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TENDON ORGAN DISCHARGE DURING VOLUNTARY MOVEMENTS IN CATS

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SUMMARY

1. The discharge activity of tendon organ afferents was recorded during voluntary movements in cats.

2. The eight tendon organ afferents in our sample all fired during isotonic movements involving active muscle shortening.

3. Firing rates usually exceeded 100 sec^{-1}, even up to the highest muscle shortening velocity observed, 1·8 resting lengths per second (l_r/sec).

4. We suggest that during voluntary, isotonic movements involving muscle shortening at velocities exceeding 0·2 l_r/sec, the net action of muscle afferents on homonymous motoneurones is often inhibition.

5. These observations on tendon organs, taken together with previous findings on muscle spindles, indicate that in normal fast movements the role of the large muscle afferents is to signal dynamic functions of muscle length and force.

INTRODUCTION

It has been suggested recently that in unobstructed movements in which muscle velocities exceed 0·2 resting lengths per second (l_r/sec), the firing rates of mammalian muscle spindles are predominantly modulated by the length variations (Prochazka, Stephens & Wand, 1979). Thus during active muscle shortening at such velocities the firing rates of spindle afferents progressively decrease.

Tendon organ afferents are known from acute studies to discharge at high rates during isometric muscle contractions (Jansen & Rudjord, 1964; Houk & Henneman, 1967). However, it is also known that the faster a contracting muscle shortens, the smaller is the force generated at its tendon, providing that the efferent excitation remains constant (Hill, 1938). Given the difficulty of estimating the inertial, viscous, elastic and contractile components of force in an *in situ* muscle during voluntary shortening contractions, it is extremely difficult to predict the behaviour of tendon organs at different speeds of shortening.

We therefore investigated the discharge behaviour of tendon organ afferents in hind-limb and tail muscles of the cat, during voluntary movements involving muscle shortening velocities ranging from 0 to 1·8 l_r/sec. It will be shown that in our sample

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all tendon organs increased their firing rates during unobstructed shortening contractions, even at the highest velocities of shortening. This is in direct contrast to both primary and secondary muscle spindles, whose firing rates generally drop when the velocity of muscle shortening exceeds 0·2 l_r/sec.

METHODS

Detailed descriptions of the afferent recording technique have appeared elsewhere (Prochazka, Westerman & Ziccone, 1976, 1977; Prochazka *et al.* 1979), and so only a summary is presented here.

Surgery. During one aseptic operation under halothane and nitrous oxide anaesthesia, pairs of fine (17 μm) wires insulated except for their tips were introduced into L7 and 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, miniature pins (1 mm diam., 3 mm long) were embedded in bone at the ischium, the head of the tibia and the calcaneum. Flexible, Teflon-coated wires (0·25 mm diam., 25 mm long) issuing from these pins, 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 6 weeks.

Recording sessions. Starting 1 day post-operatively, a small capsule containing 2 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 trains of single afferent fibres could now be recorded. In the six cats implanted for this study, stable recordings from thirty-four identified afferents were obtained. Most afferents were held for between 6 and 10 hr, but eight could be recorded over a period of days, the maximum being 15 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 extensor, a mercury-in-rubber length gauge was attached to the appropriate percutaneous fixation wires so as to be in parallel with the muscle. 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 recording in the awake animal generally lasted about 1 hr. The movements studied depended on the afferents involved. In the case of knee flexor afferents, advantage was taken of the natural tendency of cats to oppose an externally applied extension of a leg. Recordings could be obtained for a large number of flexion movements of different speeds. An FM cassette recorder (Data Acquisition, type DA 1432-2) 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

The results are drawn from taped recordings from six cats (T3, T5, T6, T8, T9, T11) in which tendon organ afferents were well represented. Of the thirty-four afferents recorded in these cats, the twenty-five which could be identified adequately were distributed as follows: eight skin or hair follicle receptors. Two spindle secondaries: one ankle extensor, one tail abductor. Seven spindle primaries: three ankle extensor, one knee flexor, three tail abductor. Eight tendon organs: two ankle extensor, one ankle flexor, four knee flexor, one hip extensor.

Fig. 1 shows the firing rate of a tendon organ located in a knee flexor. In *B*, the

unitary discharges of the afferent in response to repeated muscle twitches elicited by electrical stimulation through the e.m.g. recording electrode may be seen. The lowest threshold of response was obtained when the electrode tip was judged to be in the biceps femoris muscle.

