

TENDON ORGAN FIRING DURING ACTIVE MUSCLE LENGTHENING IN AWAKE, NORMALLY BEHAVING CATS

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SUMMARY

1. Recordings were obtained of the discharge of single tendon organ (Ib) and muscle spindle (Ia) afferents of the ankle extensor muscles during movement in normal cats.

2. During very slow, smooth increases and decreases in muscle force, Ib afferents showed from one to five stepwise changes in firing rate, attributable to the recruitment of motor units inserting into the receptor capsule.

3. These 'recruitment steps' in Ib firing rate became smoothed and tended to merge during faster variations in muscle force, and were rarely discernible in normal movements such as slow stepping.

4. Rapid imposed stretches resulted in Ib firing patterns which fitted well a dynamic function of whole muscle force.

5. Comparisons were made between the responses of Ib and Ia afferents during rapid, imposed muscle stretch. The segmentation of discharge typical of Ia afferents was not present in Ib afferents, despite segmentation of the e.m.g. of the receptor-bearing muscles. This would imply that Ib afferents exert a rapidly fluctuating reflex action against a relatively steady background of Ib input.

6. Ankle extensor Ib firing during stepping was characterized by feeble firing during the swing phase and substantial, smoothly modulated firing during the stance phase.

7. Taken together with previous chronic recordings, the data support the view that the ensemble of Ib afferents from a muscle signals a dynamic, non-linear function of whole muscle force over a wide range of normal movement.

INTRODUCTION

Compared to muscle spindle afferents, tendon organ afferents have received scant attention in published studies on afferent firing during voluntary movement. To our knowledge, only two records of presumed tendon organ firing during voluntary muscle contraction in man have appeared in the literature (Vallbo, 1970, 1974). Data from chronic recordings in normal cats have shown that, as expected from acute studies (review: Proske, 1981), tendon organ firing is usually closely coupled with e.m.g. activity of the receptor-bearing muscle (review: Prochazka & Hulliger, 1983). However, two specific questions about tendon organ firing, both arising from human

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neurography, have remained unanswered. First, during smooth increases in muscle force, do tendon organs show smooth increases in firing rate (as reported by Vallbo (1970)), or stepwise increases related to motor unit recruitment (as reported by Vallbo (1974) and Crago, Houk & Rymer (1982))? Secondly, do tendon organs respond with bursts of discharge during rapid muscle stretch as do muscle spindle primary afferents (Tracey, Walmsley & Brinkman, 1980; Hagbarth, Hägglund, Wallin & Young, 1981; Prochazka & Wand, 1981)?

Both questions are relevant to any over-all theory of the control of movement. Assuming, for example, that tendon organs had a significant reflex action on α -motoneurons, stepwise increases in tendon organ firing would tend to limit the accuracy of finely graded muscular contractions. If tendon organs responded with bursts of discharge similar to those of Ia afferents during rapid muscle stretch, this could have a considerable bearing on the interpretation of the bursts of e.m.g. in response to this stimulus, studied so intensively in recent years.

We shall present evidence from chronic recordings in normal cats that first, tendon organs do indeed exhibit 'recruitment steps' in their firing rate, but that these are generally seen only in slowly varying contractions. Secondly, the tendon organs in our sample differed considerably from Ia afferents in that they showed very little tendency to fire in bursts during rapid muscle stretch. This would imply that Ia afferents exert a rapidly fluctuating reflex action on spinal motoneurons against a relatively fixed background of Ib input during rapid muscle stretch.

METHODS

Detailed descriptions of the afferent recording technique have appeared elsewhere (Prochazka, Westerman & Ziccone, 1976; Prochazka, 1984), and so only a summary is presented here.

Summary. During an aseptic operation under pentobarbitone anaesthesia, four fine ($17\ \mu\text{m}$) wires insulated except for their tips were introduced into L7 spinal root ganglia through small slits in the dura mater. The wires were fixed to the dura with a drop of isobutylcyanoacrylate, and fine connecting cables were passed subcutaneously to a dental acrylic headpiece, along with a flexible silastic catheter from the jugular vein. In order to provide fixation points for externally attached length gauges, miniature pins (1 mm diameter, 3 mm long) were embedded in bone at the ischium, the lateral femoral epicondyle, the tibial tuberosity and the calcaneum. Flexible, nylon monofilaments (0.2 mm diameter, 25 mm long) issuing from these points, emerged percutaneously in line with the knee flexor muscles, the lateral gastrocnemius muscle and the soleus muscle respectively. On recovering from the anaesthetic, the animals showed virtually no signs of noticing the small implants and no evidence of discomfort.

