Exp. Brain Res. 14, 274—292 (1972)

Mechanical Arrangement and Transducing Properties of Golgi Tendon Organs

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Received April 23, 1971

Summary. 1. The mechanical arrangement and transducing properties of Golgi tendon organs in soleus and anterior tibial muscles of anesthetized cats have been studied by noting responses of their Ib afferents to muscle stretch (passive force) and contraction (active force) of small portions of the muscle including functionally isolated motor units.

2. Tendon organs were shown to be arranged both in-series and in-parallel with adjacent muscle fibers. There were gradations in these relations, the tightest arrangements involving the response to contraction of a single motor unit, brisk discharge from an in-series receptor and pause in the stretch-activated firing of an in-parallel receptor. Other arrangements included those in which groups of muscle fibers neither directly in-series nor in-parallel with a receptor were still found capable of influencing its firing pattern. If in-series muscle fibers maintained their contraction while in-parallel fibers were also contracting, the receptor usually responded slightly less actively than it did to the in-series force alone.

3. Tendon organs were found to have a very low threshold to in-series force developed by muscle contraction. Responses were observed to as little as 0.5 gm of twitch tension. Minimum active force thresholds were similar for the two muscles studied, but thresholds to dynamic stretch were lower for anterior tibial receptors. Division of the dynamic stretch threshold by the minimum active force threshold gave a measure of the extent to which each tendon organ was more sensitive to active than passive force. These values (generally less than 50) did not negate the physiological significance of responses to passive stretch.

4. The present data, together with those of Houk and his co-workers (1967, 1971) emphasize that tendon organs can participate in the moment to moment reflex control of normal muscle activity.

Key words: Golgi tendon organs — Group Ib input — Motor control system — Posture — Locomotion

Until recent years Golgi tendon organs were considered to be high threshold tension detectors. Matthews (1933) found that their responses to stretch and contraction were similar when contractions were produced by stimulation of the muscle nerve. It was then assumed that the discharge from Ib afferents implied a strict in-series linkage between tendon organs and the striated musculature. Due largely to the work of Houk and Henneman (1967) on cat soleus there is now indication that the mechanical arrangement of tendon organs is complex, receptors lying in-series with certain groups of muscle fibers and in-parallel with others. By stimulating the divided ventral rootlets it was shown that the threshold to active force delivered in-series was very low, to the extent that a receptor could be fired by contractions of a single motor unit. These findings supported indirect suggestions (Cruz and Hufschmidt, 1962; Eccles *et al.*, 1957; R.M. Eccles and Lundberg, 1959; Jansen and Rudjord, 1964; P. B. C. Matthews, 1964) that tendon organs might play a role in the reflex regulation of muscle activity by providing information concerning the degree of muscle contraction.

Houk and his colleagues (Houk, 1967; Houk and Henneman, 1967; Houk and Simon, 1967; Houk *et al.*, 1971) maintain that responses to active contraction constitute the only effective and important stimulus to tendon organ activity within the physiological range. We have presented evidence, however, that soleus tendon organ responses to passive muscle extension may also have functional significance (Stuart *et al.*, 1970a). Furthermore, Alnaes (1967) has reported that the majority of tendon organs in tibialis anterior give sustained discharge to passive stretch of the muscle within its physiological range. He found anterior tibial receptors to have greater stretch sensitivity than the soleus tendon organs studied in the same laboratory by Jansen and Rudjord (1964). These workers proposed that the difference in passive force threshold of soleus and anterior tibial receptors could be explained on the basis of differences in the distribution of passive tension in the two muscles (Alnaes, 1967; Jansen, 1967). It thus became of interest to determine if soleus and anterior tibial tendon organs differ in their responsiveness to active force or if differences in their firing patterns simply reflect differences in the profile of tension developing in the two muscles and their motor units.

In this paper we present observations on the mechanical arrangement of tendon organs and muscle fibers and contrast the relative sensitivity of soleus and anterior tibial receptors to passive force developed by stretch and to active force developed by contraction of isolated motor units. In a subsequent report (Mosher *et al.*, 1972) the properties of the motor units themselves are discussed. As presented in preliminary accounts (Mosher *et al.*, 1970a, b; Stuart *et al.*, 1970c, 1971) our data tend to confirm those of Houk and Henneman (1967). In some respects, notably subtleties of mechanical arrangement and stretch responsiveness, our results differ from theirs. Elsewhere (Stuart *et al.*, 1971) we have emphasized that the capacity of tendon organs to respond to stretch as well as to contraction widens the scope of their functional contribution and is consistent with recent evidence on the central organization of Ib reflexes.

