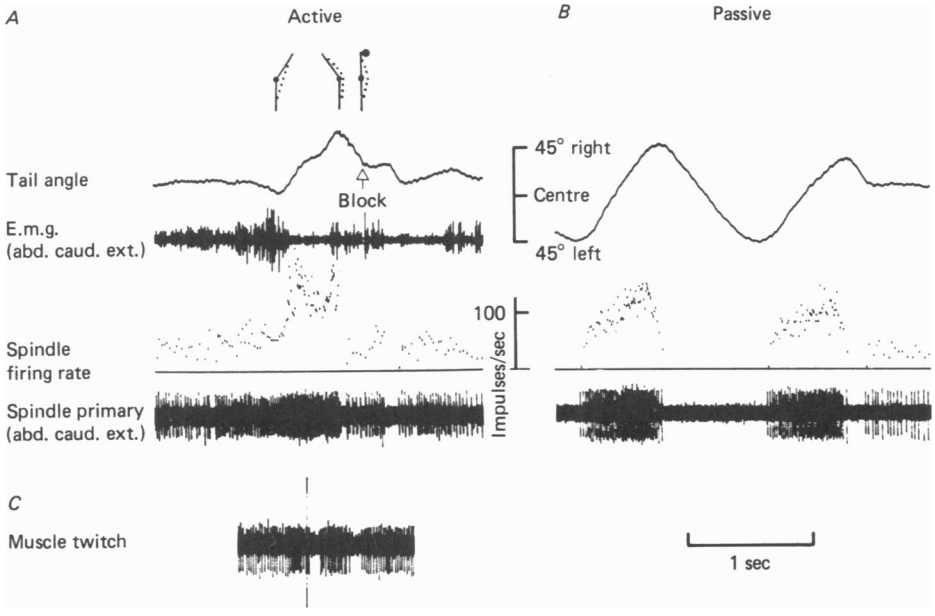

Fig. 1. Tail abductor spindle primary. *A*, voluntary lateral movements of tail. Muscle represented schematically as dotted line in schematic, length increasing for upward deflexion of length transducer signal (calibrated at 0 and ±45° lateral tail angle). Active shortening was blocked as shown, by obstacle positioned unexpectedly about 20 mm caudal to ischium. *B*, deep anaesthesia, lateral tail movements imposed by experimenter. At end of second cycle, the length variations occurring at 'block' in *A* were simulated. *C*, spindle response to electrically evoked muscle twitch.

Tail abductor spindles

Fig. 1*A* shows the activity of a spindle primary ending located in abductor caudalis externis, during lateral tail movements. As indicated in the schematic, muscle shortening was associated with a tail movement to the cat's left, and a downward deflexion of the length trace. The firing rate of this afferent was closely related to the length variations, with a high dynamic sensitivity evident during the passive lengthening phases, where e.m.g. activity was minimal. During the brief period of active shortening before the block, the afferent was initially silenced, and then resumed firing at a low rate some 100 msec before contact with the obstacle.

The obstacle consisted of a metal rod, fitted with a photo-electric sensor, which was unexpectedly positioned some 20 mm caudal to the ischium, so as to halt the

movement. The firing rate of the spindle can be seen in Fig. 1*A* to have returned to about 50 impulses/sec within about 60 msec of the first cessation of shortening. The e.m.g. activity during the 200 msec of approximately isometric conditions indicates that the animal was actively trying to overcome the obstacle.

