

Ia AFFERENT ACTIVITY DURING A VARIETY OF VOLUNTARY MOVEMENTS IN THE CAT

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SUMMARY

1. Implanted dorsal root electrodes were used to record discharge trains of single spindle primary afferents (Ia's) of the cat's hind limb during different types of movement.

2. The length of the ipsilateral ankle extensors was continuously monitored by an implanted length gauge. Length changes occurring during active stepping were subsequently passively reproduced during brief anaesthesia.

3. A comparison of the Ia responses in active and simulated step cycles revealed that moderate fusimotor drive to ankle extensor spindles probably occurred mainly, if not exclusively, during the E₁, E₂ and E₃ phases of active stepping.

4. A temporal advance in the Ia response to passive stretching in the F-phase was attributed to the after-effects of fusimotor activity in the extension phases.

5. Light thrust applied to the animal's back evoked a potent fusimotor response. This load compensation effect may provide an explanation for the apparently higher degree of α - γ co-activation seen in the mesencephalic locomotor preparation.

6. Ankle extensor Ia discharge decreased during falls, despite an increase in extensor e.m.g. This is seen as a clear example of independent α and γ control.

7. Placing reactions during walking were consistent with the notion that cutaneous inputs dominate over proprioceptive inputs in these movements.

8. α and Ia discharge during paw-shaking showed many of the characteristics of that in decerebrate and spastic clonus. The present results suggest that movements resembling clonus may be part of the animal's normal repertoire.

9. Isometric co-contraction of agonists and antagonists was found to involve α - γ co-activation.

10. Hamstring Ia discharge behaviour during stepping further highlighted the increases in firing rate which normally occur during passive muscle stretching in 'pre-programmed' movements.

INTRODUCTION

Several important recent papers have emphasized the potency, if not the dominance of α -coupled fusimotor drive on the discharge behaviour of muscle spindles during voluntary movements (Severin, Orlovsky & Shik, 1967; Phillips, 1969; Vallbo, 1973; for review, see Wetzel & Stuart, 1976).

It is evident from percutaneous single afferent recordings in humans that for the slow, weak and usually isometric contractions allowed by the technique, α - γ co-activation would indeed seem to be the rule (Vallbo, 1974; Burg, Szumski, Struppler & Velho, 1976).

However, it is also clear that the mammalian nervous system has evolved the potential for independently controlling α and γ motoneurons (see Matthews, 1972). It seems unlikely that this versatility would be neglected in movements for which the simple strategy of α - γ co-activation might not be appropriate.

By recording from single afferent fibres in the freely moving cat, it was possible in this study to observe the discharge behaviour of muscle spindles during a large variety of different movements. It was found that for certain classes of movement (e.g. paw shaking), the e.m.g., muscle length and spindle discharge patterns were usually fairly reproducible, and allowed deductions to be made about possible fusimotor involvement.

In a previous investigation (Prochazka, Westerman & Ziccone, 1976*a*), it was observed that spindle primary (Ia) afferents fired throughout the step cycle, and that firing rates during phases of passive muscle stretch were comparable with and indeed often higher than those during phases of active muscle contraction (lengthening or shortening). Significant firing rates during passive stretch have also been observed in jaw muscle spindles of conscious cats (Taylor & Cody, 1974) and monkeys (Goodwin & Luschei, 1975).

The relative importance of passive stretch in eliciting Ia discharge was further examined in the present study by analysing responses during different classes of movement.

Thus two main questions underlie this investigation. Firstly, are there classes of movement for which α - γ co-activation does not occur? Secondly, in normal movements, does muscle stretch in the absence of fusimotor

drive produce Ia firing rates comparable to those produced during fusimotor drive?

METHODS

A detailed description of the technique has appeared elsewhere (Prochazka *et al.* 1976*a*), 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 the L 7 spinal root through a small slit in the dura mater. The wires were affixed to the dura using a drop of isobutyl cyanoacrylate, and fine connecting cables were passed subcutaneously to a dental acrylic headpiece.

E.m.g. electrodes made from pairs of flexible, insulated, stainless-steel wires were implanted in the biceps femoris (BF) and lateral gastrocnemius (LG) muscles. A mercury-in-rubber length gauge was implanted between the calcaneum and the head of the tibia so as to lie in parallel with the triceps surae muscles. Connecting cables were passed subcutaneously to the head, along with an heparinized catheter from the jugular vein. After recovery from the operation, the animals bore the implants with no apparent discomfort for up to 6 weeks. Their observed hind-limb movements and recorded limb thrusts during stepping and running rapidly approached normal within the first 2 days.

Recording sessions. Starting 1 day post-operatively, a small capsule containing two FM transmitters was clipped on 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 for periods ranging from a few minutes to many hours. It has been our experience that successful recordings are most likely to occur between days 3 and 7 post-operative (the longest period after implantation during which single fibre discharges were obtained was 15 days). Electrodes can remain totally silent for days, and then, presumably as a result of small movements, suddenly produce stable single-fibre recordings.

During successful sessions, the animals walked over a flat surface to retrieve food pellets. An FM tape recorder (Tandberg 100) stored three transmitted signals: length, e.m.g. and neurogram. In the present series of experiments, recordings were made during a variety of movements in addition to those involved in stepping; for example, it was possible to elicit rapid shaking of the hind limb by applying a small square of sticking plaster to the footpads.

Afferent identification. When the full range of movements had taken place whilst recording from an afferent, the cat was anaesthetized via the indwelling jugular catheter using a short-duration anaesthetic (methohexitone: Lilly, 5 mg/kg). This enabled the afferent to be identified on the basis of its responses to a series of physiological and pharmacological tests.

(1) Palpation, joint manipulation and taps of graded intensity applied over muscle and tendon were used to locate the receptor. Spindle primaries have a high dynamic sensitivity to such stimuli. The maximum elicitable dynamic index was obtained by rapid and maintained stretches of the appropriate muscle. If the dynamic index did not exceed 100 Hz, the afferent was not classified as a spindle primary.

(2) Vibration from 10 to 1000 Hz was applied over the appropriate muscle and tendon. If the afferent discharge rate could not be driven over 100 Hz, the afferent was not classified as a spindle primary.

(3) Muscle twitches were evoked by percutaneous stimulation using a bipolar electrode consisting of two sharp stainless-steel wires 6 mm apart pressed down on to

the skin. If the afferent discharge did not pause during a minimal twitch, the afferent was not classified as a spindle primary.

(4) A dose of succinylcholine chloride (200 $\mu\text{g}/\text{kg}$) was administered via the catheter (artificial respiration was generally required for 2–3 min, the duration of muscle relaxation falling well within the period of anaesthesia). If the maximum dynamic index did not increase by at least 50 Hz, the afferent was not classified as a spindle primary.

No attempt was made to obtain conduction velocities of the afferents, as it was felt that the location along the nerve at which a percutaneous electrical stimulus would act could not be accurately estimated.

It should be emphasized that only those afferents which fulfilled all of the above identification criteria for Ia's are discussed in this report. The present observations were drawn from tape recordings of twenty-six thoroughly identified Ia afferents in twelve cats. Some aspects of the behaviour of fifteen of these afferents were described in a previous report. The results presented here refer to responses observed in the eleven subsequently recorded afferents with general conclusions applying to the whole population.

RESULTS

Active and simulated steps. Recordings have now been obtained from nine Ia afferents of the ankle extensors during stepping. As reported previously for a smaller sample of units (Prochazka *et al.* 1976*a*) all of these afferents showed the same characteristic modulations of firing frequency related to phases of the step cycle (see below).