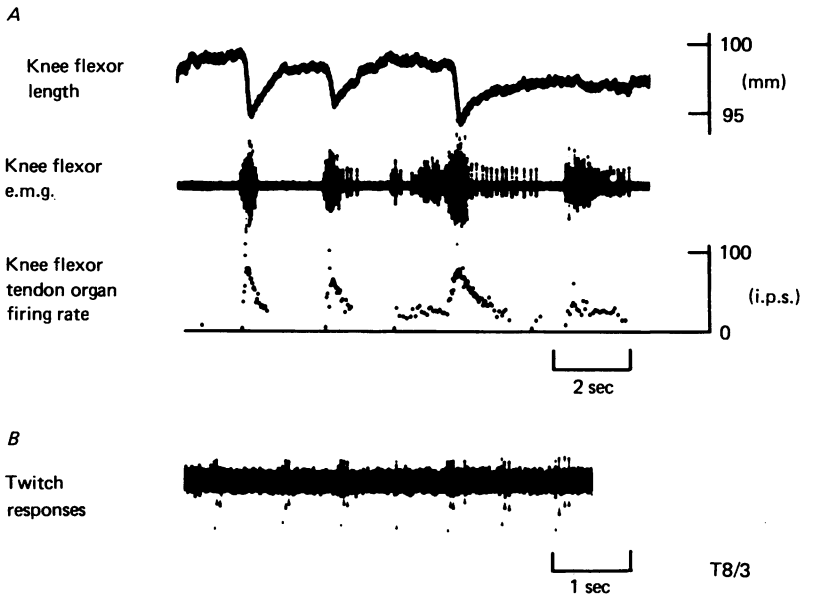

Fig. 1. *A*, firing of a knee flexor tendon organ during three voluntary flexions. Modulation of the firing rate is strongly related to the amplitude of the knee flexor e.m.g. with little dependence on muscle length. Peak firing rates occurred during active shortening. *B*, unitary discharges of the afferent in response to muscle twitches evoked by electrical stimulation through the e.m.g. electrode (large spikes are stimulus artifacts).

In the voluntary flexion movements of Fig. 1*A*, the firing rate of the tendon organ was strongly related to the amplitude of the e.m.g. The modulatory effect of the changes in muscle length appears to have been of minor importance, although the afferent was sensitive to imposed muscle stretch in the awake animal. This highlights the importance of using suxamethonium in the identification of muscle afferents (Prochazka *et al.* 1976). In our experience, a preliminary identification on the basis of palpation and muscle twitches in the awake animal was proved wrong in about 25% of cases, once the suxamethonium test had been applied during subsequent Epontol anaesthesia.

Fig. 2 shows the results of systematic trials on three different tendon organs (*A*, *B* and *C*) involving voluntary movements of increasing velocity. The peak firing rates for a given afferent were similar, whether the velocity of shortening was very low (0·1 to 0·3 l_r/sec) or very high (1·4 to 1·8 l_r/sec). In some of the records (e.g. *C*, 0·2 and 0·8 l_r/sec), it is evident that the afferent fired during the shortening provided that e.m.g. activity was present. Where the e.m.g. activity ceased, but the shortening continued (presumably ballistically), the firing of the tendon organ ceased abruptly, shortly after the cessation of e.m.g.

Similar observations were made in the case of a tendon organ in extensor digitorum longus (an ankle flexor). Recordings from two tendon organs located in ankle extensors also showed that these afferents were active during voluntary shortening contractions, but in these cases, it was not possible to study velocities above 0·8 l_r/sec, as fast voluntary extension movements were found more difficult to evoke.