Recording sessions

Starting 2 days post-operatively, a small capsule containing two FM 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 of single afferent fibres could now be recorded. Surface or needle electrodes were used for e.m.g. recordings. Muscle length was monitored with length gauges attached externally to the percutaneous fixation threads. All movements were video-taped.

Afferent identification

The criteria available for identifying afferents non-invasively in chronic microneurography have recently been collected and evaluated (Prochazka & Hulliger, 1983). It emerged that muscle spindle primary afferents may be reliably differentiated from all other afferents on the basis of their responses to muscle stretch applied from 1 to 5 min after i.v. suxamethonium (100–200 $\mu\text{g}/\text{kg}$)

during brief Epontol (Bayer) or thiopentone anaesthesia. The suxamethonium test can also be used to differentiate spindle secondary afferents from intermediate and high threshold tendon organ afferents (Dutia, 1980; Dutia & Ferrell, 1980). However, the remaining one in four tendon organs classified as low threshold (tonic firing at resting muscle length) cannot safely be differentiated from spindle secondary afferents with suxamethonium.

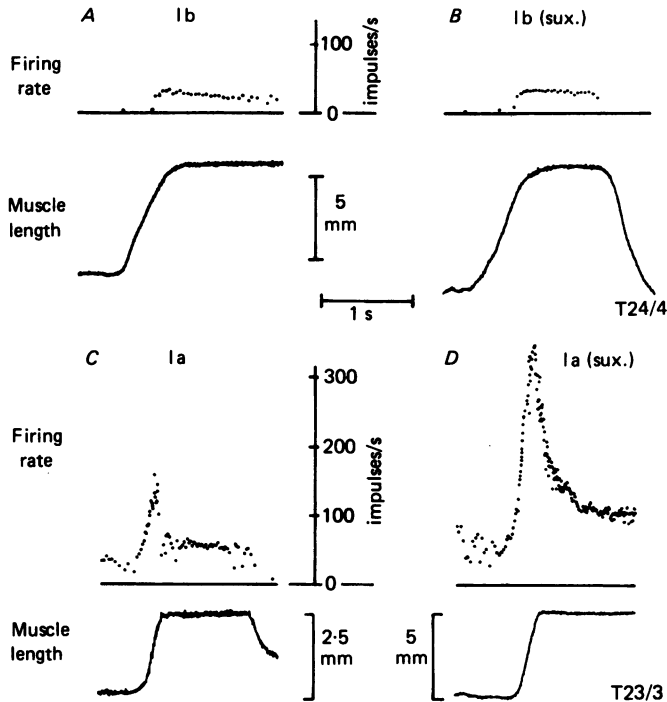


Fig. 1. Classification of afferents with suxamethonium. *A*, response (impulses/s) of a presumed gastrocnemius intermediate-threshold tendon organ afferent to muscle stretch during deep thiopentone anaesthesia. *B*, same 1 min after i.v. suxamethonium (200 $\mu\text{g}/\text{kg}$), showing negligible change in dynamic and position responses. *C* and *D*, same tests as *A* and *B* respectively for a gastrocnemius spindle primary afferent. Note dramatic increases in dynamic and position responses after suxamethonium.

The ten afferents designated as innervating tendon organs in this paper were all of the intermediate or high threshold type. Fig. 1 shows the responses of the lowest threshold afferent in our sample to stretches before (*A*) and after (*B*) i.v. suxamethonium, both tests having been carried out with the cat under deep thiopentone anaesthesia (20 mg/kg i.v. via in-dwelling jugular catheter) immediately following a chronic recording session. There was no significant change in either static or dynamic sensitivity, and so the afferent was classified as a tendon organ. In contrast, Fig. 1 *C* and *D* shows the responses of another afferent (considered again in Fig. 6) to similar tests. The dramatic increase in dynamic sensitivity in *D* clearly identifies the afferent as a spindle primary.

The tendon organ afferents in this study were drawn from taped data from seven cats (T5, T8, T9, T16, T23, T24 and T26). Seven of the ten afferents were identified as above with suxamethonium. In the remaining three, the classification was based on muscle palpation, electrically evoked muscle twitches, and the silencing effect of deep anaesthesia alone (the abolition of muscle tone greatly increasing the thresholds to imposed muscle stretch).