By using deep anaesthesia to suppress fusimotor activity we were then able in three cases to study the effects of passive limb movements on the spindle discharges. Furthermore, by practice, we were able fairly closely to simulate the temporal pattern of the length changes monitored during the active step cycle. When the length changes recorded in many simulated cycles (e.g. Fig. 1*A*) were later compared with those recorded during normal stepping (e.g. Fig. 1*B–D*), a number of cycles could be found in which good correspondence had been achieved.

In each sequence of Fig. 1, LG e.m.g., muscle length, and instantaneous firing frequency of a single Ia afferent of the ankle extensors are presented. This afferent was probably located in either soleus or gastrocnemius, as extreme toe dorsiflexion had no influence on the firing rate (in contrast with the behaviour of plantaris Ia's).

The symbols F, E₁, E₂ and E₃ in Fig. 1 indicate the four phases of the step cycle defined by Philippson (1905) (see also Goslow, Reinking & Stuart, 1973). Flexion of the ankle, knee and hip joints begins as the foot is lifted from the ground for the forward swing (upward arrow indicating start of F). The triceps muscles are passively stretched by the ankle flexors (lengthening of LG, e.m.g. silent).

The first extension phase (E₁) starts during the swing, when triceps length has reached a maximum (marked by filled circles in Fig. 1*B–D*).

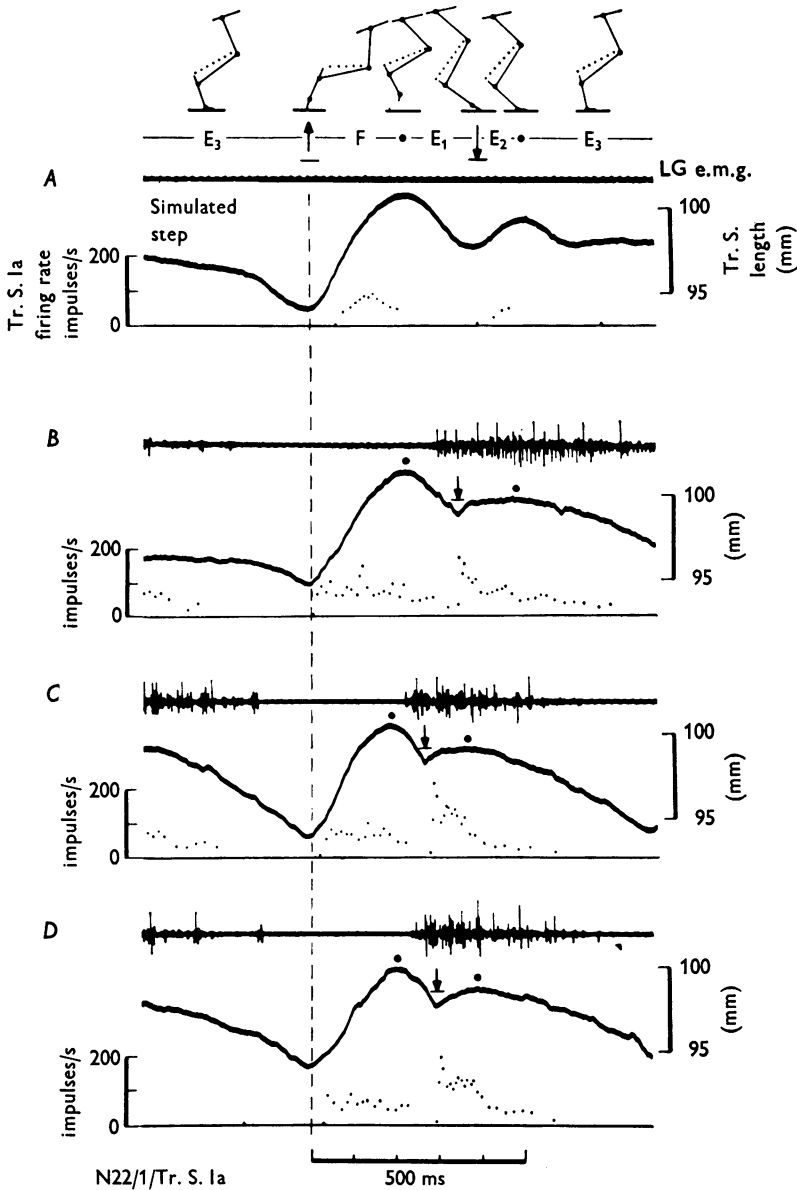


Fig. 1. Simulated and active step cycles of the ankle extensors. In each case, top trace: e.m.g. of lateral gastrocnemius; middle trace: length of ankle extensors; lower trace: instantaneous firing rate of a spindle primary afferent (Ia) of the ankle extensors. *A*, passive flexion and extension of ankle during anaesthesia (simulation of active length changes). *B-D*, active step cycles with well-matching length signals. Notice increased Ia firing during E_1 , E_2 and E_3 , and temporal advance of discharge during *F* in the active steps.

The shortening of the triceps during this phase results largely from the inertial and gravitational forces tending to swing the foot down, and this is supplemented by the onset of active contraction (LG e.m.g. in last 70 ms of E_1). After foot contact (downward arrows), the weight-bearing extensors generally yield for a short time (E_2 phase). After the peak of this lengthening contraction (filled circles in Fig. 1*B-D*), the stance phase continues for the duration of E_3 as the animal's centre of gravity moves forward.

The records of *A* were obtained during deep methohexitone anaesthesia. No resistance to passive joint rotation could be detected, and the LG e.m.g. was completely silent. The tonic discharge rate of the afferent was low and steady, and not affected by toe pinches and pinna stimulation. The available evidence suggests that under such conditions of deep barbiturate anaesthesia, fusimotor activity is minimal, if not entirely absent (see also Proske & Lewis, 1972). The responses to simulated length changes were therefore considered to be those of functionally de-efferented (passive) spindles.

Certain differences in the Ia firing patterns during active and simulated steps are evident in Fig. 1. In active stepping, the discharge during all three extension phases (E_1 , E_2 , E_3) is enhanced. All nine ankle extensor Ia's discharged during muscle shortening in the E_1 phase except when stepping was very rapid, whereas no discharges were observed in simulated E_1 phases.

Unfortunately the simulations of length changes during E_2 did not show a close correspondence with the active records. Furthermore, no attempt was made to mimic the slight jarring of distal musculature which occurs on foot contact (Film: Sontag, Cremer, Meseke, Ropte, Hoeffling, Goemann & Nowigk, 1976). It is therefore not possible to say to what extent the high discharge rates seen during the first 30 ms of E_2 in active stepping are a function of fusimotor drive. However, although the peak velocity of stretching during the simulation of E_2 (in *A*) exceeds that in the E_2 phases of *C* and *D*, the firing rate achieved during the simulation is considerably lower. This is strongly suggestive of fusimotor drive during E_2 in the active steps.

The maintained firing rates during muscle shortening (E_3) in *B*, *C* and *D* clearly indicate static fusimotor drive (Lennerstrand & Thoden, 1968). Apparently this drive is rarely organized to compensate entirely for the muscle shortening, especially during the latter part of E_3 , where, without exception, there occurred reductions in firing rate. This was true for all ankle extensor Ia's, for trotting as well as walking, irrespective of peak firing rates attained during E_3 .

Another interesting point of difference between the active and simulated records was the latency of onset of discharge during the *F* phase.