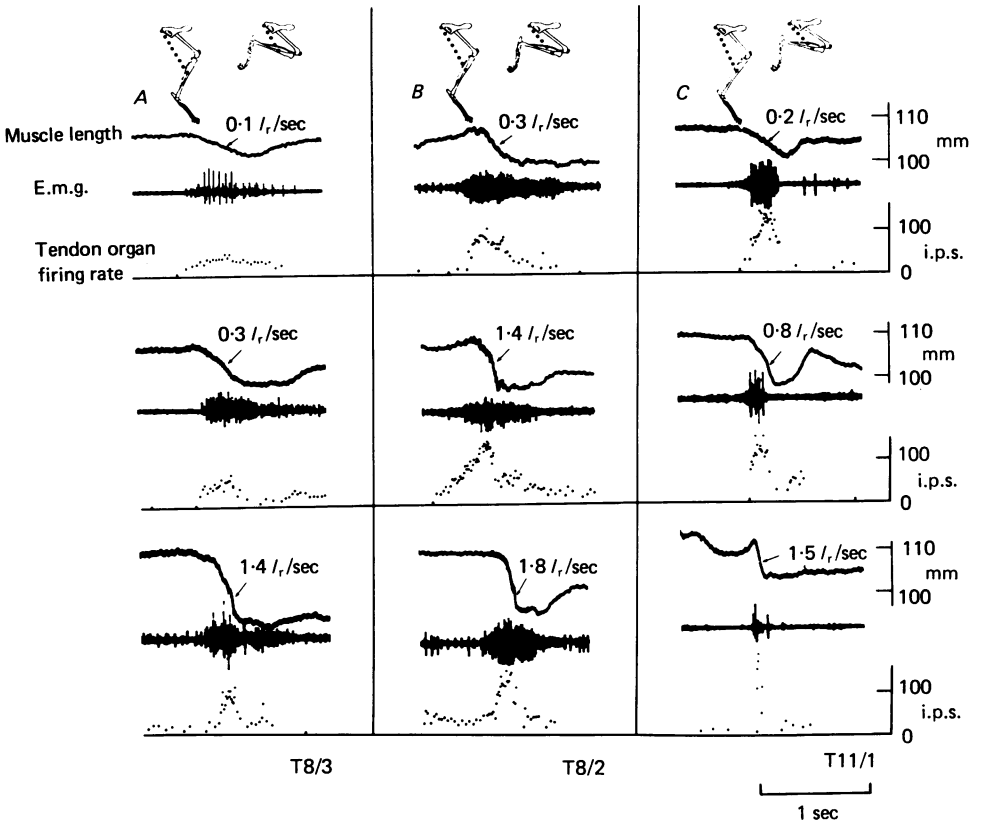

Fig. 2. Firing of three different knee flexor tendon organs (*A*, *B* and *C*), during active knee flexion involving increasing velocities of muscle shortening (as shown by arrows). Peak firing rates occurred during shortening, up to the maximum velocity observed, 1·8 l_r/sec.

DISCUSSION

Tendon organs. In contrast to muscle spindles (Prochazka *et al.* 1979), the knee flexor tendon organ afferents in our sample increased their firing rates during active muscle shortening, up to the maximum muscle velocity observed, 1·8 l_r/sec. We could not study extensor tendon organs beyond velocities of 0·8 l_r/sec, but it has previously been shown that there is little difference in the thresholds of tendon organs in cat ankle flexors and extensors to twitch contractions of the receptor-bearing muscles (Stuart, Mosher, Gerlach & Reinking, 1972), and so it seems reasonable to assume that extensor tendon organs also discharge rapidly at the faster speeds of active shortening.

In the absence of e.m.g. activity, the stretch responsiveness of the tendon organs was low. This is in agreement with the conclusions of Stephens, Reinking & Stuart (1975). Thus the modulation of firing rate of tendon organ afferents seems to be largely a function of the level of motoneuronal discharge in normal voluntary movements.

In this study, we have not attempted to analyse the influence of initial muscle length on the tendon organ responses during subsequent active shortening. Stephens *et al.* (1975) studied the dependence of tendon organ discharge on length changes during contractions of single motor units. When compared to the dependence on the number of active motor units, the length effects were relatively minor. It is therefore probable that tendon organ responses would not be significantly different from those described above, even at very small or very large initial lengths.

The tendon organs in our study showed firing rates in excess of 100 sec^{-1} during unobstructed movements involving active muscle shortening at velocities in the range 0–1·8 l_r/sec. In contrast, the firing rates of muscle spindles usually drop well below 100 sec^{-1} when shortening velocities exceed 0·2 l_r/sec (Prochazka *et al.* 1979). It is generally agreed that inhibition is the primary reflex action of tendon organ afferents on homonymous motoneurones (Lundberg, Malmgren & Schomburg, 1977), whereas the main action of homonymous spindle afferents is one of excitation. Further, the numbers of tendon organs, spindle primary endings and spindle secondary endings in a given muscle are roughly equal (Matthews, 1972). Thus the net action of muscle afferents on homonymous motoneurones during rapid active muscle shortening may well be inhibition, especially at the higher shortening velocities.

To a first approximation, the collective discharge of all of a muscle's tendon organs is a function of the tensile force in the tendon (Stephens *et al.* 1975). Inhibition of homonymous motoneurones resulting from this discharge would tend to cause muscle relaxation, and therefore represents negative force feed-back. Similarly, we believe that, at least for movements involving muscle velocities above 0·2 l_r/sec, the collective discharge of spindle afferents of a muscle is a dynamic function of muscle length (Prochazka *et al.* 1979). Excitation of homonymous motoneurones resulting from this discharge would tend to cause muscle shortening, and therefore represents negative length (and velocity) feed-back. The strength of tendon organ inhibition of homonymous motoneurones is under powerful C.N.S. control (Lundberg *et al.* 1977). Similarly, the relative sensitivity of muscle spindle afferents to length and velocity depends on static and dynamic fusimotor action. Thus the relative gains of length, velocity and force feed-back are potentially under continuous C.N.S. control.

It should be stressed that in pointing out the existence of afferent connexions and firing patterns consistent with negative feed-back of force, length and velocity during voluntary movement, we are not suggesting that all voluntary movements are controlled wholly by a C.N.S. servo. Indeed, may instances could be cited, where servo action would be most inappropriate, and has, in some cases, been shown to be overriden (Newsom, Davis & Sears, 1970; Prochazka, Sontag & Wand, 1978). However, it is equally clear, that segmental reflexes often act to impart to mammalian neuromuscular systems characteristics of response similar to those of servos (Crago, Houk & Hasan, 1976; Nichols & Houk, 1976; Ghez & Shinoda, 1978; Houk, 1979).

In conclusion, the results of this study on tendon organs, taken together with the

results of a similar study on muscle spindles (Prochazka *et al.* 1979) suggest that in movements involving muscle velocities exceeding 0·2 l_r/sec, the afferent responses are consistent with the idea that the peripheral nervous system in cats monitors continuously the length, velocity and force of limb muscles.

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