Fig. 1*B* shows the responses of the same afferent to movements imposed by the experimenter during a brief period of deep Epontol anaesthesia, in which fusimotor activity may be assumed to have been suppressed. At the end of the second cycle,

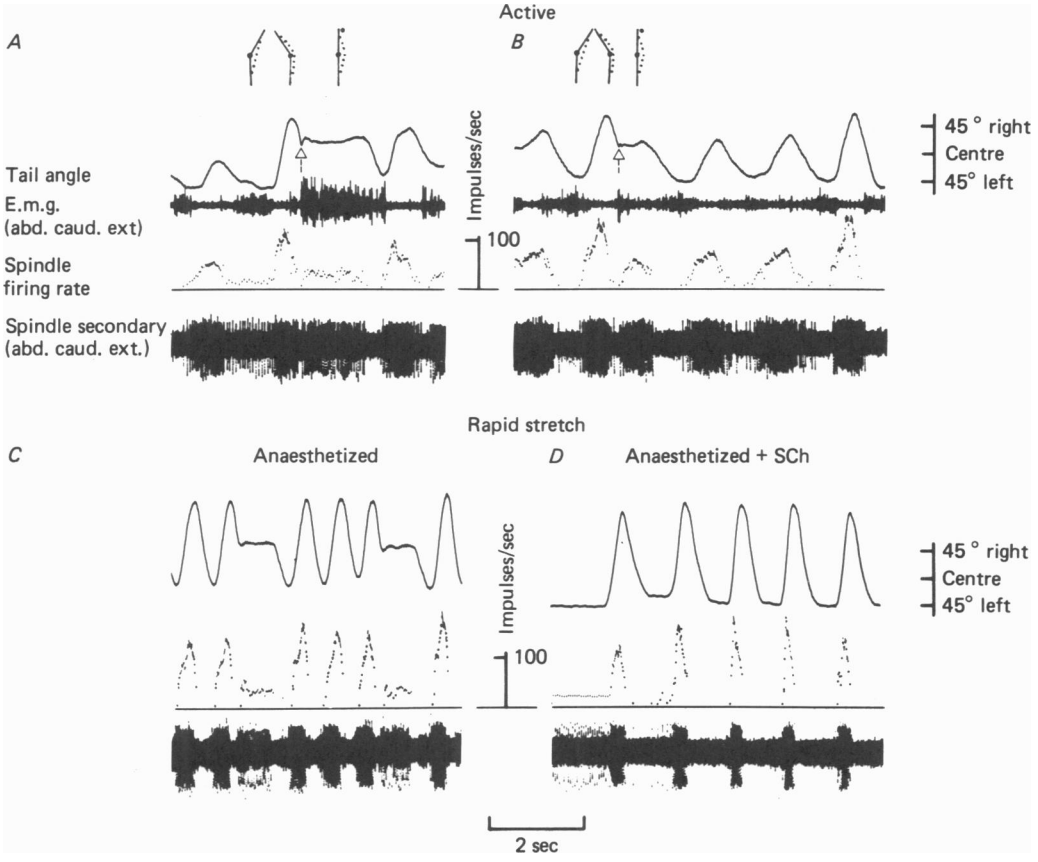

Fig. 2. Tail abductor spindle secondary. *A* and *B*, voluntary lateral movements of the tail (muscle length changes as in Fig. 1*A*). Active shortening was blocked at the arrows. *C*, deep anaesthesia, lateral tail movements imposed by experimenter, mimicking the length changes in the active movements. *D*, rapid passive stretches after I.V. succinylcholine, showing no appreciable change in dynamic sensitivity.

the length variations which had occurred during obstructed shortening, as in Fig. 1*A*, were approximately reproduced. During the last isometric period, the afferent can be seen to have resumed firing at some 30 impulses/sec. Thus fusimotor action during the block in Fig. 1*A* seems only to have increased the firing rate by some 20 impulses/sec above the passive case. Fig. 1*C* shows the result of one of the identification tests, an electrically evoked muscle twitch, which caused a pause in the firing of the afferent.

The firing patterns of a spindle secondary ending, also located in abductor caudalis externis, are shown in Fig. 2. The identification of this afferent was made on the basis of its responses to electrically evoked muscle twitches, taps applied to the muscle (not shown), and most importantly, by its unchanged dynamic responsiveness to rapid muscle stretch after I.V. succinylcholine chloride, 200 μg/kg. This may be seen by comparing the responses in Fig. 2*C* and *D*. Although it is not evident in these neurogram records, there was in fact a second afferent in the background, whose firing rate was markedly increased after succinylcholine, showing that the drug was indeed acting upon neighbouring spindle primary endings (Rack & Westbury, 1966).