RESULTS

Recruitment steps

Smoothly varying contractions can readily be evoked in normal cats by applying slow, smooth stretches and releases to the limbs. Afferents identified as tendon organs nearly always showed stepwise changes in their firing rates (presumably reflecting

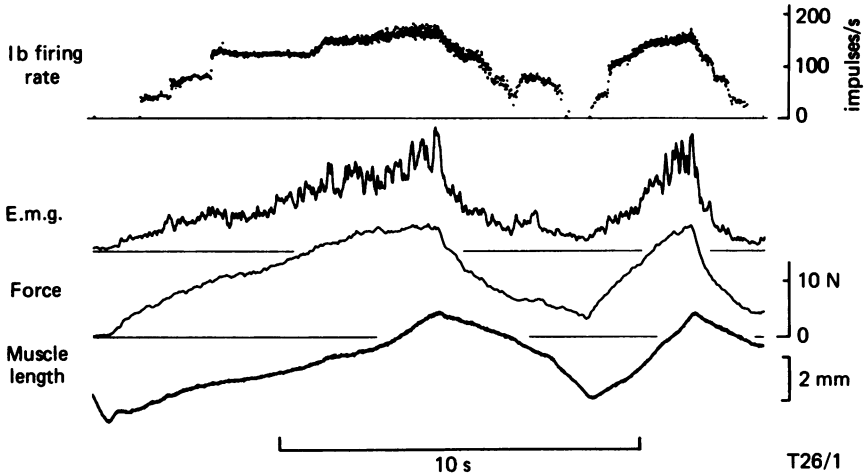


Fig. 2. Discharge of an ankle extensor tendon organ during two imposed flexion-extension movements. Traces from top to bottom: tendon organ instantaneous firing rate; rectified, low-pass filtered ($f_c = 4.5$ Hz, 40 dB/dec) surface e.m.g. from lateral gastrocnemius muscle; force applied to plantar surface of foot near metatarso-phalangeal junction; variation in length of lateral gastrocnemius muscle. Four clear stepwise increments in firing rate occurred in the first (slow) stretch, whereas in the second (faster) stretch such increments were smoothed or tended to merge and so were less distinct. Note the three clear decrements in firing rate in the final slow release.

motor unit recruitment), provided that the force variations were sufficiently slow. The tendon organ afferent of Fig. 2 showed four clear increments in firing rate during the first of two imposed muscle stretches. In the second (faster) stretch, these recruitment steps were smoothed and tended to merge. Stepwise decrements were apparent in both releases, although more clearly in the second.

The force variations were measured with a hand-held force gauge, the element of which consisted of a brass U-shaped former carrying bonded semiconductor strain gauges. The force was transmitted via a 25 mm diameter disk pressed onto the plantar surface of the foot near the footpads. The lever arm from the point of application of force to the ankle pivot was measured to be 60 mm, while the corresponding lever arm for the triceps surae muscles (proximal end of calcaneus to ankle joint) was 15 mm. Thus the peak force generated by the muscles themselves in Fig. 2 was estimated to have been about 80 N, which is 40–45% of the maximal force to be expected from the triceps surae group (Walmsley, Hodgson & Burke, 1978; assuming the lateral gastrocnemius generates the same force as the medial gastrocnemius).

Dynamic responses to rapid stretch

Fig. 3 shows the response of the same tendon organ afferent to four rapid, imposed muscle stretches. Substantial rates of discharge were evident, particularly during the dynamic phases of stretching. The patterns of response seemed superficially to follow closely the time course of force applied near the metatarso-phalangeal junction as