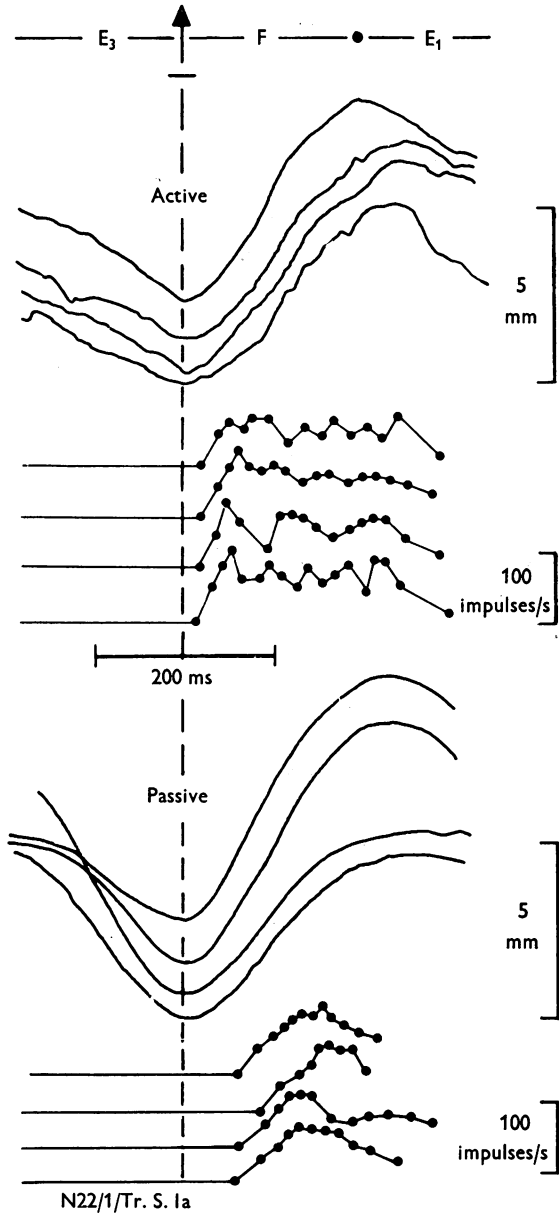


Fig. 2. Active and simulated step cycles showing temporal advance of F-phase discharge of an ankle extensor Ia. In each case, the length signals are aligned with onset of flexion, and are arranged in the same vertical order as the corresponding instantaneous firing rates beneath. Average temporal advance of first Ia discharge is 48 ms in the active records.

This is more clearly illustrated in the traced recordings of Fig. 2 (same afferent as in Fig. 1).

In this Figure, four simulated and four active step cycles were selected on the basis of length correspondence. In each case, the length and corresponding instantaneous firing rate signals were arranged in the same vertical order. The average latency of the first discharge after onset of F was 22 ms for active, and 70 ms for simulated steps. This represents an advance amounting to some 48 ms in the active cases.

It is apparent in Figs. 1 and 2 that the peak firing rates attained during F are not significantly different for the active and simulated step cycles. The receptor was therefore apparently more dynamically sensitive only during the initial 60 or 70 ms of stretch.

If significant dynamic fusimotor drive had occurred throughout F in the active steps, a much higher dynamic response might have been expected. Similarly, strong static drive would have resulted in considerably higher tonic firing rates. Furthermore, the evidence from spinal and decerebrate locomotor preparations argues against fusimotor activity in this phase of the cycle (Sjöström & Zangger, 1975; Severin, 1970).

The active responses would, however, be consistent with a slow completion during the early part of F of intrafusal contractions initiated by fusimotor drive in the preceding E phases (see Discussion).

Fig. 3 shows the discharge behaviour of a Ia afferent of the triceps surae for walking and for trotting. The receptor-bearing muscle was almost certainly plantaris, as the afferent responded to extreme dorsiflexion of the toes in addition to dorsiflexion of the ankle.

Although no e.m.g. analysis of stepping has been performed for plantaris, it seems reasonable to assume that the timing of plantaris e.m.g. would closely correspond to that of LG e.m.g. (plantaris is synergistic to FDL in its toe flexor capacity, and to gastrocnemius-soleus in ankle extension (Goslow, Stauffer, Nemeth & Stuart, 1972; Wetzel, Gerlach, Stern & Hannapel, 1973)). Engberg (1964) showed that FDL, soleus and gastrocnemius all had very similar periods of e.m.g. activity during stepping.

Three full step cycles are shown in each record, the third being the final step in a sequence ending in stance. In the first two rapid steps of the trotting record, the discharge rate of the Ia reached peaks of about 150 impulses/s during the E₂ phases. The small increases in firing rate just before foot lift-off (i.e. just before the length minima of each cycle) were very likely due to an extra stretch of plantaris occurring as a result of extreme toe dorsiflexion (Sontag *et al.* 1976). The delayed onset of firing after foot lift-off is similarly probably due to sudden passive plantarflexion of the toes. Otherwise this afferent showed the typical discharge behaviour of a pure ankle extensor Ia under an apparently moderate degree of fusimotor drive.

Load compensation. For a total of 7 Ia's, it was possible to elicit active contractions of the receptor-bearing muscles in response to external loading. For ankle extensors, a convenient approach was to lightly press down on the animal's back during stepping (Fig. 4*A*) or during stance (Fig. 4*B*). Such loading was often countered by small increases in extensor activity, as judged by increased LG e.m.g. and resistance to the push.

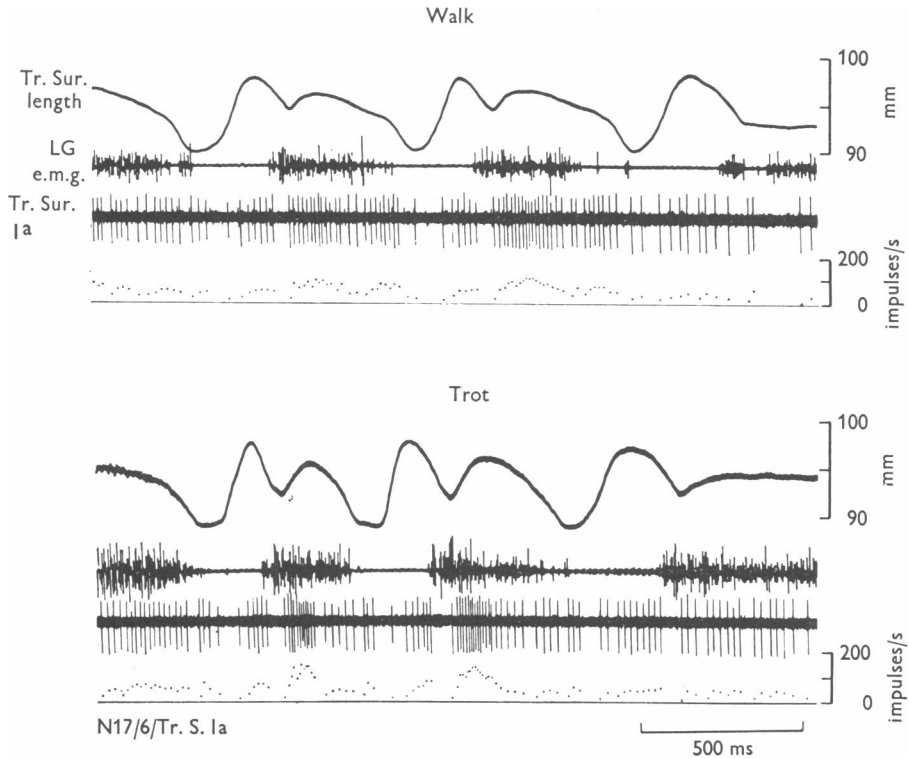


Fig. 3. Discharge behaviour of a plantaris Ia during walk and trot. Instantaneous frequencies refer to the Ia discharge train. With some small differences, the firing pattern closely resembles that of 'pure' ankle extensor Ia's.