In Fig. 2*A* and *B*, a number of unobstructed tail-wags are illustrated, together with two obstructed shortening movements (arrows indicate onset of block). The firing rate of this afferent was clearly very closely related to muscle length, with a small dynamic component of sensitivity. There was little evidence for the notion that the unloading of the spindle during active shortening was being compensated for by fusimotor action. In the blocked movements of Fig. 2*A* and *B*, the animal tried to overcome the obstacle, as evidenced by the persisting e.m.g. activity. The firing rate of the secondary ending during these periods of isometric activity was not substantially greater than that in comparable segments of Fig. 2*C*, where fusimotor action was presumably suppressed.

Hind limb muscles

Fig. 3 shows the variations in firing rate of a spindle primary afferent located in a knee flexor muscle, most probably biceps femoris posterior. The dramatic effect of succinylcholine on the dynamic responsiveness of this afferent to rapid, maintained stretches may be seen in Fig. 3*B*. The segment of record of Fig. 3*A* illustrates a sequence of knee extensions (upward deflexion of length trace) and flexions, the animal lying comfortably on the experimenter's lap. In the first movement, starting from almost complete flexion, the leg was extended by pulling on the cat's paw. This was moderately resisted by the animal, and after some 3·5 sec, the paw was released. Rapid, active flexion ensued, but full flexion was prevented by the unexpected placing of a metal rod in the path of the calcaneum. Contact with the obstacle produced the impulses shown under the length trace.

During the initial extension, the primary ending accelerated its firing to about 50 impulses/sec. There was a cessation of firing during the active shortening, and a resumption of discharge after contact with the obstacle.

The subsequent three extension–flexion cycles were not resisted by the cat. The rapid flexions were imposed by the experimenter, and there was no detectable muscle tone. Despite this large difference in the 'set' of the animal, the resumption of discharge after sudden halts to shortening was not significantly different in the active and passive movements. The final extension–flexion trial was similar to the first, except that in this case, just prior to its release, the paw was pinched slightly. This produced an acceleration in firing of about 25 impulses/sec, but the afferent was still silenced during the subsequent active shortening, and the resumption of firing after the block was similar to those in the previous trials.

Fig. 4 shows the discharge activity of a spindle secondary ending located in an

ankle extensor muscle, most probably medial gastrocnemius. The responses of this ending to rapid, maintained stretches before and after 200 μg/kg, I.V. succinylcholine chloride (Fig. 4*C*) indicate that the dynamic responsiveness of the ending was similar in the two cases (the rate of stretching in the succinylcholine trial was somewhat lower than in the other trial). Electrically evoked twitches of medial gastrocnemius caused pauses in firing which were typical of a secondary ending (Fig. 4*D*).