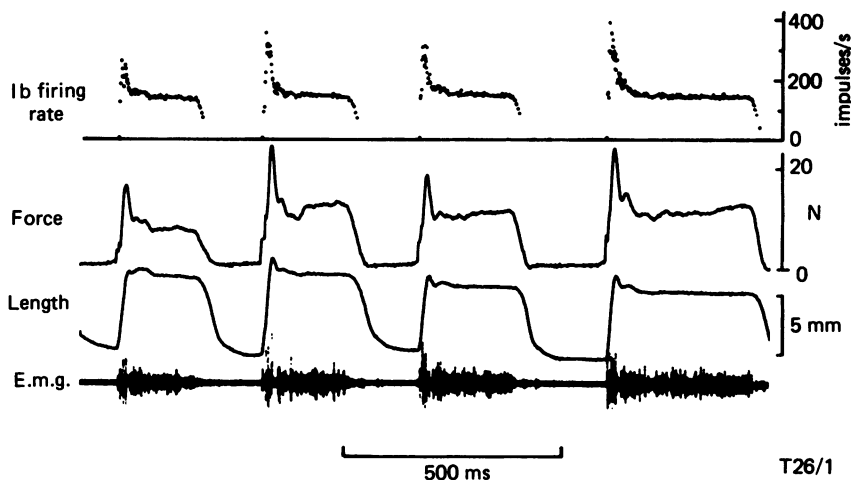


Fig. 3. Same tendon organ afferent as in Fig. 2, responding to four rapid, imposed ankle dorsiflexions. Top to bottom: tendon organ firing rate; force applied to plantar surface of foot near metatarso-phalangeal junction; variation in length of lateral gastrocnemius muscle; surface e.m.g. from lateral gastrocnemius. The dynamic responses of the afferent were much more similar to the force than to the length variations.

described above. On closer inspection, it is evident that some of the force variations during the hold phases of stretch were not mirrored in the afferent firing rate. Furthermore, on expanding the time scale, there was a noticeable phase advance of the peak of afferent firing on the peak force (shown in Fig. 4.).

Previous acute studies have indicated that tendon organ afferents exhibit characteristic transfer functions relating their firing to time-varying functions of muscle force (Houk & Simon, 1967; Anderson, 1974; Crago *et al.* 1982). We tested the two models cited by Crago *et al.* (1982) on our data by playing the force records through filters with the appropriate transfer functions. While both models resulted in improved fits to the time course of afferent firing in the dynamic phase of stretching, the best fits (Fig. 4B) were obtained with a modified version of the Anderson model, namely:

$$H(s) = K \frac{(s + 0.63)(s + 3.14)(s + 60)}{(s + 0.82)(s + 3.88)(s + 210)}$$

where s is the Laplace variable, K is the static gain and $H(s)$ is the tendon organ transfer function in the frequency domain. The high-frequency pole ($s + 210$) was only included in order to suppress noise in the recording. The zero ($s + 60$) was the

singularity most responsible for the phase advance during the rapid phase of stretch, and corresponds to the $(s + 25.1)$ zero in the Anderson model.

Bursting discharge during muscle stretch?

Spindle primary afferents generally fire in well-defined, high-frequency bursts during muscle stretch at speeds above about 1 resting length/s (Tracey *et al.* 1980;

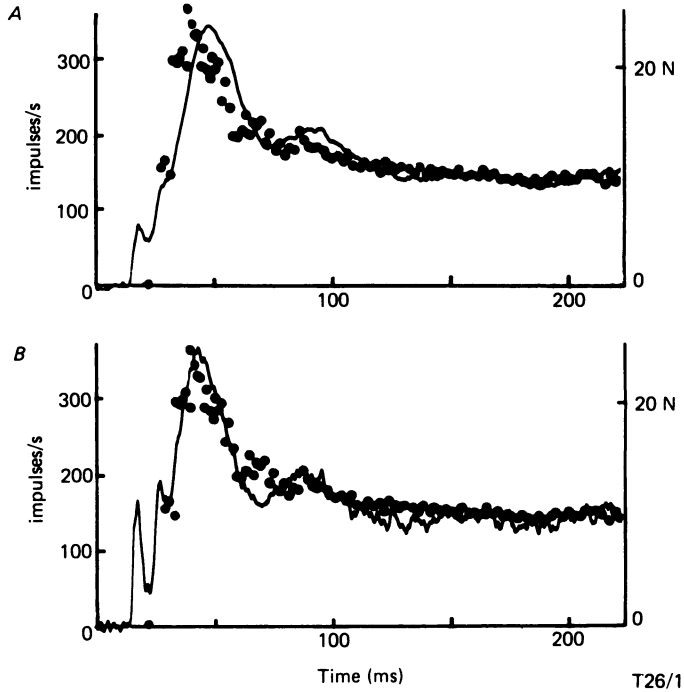


Fig. 4. Second imposed movement of Fig. 2, showing tendon organ firing rate superimposed *A*, on the force record *B*, on a trace obtained by filtering the force record according to a transfer function similar to the Anderson (1980) model of tendon organs.