The vertical dashed lines in Fig. 4 give an approximate indication of the onset and termination of back thrust. It is estimated that the applied force did not exceed 5 N. In *A*, a rapid step (swing phase: F and E₁) occurred just before the thrust. The ankle extensor Ia showed the usual firing pattern for these phases: a decreased firing rate just before F, an increased rate during F, a high-frequency burst on foot contact. For the duration of thrust, however, the firing rate was much higher than that in normal stance phases of unrestricted stepping (e.g. compare the discharge

rates during thrust in Fig. 4A with those in the E₂-E₃ phases of Fig. 1B-D).

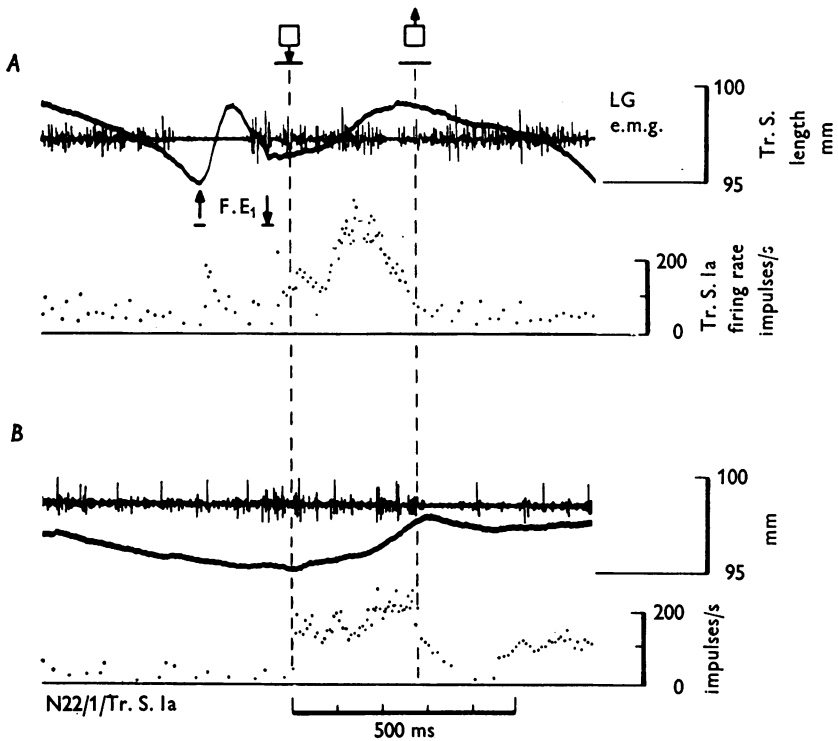


Fig. 4. Ankle extensor Ia discharge during application of light thrust to animal's back. *A*, thrust applied just after onset of E₂ phase of a step. *B*, thrust applied during a slow extension (animal standing). The high and maintained Ia discharge rates, presumably resulting from fusimotor drive, may be viewed as part of a 'load compensation response'.

In *A* the velocity of muscle stretching during the F phase at a length of 96 mm was 88 mm/s, the resulting firing rate being 180 impulses/s. In contrast, during the first 100 ms of thrust, where the velocity at the same length was only 5 mm/s, the firing rate was only slightly lower (170 impulses/s). As it happens, the dynamic sensitivity in this F-phase is almost identical to that of a soleus Ia investigated by Crowe & Matthews (1964; their Fig. 5C: peak firing frequency 179 impulses/s at 88 mm/s). In that experiment, the same firing rate could be achieved in response to stretching at 5 mm/s by stimulating a single dynamic fusimotor fibre at 70 impulses/s.

In the record of Fig. 4A, it is not possible to say to what extent static fusimotor recruitment contributed to the increased firing, nor whether the balance between static and dynamic drive remained constant. Clearly, however, the drive was extremely potent, and the responses indicate a high dynamic sensitivity.

In *B* the thrust was applied during stance. The animal happened to be gradually lifting itself from a partly crouched position, this being reflected in the slow shortening of the ankle extensors. During the period

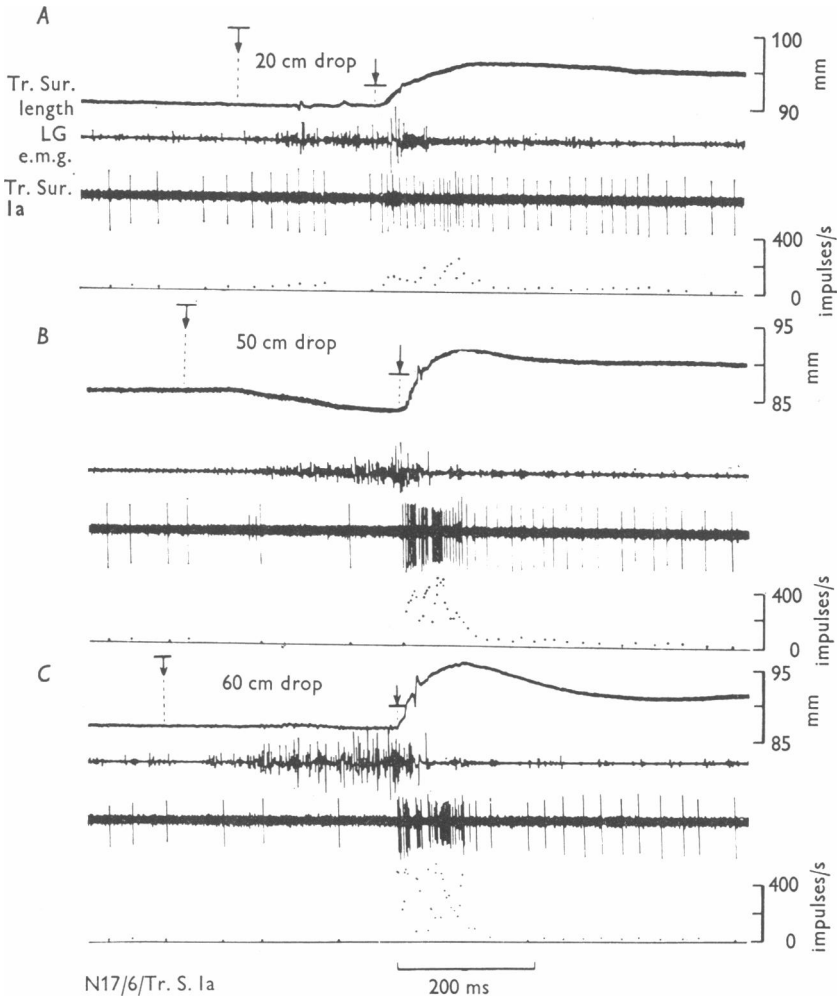


Fig. 5. Ankle extensor Ia discharge recorded during three falls on to a flat surface from the heights indicated. Times of release are estimates based on 1 *g* acceleration. Note reduction in Ia firing rate before landing, even for nearly isometric contractions of the extrafusal muscle (*A* and *C*).

of back thrust, the firing rates in *B* were similar to those in *A* for similar velocities of stretching. Under these conditions, then, the responses did not seem to depend substantially on the type of preceding movement, nor on the firing rate just prior to thrust.

The large modulations in spindle firing rate were not generally accompanied by comparable changes in e.m.g. activity in this experimental situation and similar findings have been noted previously (Taylor & Cody, 1974; Goodwin & Luschei, 1975; Prochazka *et al.* 1976*a*). However, when strong, nearly-isometric flexor contractions were elicited by pulling the paw, the amplitude of knee flexor (biceps femoris) e.m.g. and the firing rates of knee flexor Ia's often showed large modulations occurring in parallel.