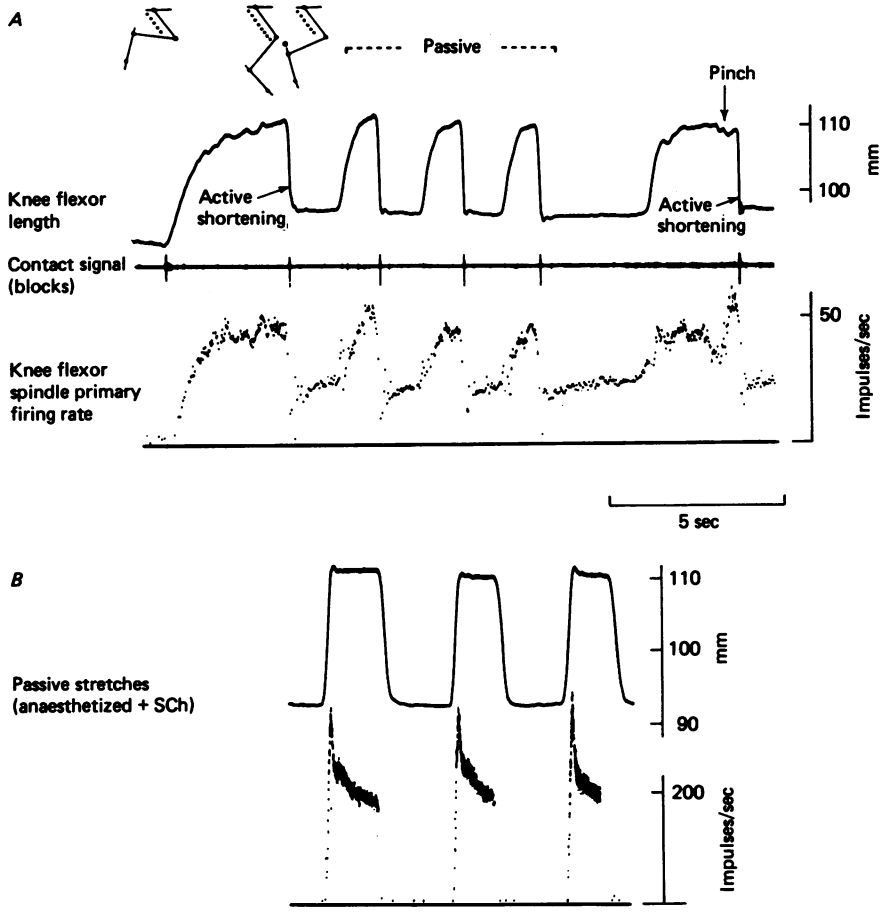

Fig. 3. Knee flexor spindle primary. *A*, knee extension (upward deflexion of length signal) and flexion, repeated five times. In the first and last trials, the cat resisted extension and actively flexed as soon as its paw was released (sloping arrows), the active shortening being blocked at contact signals in second trace. In the middle three trials ('passive'), the cat did not resist extension, and flexion was imposed by experimenter. *B*, deep anaesthesia, 1 min after I.V. succinylcholine, showing large dynamic sensitivity to rapid stretches.

The segment of recording in Fig. 4*A* represents two horizontal placing reactions. The cat was held by the experimenter, and was moved horizontally forward until the dorsum of its paw touched the edge of a table. Placing reactions then ensued, the foot making contact with the table surface at the times indicated by the arrows.

The height of the animal above the surface of the table varied from trial to trial, and it seems reasonable to assume that the exact moment of foot contact could not be predicted by the animal. The sudden cessation of shortening is therefore comparable to that in the blocked shortening trials in Figs. 1–3.

Again we see a silencing of the afferent during active extrafusal shortening, and only a modest resumption of firing after foot contact, although the e.m.g. activity of medial gastrocnemius indicates that appreciable voluntary effort was involved.