Prochazka & Wand, 1981). Fig. 5*B* illustrates this behaviour in a gastrocnemius Ia afferent recorded during a rapid imposed foot dorsiflexion, and shows the accompanying segmentation of the gastrocnemius e.m.g. The tendon organ afferents in our sample had a very different form of response, as shown by the afferent of Fig. 5*A*. While there was a noticeable phasic peak of firing rate, this was followed by fairly steady firing rather than by bursts of discharge.

The afferent of Fig. 5 had the lowest threshold and reached the highest firing rates in response to muscle stretch of the ten tendon organ afferents in our sample. The responses of two higher threshold tendon organs to similar imposed movements are shown in Fig. 6*A* and *C*. By way of comparison, Fig. 6*B* and *D* shows two further spindle primary afferent responses under similar conditions. The tendon organ of Fig. 6*A* responded to the stretch with a low and fairly steady firing rate. The response of the afferent in Fig. 6*C* came the closest to a bursting pattern of all the tendon organs

in our sample. Yet compared to any of the eight spindle primary afferents observed with this form of stimulus, the bursting tendency was minimal. The spindle primary response of Fig. 6D is illustrated here to show that the interval between bursts may differ from one spindle afferent to another (as well as being dependent upon the maximal speed and indeed the over-all time course of muscle stretch (as shown previously: Prochazka & Wand, 1981)).

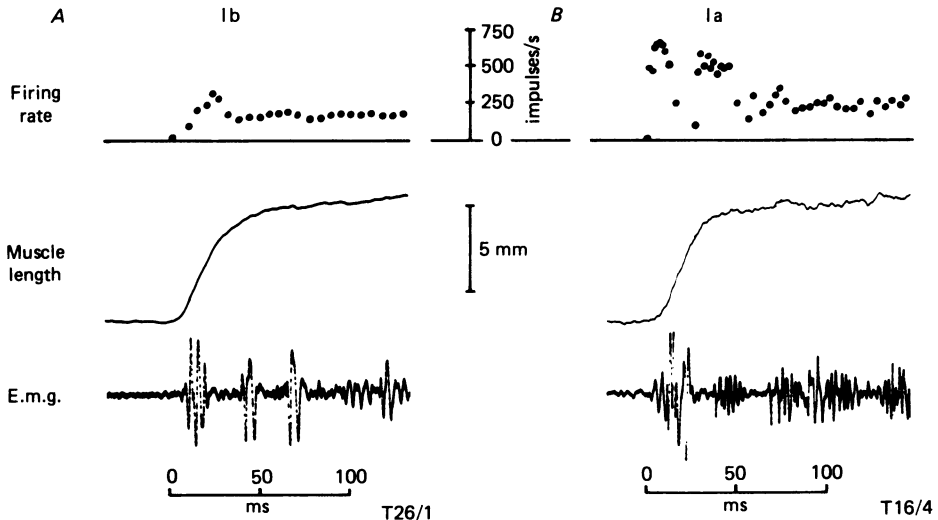


Fig. 5. Rapid, imposed muscle stretch. *A*, response of the same tendon organ afferent as in Figs. 2–4 to a rapid imposed ankle dorsiflexion. There was little tendency for bursting in the afferent response, although the e.m.g. showed clear segmentation. *B*, response of a gastrocnemius spindle primary afferent to a similar imposed movement. There was a strong bursting tendency, the first phase encompassing the peak speed of stretch (approx. 250 mm/s: equivalent to 2.4 resting lengths/s, resting length 105 mm measured from lateral femoral epicondyle to calcaneum).

Tendon organ firing during stepping

Surprisingly, there are only eight published records of tendon organ afferent discharge during normal locomotion: four reported by Loeb & Duysens (1979) and Loeb (1980) and four by Prochazka *et al.* (1976) and Westerman, Prochazka & Ziccone (1976). None of these records included the monitored length variations of the receptor-bearing muscle, and so phases of muscle lengthening and shortening had to be estimated qualitatively.