Free-fall and landing. E.m.g. and muscle length recordings were obtained during free fall and landing in four cats. Additionally, in two cats, the discharge trains of two ankle extensor Ia's were recorded for a total of 18 drops from heights ranging from 5 to 60 cm (Prochazka, Westerman & Ziccone, 1976*b*).

Fig. 5 shows the responses for three such trials. In agreement with Watt (1976), the LG e.m.g. increased significantly from between 40 and 70 ms after release. Presumably a co-contraction of the ankle flexors prevented significant length changes in *A* and *C* before foot contact.

In all falls, the Ia firing rate decreased significantly before the moment of foot contact. Generally the length changes were similar to those in *B* (suggesting a slight predominance of extensor tension resulting in slow ankle extension prior to foot contact). Records *A* and *C* were chosen to demonstrate that the decrease in Ia discharge also occurred for substantially isometric contractions.

The very rapid muscle stretching after foot contact always resulted in extremely high Ia firing rates (e.g. in excess of 500 impulses/s in *B* and *C* in response to maximum stretch rates of 500 mm/s). The occurrence of two or three longer intervals during such high frequency discharge suggested an abrupt change in dynamic sensitivity during the stretch. When similar very rapid stretches were applied during anaesthesia, no such discontinuities were observed. Similar abrupt transitions in sensitivity may often be seen in the responses of Ia's to rapid muscle stretch in the decerebrate cat (Eldred, Granit & Merton, 1953; personal observations).

Placing reaction during walking. Tactile stimulation applied to the dorsum of the foot during the swing phase has been shown to cause a rapid, coordinated set of contractions resulting in the limb being lifted over the 'obstacle' (Forssberg, Grillner & Rossignol, 1975). The response was shown to depend on an intact cutaneous input (chronic spinal preparation).

In the present experiments, a length of 1 cm tubing fitted with a contact switch was rapidly moved into position just in front of the left hind limb during the stance phase of stepping (Fig. 6). The dorsum of the foot came up against this obstacle in the ensuing F-phase.

The length trace in *A* shows that after the moment of contact with the obstacle (indicated by the vertical dashed line), there was an initial brief period (*ca.* 30 ms) of shortening of the ankle extensors. Presumably this extension was caused by the decelerating effect of the obstacle on the foot.

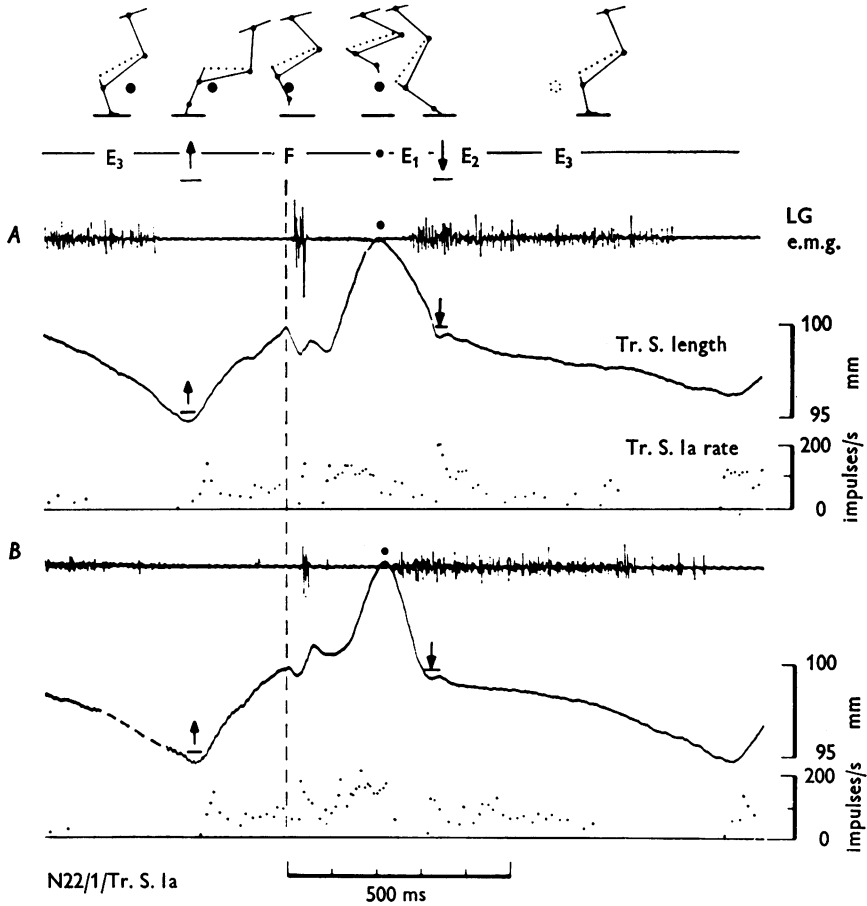


Fig. 6. Placing reaction during stepping. Stick figures indicate relative position of 'obstacle'. E.m.g., length and Ia discharge refer to ankle extensors. Note rapid LG e.m.g. response after contact in *A*, despite Ia silence. *B*, different step, showing consistency of response. In both cases, the main post-contact flexion is delayed by about 100 ms, presumably allowing time for knee flexors to lift the foot clear.

During this shortening, some 15 ms after contact, intense e.m.g. activity commenced in LG. This would normally be expected to produce further rapid shortening. However, the antagonistic flexors almost certainly became strongly active at the same time, their activity persisting beyond that of LG (Forssberg *et al.* 1975).

From the length record, it would therefore seem that the net effect was a 'locking' of the ankle for the first 100 ms after contact, followed by a large additional flexion completing the F-phase.

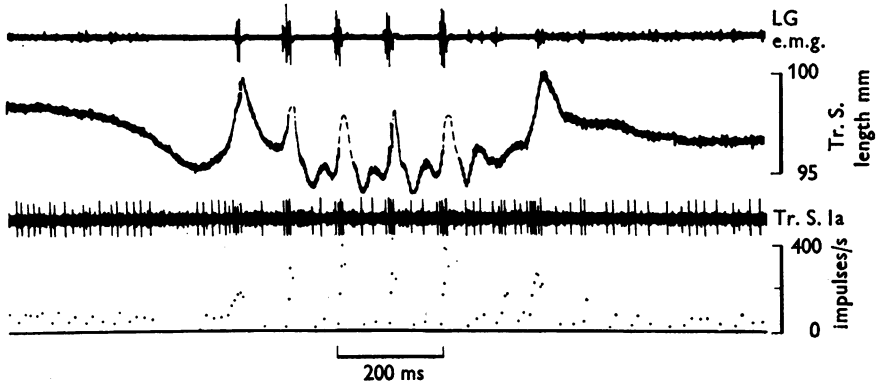


Fig. 7. Rapid paw-shaking. Due to amplifier 'cross-talk', it was necessary to estimate some of the length record (dashed lines). Ia discharge occurred almost exclusively during muscle lengthening. Length, e.m.g. and Ia discharge strongly resembled the patterns seen in decerebrate clonus.

The firing frequency of the ankle extensor Ia in Fig. 6 followed all of these length changes as would be expected of an essentially passive stretch receptor with high dynamic sensitivity. It is of particular interest, however, that the burst of LG e.m.g. started during a pause in spindle firing.