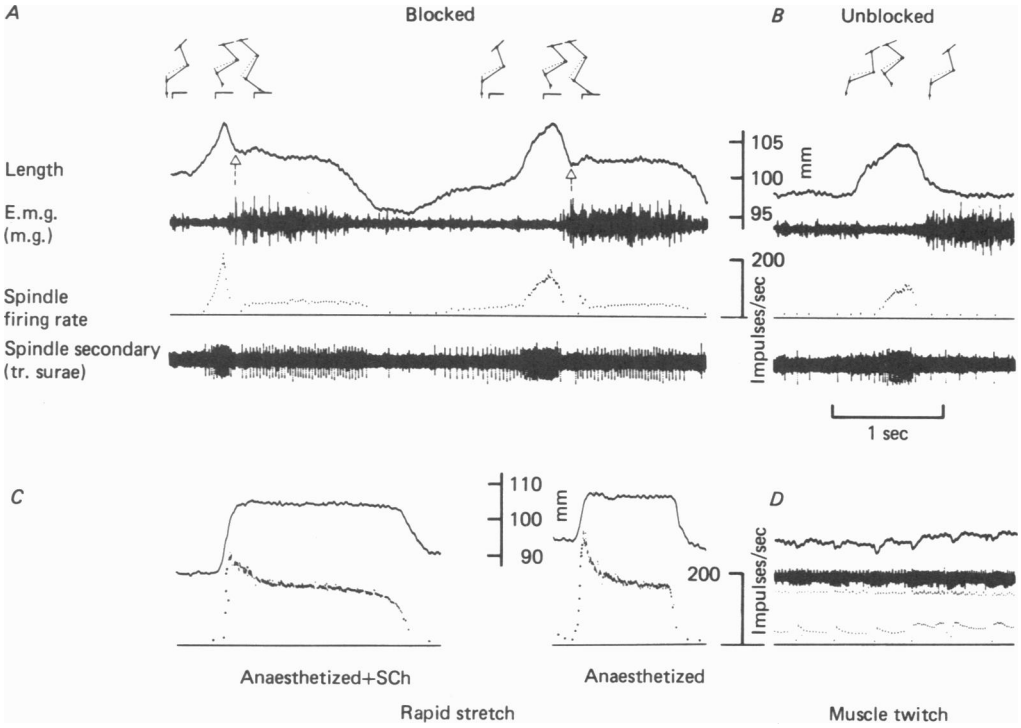

Fig. 4. Ankle extensor spindle secondary. *A*, two horizontal placing reactions elicited by touching dorsum of paw against side of table. Shortening stopped at moment of foot contact (arrows), with only a small increase in firing during the subsequent periods of weight-bearing. *B*, placing reaction without final foot contact. *C*, rapid passive stretch after I.V. succinylcholine (left), showing only a small dynamic sensitivity, not appreciably different than before succinylcholine (right). Note that rate of stretch was larger in this latter trial. *D*, responses of the afferent to electrically evoked muscle twitches (top: length trace; middle: afferent spikes; bottom: afferent firing rate).

Fig. 4*B* shows a trial in which a placing reaction occurred without subsequent foot contact. The resumption of afferent firing towards the end of this segment was at a very low rate. Taken together, these results suggest that this afferent responded largely to variations in muscle length, with little evidence for skeletomotor-coupled fusimotor action.

DISCUSSION

Unobstructed shortening

In this study, we have tried to establish the degree to which fusimotor action compensates for spindle unloading during active muscle shortening. In general, the results show that for the types of movement studied, both primary and secondary endings tend to fall silent during unobstructed extrafusal shortening. This is in agreement with Taylor & Cody (1974), Goodwin & Luschei (1975) and Prochazka *et al.* (1976, 1977), but, at first sight, contrasts with the respiratory studies of Critchlow & Euler (1963) and the human neurography data of Vallbo (1973) and Hagbarth, Wallin & Löfstedt (1975).

However, in the following, we will attempt to show that the apparent differences can be largely resolved by taking into account the rates of change of muscle length in the various experiments. Clearly, the rate at which a muscle shortens is a key factor in the silencing effect on its spindles (present results; Cody, Harrison & Taylor, 1975). In order to compare data from muscles of different lengths, we shall express muscle velocities in relation to the resting lengths (l_r) of the muscles involved. Although it has not been rigorously demonstrated, it is reasonable to suppose that a spindle ending responds to the proportional length change of that portion of the muscle along which the spindle extends (Andersson, Lennerstrand & Thoden, 1968). Assuming that the proportional length change has a fairly constant value along the length of the muscle, this is equal to the proportional length change of the muscle as a whole, irrespective of its initial l_r. Thus if one muscle has a l_r ten times that of another, the first would need to be stretched at ten times the rate of the second in order to produce comparable firing rates of spindle endings in the two muscles. This has indeed been shown in comparisons between ankle extensor spindles and intercostal spindles (Lennerstrand, 1968; Andersson *et al.* 1968).