Fig. 7 shows the firing of a tendon organ afferent recorded in three step cycles along with the e.m.g. and length variations of the receptor-bearing muscle (lateral gastrocnemius). Each step was recorded during normal walking across a flat surface. The three records were selected from many similar segments as being representative of the range of both length variations and afferent firing. Video recordings were checked to exclude abnormal steps. The afferent of Fig. 7 typically fired two or three times just prior to foot touch-down. In the subsequent yield phases there was usually a phasic peak of firing, followed immediately by fairly steady firing, the rate of which

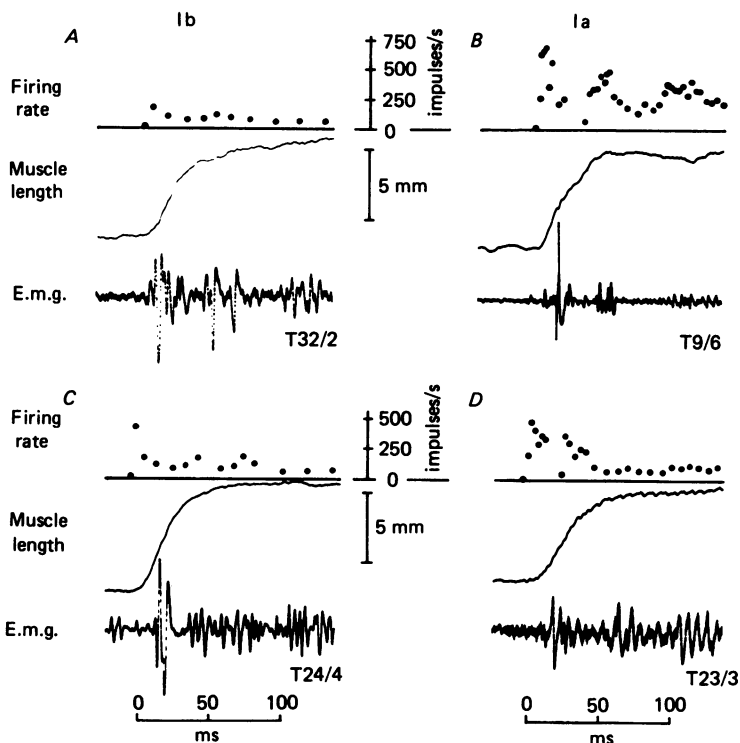


Fig. 6. Rapid, imposed muscle stretch. *A* and *C*, higher threshold gastrocnemius tendon organ afferents responding with low rates of firing to rapid ankle dorsiflexion. *B* and *D*, spindle primary afferents of gastrocnemius exhibiting segmented discharge during similar muscle stretches. The pauses between bursts were significantly different in the two spindles.

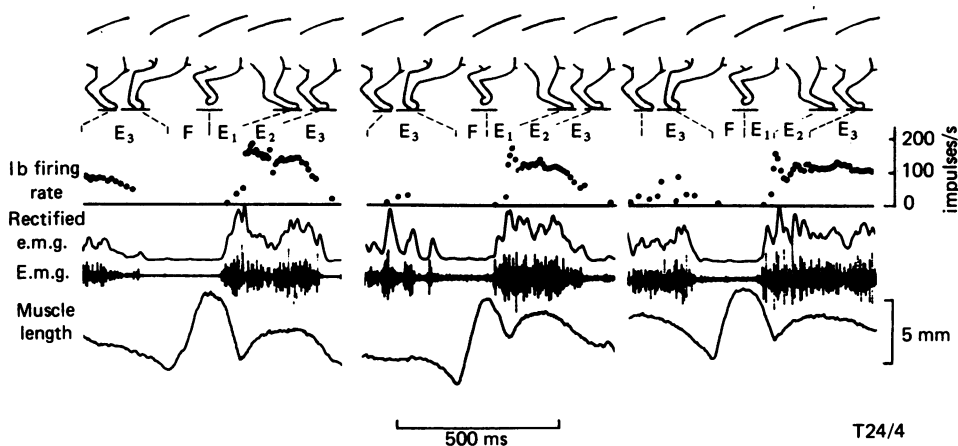


Fig. 7. Tendon organ firing during locomotion. Three separate step cycles showing from top to bottom: phase of cycle; firing rate of lateral gastrocnemius tendon organ; rectified, low-pass filtered lateral gastrocnemius e.m.g. (Butterworth, $f_c = 22$ Hz); lateral gastrocnemius e.m.g.; lateral gastrocnemius muscle length. The firing rate approximated fairly closely the e.m.g. during the stance phase of the cycles, and there was little evidence of bursting discharge or recruitment steps.

declined slowly towards the end of the stance phase of each step cycle. Clear recruitment steps in firing rate of the sort shown in Fig. 2 were very rarely seen during stepping, but were sometimes observed in stance, usually in association with slow postural shifts. Firing during the F phase only occurred occasionally in the afferent of Fig. 7 (e.g. third step cycle). Feeble F-phase firing (maximally 4 or 5 impulses) was seen in two other Ib afferents, and was more likely to occur in crouched gait.