The maximum rate of muscle lengthening during the additional flexion in *A* was 70 mm/s, and this resulted in a firing rate of 120 impulses/s. Thus it is unlikely that any substantial fusimotor drive was generated after contact with the obstacle.

The sequence of length changes in *B* was similar to that in *A*. Contact with the obstacle caused somewhat less shortening in this case, and the e.m.g. response was smaller and had a longer latency. The slightly higher Ia firing rates suggest that a small amount of fusimotor drive may have been evoked after contact. Again, the large additional flexion did not begin until about 100 ms after the stimulus.

Paw shaking. The discharge trains of three ankle extensor Ia's were recorded during many sequences of rapid shaking movements such as that illustrated in Fig. 7. Paw shaking was elicited either by the squirting of a small quantity of water on to the foot, or, more effectively, by applying a small square of sticking plaster to the foot pads.

As has been amply demonstrated previously (e.g. Deliagina, Feldman, Gelfand & Orlovsky, 1975), rapid alternating movements such as scratching and shaking of the hind limb are associated with extremely phasic

bursts of LG e.m.g. commencing during flexion. The bursts recorded in the present experiments were generally so large as to partially interfere with the telemetered length signals (dashed lines in Fig. 7 are estimates only).

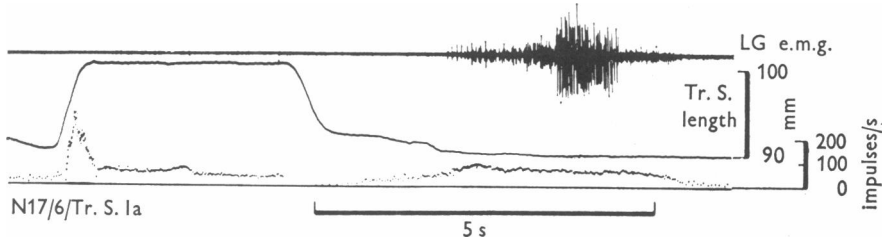


Fig. 8. Ankle extensor Ia. Cat lying on side. First part of record shows responses to passive dorsiflexion, followed by passive plantar flexion of ankle. In second part, cat stretched out, resulting in isometric contractions of LG. Increase in Ia discharge reflects α - γ co-activation in absence of external obstacle or 'length misalignment' (see Discussion).

As seen in Fig. 7, ankle extensor Ia's discharged almost exclusively in the stretching phases of such movements. This pattern is very similar to that reported by Hagbarth, Wallin & Löfstedt (1975) for finger flexor Ia's recorded during rapid alternating movements in man (their Fig. 4A).

The maximum rate of stretching in the last cycle of Fig. 7 ('clean' length signal) was 160 mm/s, the corresponding Ia firing rate being 260 impulses/s. This was the same afferent as in Fig. 4, so it is unlikely that a very powerful fusimotor effect was involved in this cycle. However, the extremely high firing rates seen in some cycles where stretch rates could not be obtained suggest that dynamic drive should not be ruled out.

Co-contraction about a joint. As alluded to in the introduction, α - γ co-activation was sometimes seen when agonist-antagonist contractions about a joint resulted in virtually isometric conditions.

In the record of Fig. 8, the ankle was initially passively dorsiflexed and then re-extended, with the cat lying on its side in a relaxed position. In the second half of the record, the cat stretched out, resulting in an obvious co-contraction of muscles in the forelimbs, neck, torso and hind limbs.

The length record shows that for the duration of increased LG e.m.g. activity, the contraction was nearly isometric. Under these conditions, the firing rate of the ankle extensor Ia increased to 90 impulses/s, i.e. considerably higher than the steady firing rate of 45 impulses/s attained after 10 mm of stretching in the passive part of the record.

A comparison of times of onset of e.m.g. and increased firing rate would not be appropriate in this case, as the e.m.g. may not have been that of the

receptor-bearing muscle, and there may have been significant differences in onset times between members of the triceps surae group.

Dorsal femoral (hamstring) Ia's. The discharge behaviour during stepping of Ia's of the bi-articulate hamstring group (knee flexors, hip exten-

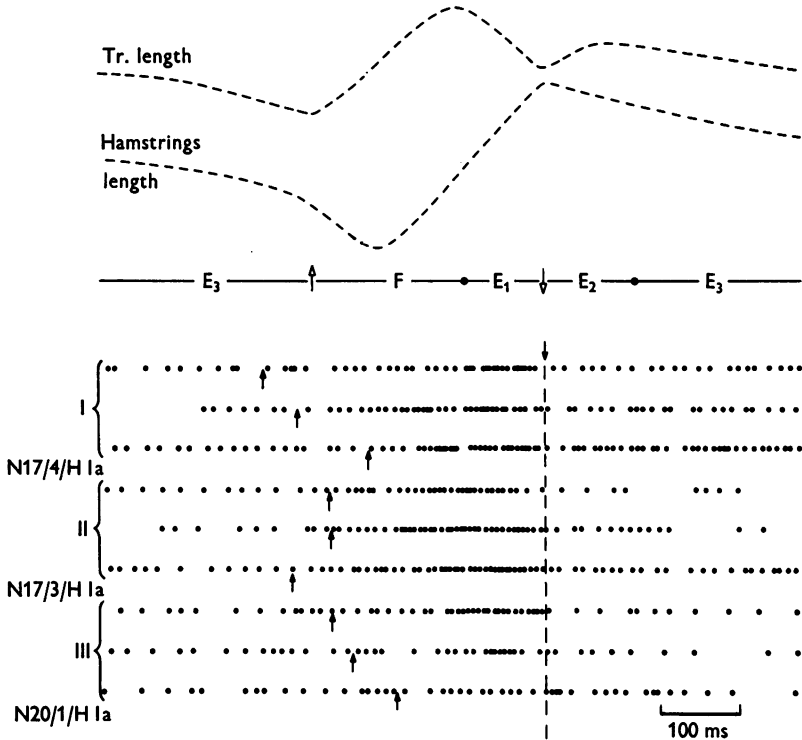


Fig. 9. Firing patterns of three bi-articulate hamstring Ia's, (I, II and III) in each case for three step cycles. Spike trains represented as horizontal rows of dots. Times of foot lift-off and contact shown as upward and downward arrows respectively, these being taken from the ankle extensor length record. Hamstring lengths estimated from the latter. Note high discharge rates during (predominantly) passive stretching in F and E_1 phases. Maintained discharge during E_3 indicates moderate fusimotor drive.

sors) was described in a previous report (Prochazka *et al.* 1976a). Ten such afferents have now been studied in 8 cats. Fig. 9 shows the firing patterns of three of these afferents, in each case for three step cycles.

In the present study, only the length of the ankle extensors was monitored. However, from the data of Goslow, Reinking & Stuart (1973) estimates were made of the corresponding length changes of the hamstrings.

The main features of the firing behaviour of hamstring Ia's during step-

ping were so uniform and consistent that no particular ordering was indicated for Fig. 9. The hamstrings are stretched more rapidly than the ankle extensors during stepping (Goslow, Reinking & Stuart, 1973). The high discharge rates attained during stretching in F and E_1 (often surpassing 250 impulses/s) are consistent with this higher rate of stretching.

The main period of e.m.g. activity of this muscle group occurs during a 200 ms period centred around foot lift-off (upward arrows). The Ia firing rate is usually somewhat elevated during this time, but never approaches that attained in the predominantly passive lengthening phase.