Let us now compare the rates of shortening observed in the relevant investigations. In all the published human afferent recordings, the fastest rate of shortening was about 0·1 l_r/sec (Hagbarth *et al.* 1975: finger flexor, l_r about 300 mm, rate of shortening about 25 mm/sec, assuming 5° flexion = 1 mm length change (Vallbo, 1974)). In the intercostal studies, the maximum rate of shortening of inspiratory muscles was about 0·2 l_r/sec (Critchlow & Euler, 1963: l_r about 15 mm, rate of shortening about 3 mm/sec, change in shortest distance between ribs = twice change in external intercostal muscle length (personal measurements)). In the jaw muscle studies, the maximum rate of shortening of temporalis was between 3 and 5 l_r/sec (Taylor & Cody, 1974: l_r about 20 mm, rate of shortening about 100 mm/sec, assuming 5° jaw rotation = 1 mm length change; Goodwin & Luschei, 1975: l_r about 20 mm, rate of shortening about 60 mm/sec).

In the present study, the rate of shortening of the knee flexors in Fig. 3*A*, last trial, was about 2 l_r/sec (l_r about 110 mm, rate of shortening measured on expanded scale about 200 mm/sec). In Fig. 4*A*, before contact, the rate of shortening of the ankle extensors was about 0·4 l_r/sec (l_r about 100 mm, rate of shortening about 40 mm/sec).

It now becomes evident that in the conscious cat and monkey experiments, where spindle afferents fell silent during active shortening, muscle velocities were in the

range 0·4–5 l_r/sec. In the respiratory studies, with maximal shortening rates of about 0·2 l_r/sec, spindle firing during shortening was often maintained. In the human neurography experiments, in which the maximal rates of shortening (0·1 l_r/sec) were about one fiftieth of those in the cat and monkey experiments, spindle afferents usually fired during shortening. Indeed at such low rates, the animal recordings show precisely the same effect (e.g. compare the first, slow shortening in Fig. 1*A* with the subsequent rapid shortenings). We therefore suggest that the following generalization can be made: in normal unobstructed movements in which muscle velocities exceed 0·2 l_r/sec, increases in muscle length will cause increases in spindle discharge, and decreases in muscle length will cause decreases in spindle discharge. The depth of this modulation will of course be dependent on the concurrent level of fusimotor activity. Such a generalization cannot be made for movements in which muscle velocities are lower than 0·2 l_r/sec. Under these circumstances, fusimotor action may often have a more powerful modulating effect on spindle discharge than do the extrafusal length changes. Consequently, during such slow movements, increases and decreases in muscle length cannot be assumed to result in increases and decreases in spindle firing.

Obstructed shortening

Both primary and secondary endings showed resumption of firing when active shortening was blocked. However, the increases in firing rate were usually only moderately larger than those occurring when similar length variations were imposed on the receptor-bearing muscles during deep anaesthesia.

We did not observe the abrupt rises in discharge of spindle afferents which would have been expected had there been graded co-activation of skeletomotor and fusimotor neurones. Rather, for the types of movements studied, fusimotor action appears to have been quite modest.

It should be pointed out that in our study, the animals were relaxed, and rarely exerted powerful force to overcome the obstacles. That these conditions might result in increased fusimotor action was suggested to us by the following observations. First, if the animals were lifted away from the normal experimental bench-top to an unfamiliar part of the room, spindle afferent discharge at constant muscle length often increased considerably. This was not usually accompanied by a comparable increase in the amplitude of the e.m.g. Secondly, if a very powerful isometric contraction was elicited, e.g. in the tail abductors by persistent holding of the tail over to the contralateral side, spindle discharge could also show large increases.