DISCUSSION

Recruitment steps. The stepwise increments in firing rate of the tendon organ in Fig. 2 are qualitatively similar to those recorded in a presumed tendon organ in man (Vallbo, 1974), and quantitatively comparable to those recorded in the decerebrate cat by Crago *et al.* (1982). In agreement with the latter authors, we found that the number of discernible increments was typically two or three, and in our sample maximally five. Crago *et al.* (1982) pointed out that this was far less than the ten to fifteen motor units estimated to lie in series with ankle extensor tendon organs, and suggested that this might be due in part to simultaneous recruitment of two or more motor units resulting in skipped or combined steps in Ib firing rate. Indeed Fig. 2 demonstrates this phenomenon clearly, in that steps present in the Ib firing rate in the first stretch evidently merged in the second stretch. The rate of change of torque was the chief determinant of whether recruitment steps would be noticeable. With rapid variations in torque (above about 0.5 Nm/s about the ankle) Ib firing rates showed an increasing tendency to follow smoothly the time course of applied torque. In our experiment this was presumably due in part to the dynamic effect on muscle force of changes in muscle length.

Although in conscious cats muscle spindle afferents not infrequently show abrupt transitions in the regularity of their firing or, much more rarely, single stepwise increments in firing rate, a staircase-like pattern such as that in Fig. 2 has not, to our knowledge, been observed in spindles. Indeed, the presence of this pattern in response to very slow muscle stretch in the normal cat is a helpful preliminary indication that the afferent is a tendon organ. It would be most useful if this dichotomy between spindles and tendon organs were clarified on a large sample of afferents (in the decerebrate cat, for example), as it might serve to complement, if not replace, the suxamethonium test, and provide a means for differentiating between low-threshold organ afferents and spindle secondary afferents.

Rapid stretch. The tendon organ illustrated in Fig. 3 fired with a time course reasonably similar to that of the force applied to the foot, even though, in addition to the receptor-bearing muscle, at least two synergists were likely to have contributed to the reaction. Slow, small variations in force during the hold phases of stretch were not reflected in the Ib discharge. Presumably these force variations were not accompanied by recruitment or de-recruitment of motor units affecting the afferent in question (Crago *et al.* 1982).

We were surprised to find that the dynamic nature of the tendon organ response could be clearly detected with the filter analysis illustrated in Fig. 4. The inertia of the bones and tissues might have been expected to dampen the transmission of force to the tendons, and effectively counteract the high-frequency zero in the force-response

transfer function. Evidently the active force generated by the extensor muscles outweighed the inertial forces sufficiently to allow a reasonable fit with the Anderson model.

Bursts during muscle stretch? Our data indicate that, unlike spindle primary endings, tendon organ afferents have little or no tendency to fire in bursts during rapid muscle stretch (in the range 1–5 resting lengths/s).

Figs. 5 and 6 also reveal large disparities in mean and peak firing rates between spindle primary and tendon organ endings for similar time courses of rapid stretch (mean Ia firing rates in first 50 ms: 360 impulses/s; cf. mean Ib firing rates: 160 impulses/s). Since spindle primary endings outnumber tendon organs approximately in the ratio 3:2 (Barker, 1962), this means that, at least in terms of total impulses/s, the ankle extensor spindle afferents must dominate the group I afferent input to the spinal cord during a rapid muscle stretch.