DISCUSSION

Active vs. passive Ia discharge. Comparing Ia activity during active and simulated stepping revealed that fusimotor drive to ankle extensor spindles probably occurred mainly, if not exclusively, during the E_1 , E_2 and E_3 phases. A similar comparison has been made for stepping in the decerebrate cat between the firing patterns of an ankle extensor Ia before and after selective fusimotor blockade (Severin, 1970, fig. 1). The decerebrate recordings are remarkably similar to those in our conscious animals and indicate that the timing of fusimotor drive to ankle extensor spindles during stepping is essentially the same in conscious and decerebrate cats.

In both cases, functional de-efferentation of the spindle abolished the discharge normally seen during muscle shortening in the E_1 phase and greatly diminished discharge during E_2 and E_3 . Discharge during the second half of F was largely unchanged. In the curarized spinal cat treated with DOPA and nialamide, γ -motoneurons to LG have been shown to fire in the same phases of 'fictive' locomotion as LG α -motoneurons (i.e. equivalent to E_1 , E_2 and E_3) and indeed to start firing some 150 ms before α -onset (Sjöström & Zangger, 1975). In rhythmical 'locomotor' contractions of gastrocnemius in the decorticate cat, both static and dynamic fusimotor coactivation has been implicated (Perret & Berthoz, 1973).

It was previously noted that ankle extensor Ia firing often abruptly decreased towards the end of E_1 , even at constant velocities of shortening (Prochazka *et al.* 1976*a*). This was again seen in the new material (e.g. Fig. 1*B*) and is also clearly evident in Severin's (1970) recording. This would be consistent with a simultaneous co-activation of static and dynamic fusimotor fibres at the peak of flexion (end of F), as the static effect would be expected to dominate over the dynamic effect for at least the first 25 ms (Crowe & Matthews, 1964; Smith, 1966; Bessou & Pagès, 1975).

An alternative explanation for these pauses is that localized spindle unloading occurred within the muscle as a result of the very first

extrafusional contractions (Burg *et al.* 1976; Binder, Kroin, Moore, Stauffer & Stuart, 1976). The question might possibly be resolved by comparing the potency of intrafusal and extrafusal contractions on Ia discharge during muscle shortening in acute preparations.

Advance in F-phase response. A phenomenon which might be involved in many movements of a rhythmical nature was uncovered by the comparison between active and simulated stepping. This was the temporal advance of Ia discharge to passive stretching after an apparent α - γ coupled shortening contraction (Fig. 1).

In acute experiments in which length changes similar to those of Fig. 1A were applied after a preceding period of fusimotor stimulation, almost identical (up to 40 ms) temporal advances were seen in the onset of Ia firing in response to the subsequent stretch (J. E. Gregory, A. Prochazka and U. Proske, unpublished). The time course of the fusimotor after-effect suggested that the advance resulted mainly from the slow completion of intrafusal relaxation (Bessou, Laporte & Pagès, 1968; Lewis & Proske, 1972).

Goslow, Stauffer, Nemeth & Stuart (1973) recognized that preceding fusimotor drive during the E-phases would have some effect on the Ia responses to stretch in the F-phase, but they felt that stiction and viscoelasticity were potentially more powerful influences.

As mentioned earlier, it is unlikely that strong fusimotor drive extends into the F-phase of active stepping. It is not impossible that the temporal advance and subsequent firing pattern could be the result of an on-going low level of static and/or dynamic drive. However, it seems probable that fusimotor activity during the E-phases would in any case have the effect of advancing the response during F.

It is important to realize that many movements involve discrete contractions of muscles, which result in their shortening, followed sooner or later by their being passively stretched by the action of their antagonists. Assuming that the original contractions are α - γ coupled, the fusimotor after-effects would ensure a large temporal advance in Ia discharge for immediately ensuing stretches, and initial burst responses for more delayed stretches. In servo-loops, phase advances in the feed-back pathway generally have the effect of damping and stabilizing the response of the servo to rapidly changing inputs (Matthews, 1972; Goodwin, Hulliger & Matthews, 1975). It should also be stressed that the observed advances are quite large compared to nerve conduction delays, and could well be used to compensate for the latter.

At a segmental level, the sudden increase in ankle extensor Ia activity at the start of F could, via Ia interneurons, reciprocally inhibit the ankle flexors, which at this time are maximally active (Engberg, 1964). Two further factors point to a relative

inhibition of the flexors: (1) ankle extensor activity ceases before F, and with it, presumably, the recurrent inhibition of the above-mentioned Ia interneurons (Hultborn, Jankowska & Lindström, 1971); (2) the flexors' own Ib afferents can be assumed to be firing maximally at the start of F (Houk, Singer & Henneman, 1971; Stephens, Reinking & Stuart, 1975), whereas their spindles would tend to be unloaded.

Engberg's records do indeed show a reduction in tibialis anterior e.m.g. after the onset of flexion, although an analysis of many more step cycles would be needed to confirm this point. Supraspinal and propriospinal influences could swamp any such inhibition (Aoki & McIntyre, 1975; Miller & Van der Burg, 1973) and it may be instructive to first look for the effect in decerebrate or spinal locomotor preparations.

The above deductions were made on the basis of comparing Ia responses during active and simulated steps. It should be mentioned that more accurate simulations would reduce uncertainties in the interpretations. Cody, Harrison & Taylor (1975) have tape-recorded jaw angle variations during chewing in cats and have used these taped signals to drive an electromagnetic device to reproduce faithfully these variations in other anaesthetized cats.

A similar arrangement has now been developed by the present authors, using the signal telemetered from the implanted length gauge as the feed-back signal for the electromagnetic device. In this way, length variations of the triceps muscles recorded during stepping have been immediately reproduced in the same cat during brief anaesthesia. It is anticipated that this technique will allow the passive simulation of a full repertoire of active movements, whilst recordings from a given afferent are maintained.

Load compensation. Light thrust applied to the animal's back was clearly a very strong stimulus to fusimotor activity. Whether the high Ia firing rates should be looked upon as part of a 'load compensation response' or whether they were involved in general arousal is debatable (Granit, 1975).

Strictly speaking, load compensation refers to the stabilization of position in the face of changes in tension: the function of a length servo (Merton, 1951). From the e.m.g. and length changes in Fig. 4, it would seem that the efficiency (gain) of load compensation in this situation was low. However, it has been shown by Hammond (1956) and Newsom Davis & Sears (1970) that gating of reflex responses is strongly influenced by previous instruction and volition. The e.m.g. responses would clearly depend heavily on centrifugal drive, which would in turn depend on the way in which the cat intended to respond to back thrust (e.g. by passively yielding, actively extending, etc.). Nichols & Houk (1976) have proposed that motoneuronal output might change only when the mechanical stiffness presented by the muscle fails to conform to the reference, or regulated stiffness.

At first sight, the lack of a large increase in e.m.g. to parallel the increase

in Ia discharge would seem to argue against α - γ co-activation. However, other factors are involved. It is possible, for example, that the e.m.g. activity between the dashed lines resulted in part from a stretch reflex evoking activity in a muscle that would otherwise have fallen silent. Furthermore, assuming that the recruitment of only one or two fusimotor fibres need be invoked to account for the high Ia firing rate (as argued above), a co-recruitment of a small number of α -motoneurons would not significantly increase the amplitude of the mass e.m.g.

Knee flexor responses to paw-pulling, being powerful in preventing significant movement, and occurring in a very reproducible manner, are probably better examples of load compensation. However, the length variations of these muscles were not monitored. As mentioned above, the firing rate of knee flexor Ia's increased in parallel with the flexor e.m.g. during this manoeuvre, which is consistent with α - γ co-activation.