The conclusions of this investigation may therefore not apply to movements involving unusual levels of arousal, apprehension, or very strong voluntary contractions. However, for most normal movements in which muscle shortening is suddenly and unexpectedly halted, the resumption of spindle afferent discharge after the halt cannot be expected to show an abrupt increase due to fusimotor action.

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REFERENCES

ANDERSSON, B. F., LENNERSTRAND, G. & THODEN, U. (1968). Fusimotor effects on position and velocity sensitivity of spindle endings in the external intercostal muscle of the cat. *Acta physiol. scand.* **74**, 285–300.

CODY, F. W. J., HARRISON, L. M. & TAYLOR, A. (1975). Analysis of activity of muscle spindles of the jaw-closing muscles during normal movements in the cat. *J. Physiol.* **253**, 565–582.

CRITCHLOW, V. & EULER, C. V. (1963). Intercostal muscle spindle activity and its γ motor control. *J. Physiol.* **168**, 820–847.

CROWE, A. & MATTHEWS, P. B. C. (1964). Further studies of static and dynamic fusimotor fibres *J. Physiol.* **174**, 132–151.

EASTMAN, M. J., PROCHAZKA, A., STEPHENS, J. A. & WAND, P. (1978). Spindle afferent discharge during normal and obstructed movements. *J. Physiol.* **282**, 32*P*.

GOODWIN, G. M. & LUSCHEI, E. S. (1975). Discharge of spindle afferents from jaw-closing muscles during chewing in alert monkeys. *J. Neurophysiol.* **38**, 560–571.

HAGBARTH, K.-E., WALLIN, G. & LÖFSTEDT, L. (1975). Muscle spindle activity in man during voluntary fast alternating movements. *J. Neurol. Neurosurg. Psychiat.* **38**, 625–635.

LENNERSTRAND, G. (1968). Position and velocity sensitivity of muscle spindles in the cat. 1. Primary and secondary endings deprived of fusimotor activation. *Acta physiol. scand.* **73**, 281–299.

LENNERSTRAND, G. & THODEN, U. (1968). Muscle spindle responses to concomitant variations in length and in fusimotor activation. *Acta physiol. scand.* **74**, 153–165.

LOEB, G. E., BAK, M. J. & DUYSENS, J. (1977). Long-term unit recording from somatosensory neurons in the spinal ganglia of the freely walking cat. *Science, N.Y.* **197**, 1192–1194.

MATTHEWS, P. B. C. (1964). Muscle spindles and their motor control. *Physiol. Rev.* **44**, 219–288.

PHILLIPS, C. G. (1969). Motor apparatus of the baboon's hand. The Ferrier Lecture, 1968. *Proc. R. Soc.* B **173**, 141–174.

PROCHAZKA, A., WESTERMAN, R. A. & ZICCONE, S. P. (1976). Discharges of single hindlimb afferents in the freely moving cat. *J. Neurophysiol.* **39**, 1090–1104.

PROCHAZKA, A., WESTERMAN, R. A. & ZICCONE, S. P. (1977). Ia afferent activity during a variety of voluntary movements in the cat. *J. Physiol.* **268**, 423–448.

RACK, P. M. H. & WESTBURY, D. R. (1966). The effects of suxamethonium and acetylcholine on the behaviour of cat muscle spindles during dynamic stretching, and during fusimotor stimulation. *J. Physiol.* **186**, 698–713.

TAYLOR, A. & CODY, F. W. J. (1974). Jaw muscle spindle activity in the cat during normal movements of eating and drinking. *Brain Res.* **71**, 523–530.

VALLBO, Å. B. (1973). Muscle spindle afferent discharge from resting and contracting muscles in normal human subjects. In *New Developments in Electromyography and Clinical Neurophysiology*, vol. 3, ed. DESMEDT, J. E., pp. 251–262. Basel: Karger.

VALLBO, Å. B. (1974). Afferent discharge from human muscle spindles in non-contracting muscles. Steady state impulse frequency as a function of joint angle. *Acta physiol. scand.* **90**, 303–318.