It has been noted previously that the e.m.g. bursts in response to rapid muscle stretch in man (Hagbarth *et al.* 1981), in the spinal cat (Tracey *et al.* 1980) and in the awake cat (Prochazka & Wand, 1981) follow at reflex latency the bursts of Ia discharge. It is tempting to conclude that the e.m.g. responses (including those at latencies beyond 50 ms) are, at least in part, continuing monosynaptic reflexes. On the assumption that extensor tendon organ afferents reflexly inhibit homonymous (as well as synergistic) muscles (Harrison, Jankowska & Johansson, 1983) the Ib firing patterns of Figs. 5 and 6 would be consistent with this idea. The Ib component of reflex action would be relatively fixed, and at a low level compared to the intensely fluctuating Ia component. On the other hand, it is also apparent from Fig. 6D that some spindle primaries may fire in bursts whose repetition rate is faster than that of the e.m.g. bursts of the parent muscle. In our sample of eight Ia afferents, two showed a marked disparity with the e.m.g. in this respect. A larger sample would be needed in order to decide whether this constitutes a serious difficulty for the argument relating e.m.g. responses directly to Ia afferent responses during rapid stretch. Unfortunately, data from reduced preparations would be of little help, because there would be little guarantee that the fusimotor and reflex set of a conscious animal could be reproduced.

Tendon organ firing during stepping. Tendon organ afferents have received far less attention in chronic recordings than spindle afferents. This is possibly due to the mistaken view that their firing patterns are easily predictable from the e.m.g. and length variations of the receptor-bearing muscles. Fig. 7 provides a reasonably clear picture of the firing of an ankle extensor tendon organ during stepping. The relationship between the firing of this afferent and the e.m.g. is very similar to that of a tendon organ recorded by Loeb (1980). The same general features of response are present, namely two or three discharges (shown from our length traces to have occurred in the E_1 phases) prior to the main sustained firing in the stance phases (E_2 and E_3), little evidence of recruitment steps, and minimal firing during the F phases. The afferent of Fig. 7 was at the low end of the intermediate threshold range, and fired somewhat more rapidly than the afferent illustrated by Loeb (1980). We have observed occasional high threshold extensor tendon organ afferents which only fired 1–5 impulses per step cycle, but the majority showed sustained discharge of the general form seen in Fig. 7.

Goslow, Stauffer, Nemeth & Stuart (1973) simulated the length variations of cat soleus and gastrocnemius muscles during the swing phase of the step cycle. They found that 67 % of Ib afferents responded to a passive stretch mimicking the F phase of a slow walk. Typically, three or four impulses were observed per stretch. In our recordings, three intermediate threshold ankle extensor tendon organs fired occasional impulses during the F phases of slow stepping (e.g. Fig. 7, third trace). The more crouched the gait, the more likely it was to encounter F-phase firing (although this never amounted to more than 4 or 5 impulses). Our observations are consistent with those of Goslow *et al.* (1973), in that the ankle angle at the onset of the F phase was generally in the range 110–130 deg in our cats, which would correspond to a somewhat shorter initial muscle length than in the study of Goslow *et al.* (1973).

The firing during E_1 and in particular the sudden increase at the onset of E_2 (Fig. 7) is perhaps of more functional significance. Muscle spindle primary afferents of the ankle extensors usually fall silent towards the end of E_1 (Prochazka, 1980), so if most tendon organs of these muscles responded as in Fig. 7, net Ib activity might dominate over net Ia activity (Prochazka & Wand, 1980). This situation would suddenly reverse on foot contact, when most ankle extensor Ia afferents fire high-frequency bursts of discharge (Prochazka *et al.* 1976: Prochazka, 1980). This relationship between Ia and Ib firing might well be used by the C.N.S. as a marker for the onset of the stance phase of a step (particularly in view of the surprisingly small role apparently played by footpad afferents in the control of the step cycle (Engberg, 1964)).

Concluding remarks. There is now sufficient evidence in normally behaving cats to support the idea that the majority of tendon organ afferents discharge during movements involving low levels of active muscle force (Houk & Henneman, 1967). Nevertheless, it is apparent from this and previous chronic studies that in terms of mean firing rates, and the depth of modulation of firing, Ia afferents usually outweigh Ib afferents. This is particularly marked in the responses to rapid imposed muscle stretch shown above. Whereas segmentation of Ia discharge will continue to pose problems of interpretation in stretch reflex studies, the further possible complication of the existence of segmented Ib discharge now seems unlikely. As regards the nature of the variable monitored by the ensemble of tendon organs of a muscle, the chronic data support the view of Crago *et al.* (1982) that, recruitment steps notwithstanding, Ib afferents signal a dynamic, non-linear function of whole muscle force over a range encompassing movements involving very low to very high force levels.

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