One important ramification of the loading experiment relates to the effect of spine fixation in decerebrate and spinal locomotor preparations (Severin *et al.* 1967). As previously pointed out by Goslow *et al.* (1973): 'fixation of the lower spine in the mesencephalic cat would tend to limit full completion of the F phase of the step and prolong the E₂ phase'. It is exactly this latter effect which gave rise to the very high Ia discharge rates of Fig. 4A.

It is, of course, more than likely that the fusimotor drive in the conscious cat was at least in part cortically mediated (Vedel, 1973). However, the fact remains that the only significant difference between the behaviour of ankle extensor Ia's during the step cycle in the conscious and in the mesencephalic preparation is the much higher discharge rate during E₂ and E₃ in the latter (Prochazka *et al.* 1976a).

If an unintended fusimotor - mediated load compensation response is indeed present in this preparation, this should at least be taken into account when interpreting those studies on the activity during locomotion of central structures known to be influenced by spindle afferents (for review, see Wetzel & Stuart, 1976).

Free-fall and landing. In man, tendon and H reflexes in the ankle extensors are greatly reduced during unexpected free falls (Matthews & Whiteside, 1960). This would be entirely consistent with the reduction in ankle extensor Ia discharge evident in our recordings (Fig. 5).

The decrease in firing rate could be due to reduced fusimotor drive, or to a slight unloading of the receptors as a result of localized extrafusal shortening (Matthews & Whiteside, 1960; Burg *et al.* 1976; Binder *et al.* 1976).

In any case, the large increase in e.m.g. of the extrafusal muscle is apparently not accompanied by any increase in fusimotor drive. Similar

independence in the control of α and γ motoneurons has been demonstrated in the decerebrate cat by cooling or ablating the anterior lobe of the cerebellum (Granit, Holmgren & Merton, 1955).

Relative Ia quiescence during the fall may seem surprising in the light of the parallel, and strongly excitatory influence of vestibulo-spinal pathways on α and γ_s motoneurons (Grillner, Hongo & Lund, 1969). However, it seems that only the early phase of the α -motoneuronal response to sudden drops is strongly dependent on vestibular activity (Melvill Jones & Watt, 1971*b*; Greenwood & Hopkins, 1976; Watt, 1976). Furthermore, the long and variable e.m.g. latencies in this early phase argue against a direct vestibulo-spinal response, and point to a polysynaptic pathway with possible corticofugal and other supraspinal participation (Watt, 1976; Gernandt & Gilman, 1959).

The very high discharge rates observed after foot contact might be expected to give rise to a strong functional stretch reflex in the extensors, and a corresponding reciprocal inhibition of the flexors. In humans, a significant functional stretch reflex is apparently absent, both for self-initiated and unexpected drops (Melvill Jones & Watt, 1971*a, b*; R. Herman, personal communication). However, our own observations on averaged LG e.m.g. responses aligned with the moment of foot contact suggest a strong functional stretch reflex after landing in the cat (unpublished observations). Indeed, in one case where similar averages were made of the human recordings (Melvill Jones & Watt, 1971*a*, fig. 8), the e.m.g. amplitude was still significantly high at the previously determined latency of the functional stretch reflex (119.5 ms). Furthermore these authors considered that the e.m.g. responses observed during repetitive hopping indicated strong functional stretch reflexes.

Fromm & Noth (1976) have predicted a facilitation of homonymous dynamic fusimotoneurons after landing from a fall. In the present recordings, the high dynamic sensitivity evident after landing may indeed have resulted from such a facilitation, but it should be stressed that dynamic fusimotor effects have a relatively slow onset (Bessou *et al.* 1968).

In terms of function, it should be pointed out that the lack of increased fusimotor drive to extensor Ia's during the fall would make available a larger range of response after landing. This would ensure rapid and powerful reflex compensations for wrongly predicted supporting responses of the landing surface.

Placing reaction during walking. The 'locking' of the ankle for the first 100 ms of the placing reaction is seen as essential if the obstacle is to be surmounted with as little disturbance as possible. The delay would allow the knee flexors to move the foot backwards and upwards relative to the forward direction of trunk movement.

It is clear from Fig. 6A that the first LG e.m.g. response was not caused by Ia excitation. This further supports the contention of Forssberg *et al.* (1975) and Duysens & Pearson (1976) that the placing reaction is largely initiated by cutaneous input.

The power of the cutaneous response becomes apparent when it is realised that the decrease in ankle extensor Ia discharge is probably paralleled by an increase in flexor Ia discharge, both of which would tend to inhibit LG motoneurons.

Paw shaking. The generation of decerebrate and spastic clonus has been attributed to high Ia dynamic sensitivities resulting from an elevated dynamic fusimotor drive (Granit, 1969; Szumski, Burg, Struppler & Velho, 1974). Granit considered that Ia discharge rates exceeding 400 impulses/s were 'a step on the way toward a clonic response'.

It is clear from Fig. 7 that such Ia discharge frequencies can be expected in the normal conscious cat. Furthermore, the rhythm of oscillation in Fig. 7 (10 Hz) is the same as that of decerebrate clonus (Granit, 1969). It seems likely that the reflex loop in the decerebrate is normally on the verge of instability (the underlying Horsley-Schäfer rhythm of 10 Hz being the resonant frequency). Mechanical or neural transients can be shown to tip the balance into regenerative oscillation (clonus). It does not seem unreasonable to assume that in the conscious animal, the nervous system could utilize this mode of operation of the myotatic loop by appropriate reflex facilitation.

The deafferented spinal cord is capable of generating a 'fictive' scratching rhythm (Deliagina *et al.* 1975; Arshavsky, Gelfand, Orlovsky & Pavlova, 1976), but the frequency in this case is considerably lower (4 Hz), which suggests a different underlying mechanism.

According to Hagbarth (1973), clonus can occasionally be initiated by vibration in normal subjects. The present results further suggest that 'clonus' may in fact be part of the normal repertoire of movements of an animal.

Co-contraction about a joint. The responses of Fig. 8 give a clear example of α - γ co-activation in a situation not specifically covered by 'length servo' hypotheses. Many movements result from slightly unbalanced co-contractions of agonists and antagonists. This example should therefore serve as a reminder that large modulations in Ia firing rate do not necessarily imply 'misalignments'.

Dorsal femoral Ia's. The importance of passive stretch to Ia responses in stepping is again highlighted in Fig. 9. Instantaneous firing frequency records did not reveal 'initial burst' responses such as those seen in ankle extensor Ia's. This could well be explained by the persistence of fusimotor drive after the beginning of stretch (Brown, Goodwin & Matthews, 1969).

The present results further confirm the pattern of discharge of dorsal femoral Ia's previously described for the step cycle of the conscious cat (Prochazka *et al.* 1976a).

Concluding remarks. Two general principles seem to underly the Ia discharge behaviour we have observed. Firstly, passive length changes of the receptor-bearing muscles usually result in large and functionally significant changes in Ia discharge frequency. Secondly, there is apparently a considerable independence in the control of mammalian α -motoneurons and fusimotoneurons, which allows their respective contributions to be made appropriate to a given movement.

Clearly the Ia responses seen during stepping tend to conform to the ideas of servo-assistance and α - γ co-activation. It is equally evident, however, that the impressive Ia stretch responses in these and other movements must be included in any theory of α - γ interaction.

It may indeed be instructive to treat different classes of movements separately, as has been attempted in this paper. It seems very likely that in the face of different requirements, the nervous system would not restrict itself to any one strategy of α - γ control. For example, it has been argued above that even the inherent instabilities of the stretch reflex might be utilized in the generation of oscillatory movements. Thus by taking into consideration the type of movement as well as the afferent and efferent responses, certain apparent contradictions in the literature may be resolved.

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