Methods

Experiments have been performed on 27 2.5—5.5 kg cats which were deeply anesthetized with pentobarbital sodium. The recording arrangement and experimental procedures are shown in Fig. 1. In all experiments it was necessary first to accomplish functional isolation of a Ib afferent from the de-efferented soleus or tibialis anterior. The location of the receptors could often be approximated by determining the point of maximum sensitivity to pressure applied directly to the muscle with a fine probe. For experiments on the arrangement of tendon

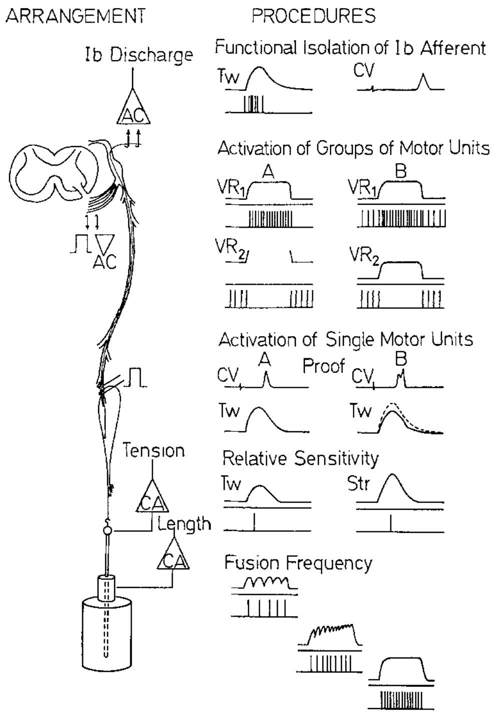

Fig. 1. *Experimental arrangement and procedures.* AC, a—c coupled amplifier; CA, carrier amplifier; Tw, twitch; CV, conduction velocity; VR, ventral root filament including groups of motor units; Str, dynamic stretch of total muscle. Discharge of functionally single Ib afferents from soleus or tibialis anterior recorded from dorsal root filaments. Provision made to stimulate or record from ventral root filaments. Muscle attached to strain ring mounted on shaft of electromagnetic vibrator. Length measured by a co-axial variable capacitor mounted around the vibrator's shaft. Vibrator maintained in length-servo. Ib afferent identified by acceleration of discharge during rising phase of twitch. Conduction velocity also measured. In some experiments groups of motor units activated by stimulating divided ventral roots. Both high (A) and low (B) threshold receptors responded with either acceleration (VR_1) or deceleration (VR_2) thereby indicating "in-series" or "in-parallel" alignment with the contracting motor units. In other experiments functionally single motor units were isolated. Ideally (A) the proof involved recording an action potential from a ventral root filament which remained single with increasing strength of stimulus to muscle nerve, and a twitch of fixed amplitude with increasing strength of stimulus to the ventral root filament. Sometimes it was possible only to split down to two axons as shown in B. In this latter case the lower threshold unit could be studied if the difference in electrical threshold remained constant before, during and after testing procedures. To examine relative sensitivity of receptors to active and passive forces, responses were contrasted to tension developed to twitch and by a dynamic stretch. Firing pattern of the receptor was noted during repetitive stimulation of each motor unit up to that frequency producing the peak tetanic tension

organs, appropriate ventral roots (L_6 and L_7 for tibialis anterior, L_7 and S_1 for soleus) were subdivided into 30 to 50 filaments (i. e. natural subdivisions, Swett *et al.*, 1970) each one of which supplied one or more motor units within the muscle. Firing patterns of Ib afferents were then observed during stimulation of these filaments. For experiments on the relative sensitivity to active and passive forces, we followed the techniques outlined by McPhedran *et al.* (1965) for the functional isolation of ventral root filaments containing single alpha axons.

It was possible to analyze the response of a receptor to twitch and tetanus of an isolated motor unit and to compare the active force threshold during a twitch to the passive force threshold during a dynamic stretch. With this approach we were not able to analyze the response of a tendon organ to all the motor units capable of driving the receptor. Unavoidably in the process of identifying single alpha axons, many filaments were damaged.

While all the techniques and procedures used in this study were conventional, certain features deserve special comment:

1. section of all nerves to tail, hip and hind limb except the one to the muscle under study;

2. an almost total freeing of the muscle under study from its surrounding attachments without compromising the blood supply. This dissection facilitates determination of receptor location and also contributes to reliable threshold measurements for dynamic stretch;

3. a rigidly stabilized leg accomplished by use of steel clamps at both ends of the tibia and at the caudal end of the sacrum. These clamps were anchored to a solid metal frame;

4. flexion of the left knee so that the line of muscle pull was about 30° from the horizontal. This angulation allowed formation of a deep mineral oil pool over the muscle being studied;

5. independent regulation of rectal, spinal cord and muscle oil pool temperature at $37 \pm 1\,^\circ C$ by use of a proportional DC system (Mills and Swett, 1964). To maintain temperature in the muscle oil pool a flexible rubber mat, wired for Joule heating, was wrapped around the anterior surface of the leg;

6. a versatile tension recording and muscle stretching system. Ours involves tying the muscle tendon by a short length of dacron line (compliance 25 μ/kg/cm) to a strain ring (compliance 30 μ/kg) attached to the end of the shaft of a servo-regulated vibrator (Stuart *et al.*, 1970b). The length of the tendon between the muscle and tendon tie was minimal to prevent the compliance of the longer anterior tibial tendon from complicating the results (Buller and Lewis, 1965). Total compliance of this tension recording system with the vibrator shaft under servo-control was an acceptable 0.5 mm/kg;

7. a tension recording system ranging in sensitivity from 2 kg/cm to 0.25 gm/cm of oscilloscope deflection. High gain measurements were facilitated by use of an operational amplifier low pass filter circuit that introduced negligible distortion in the tension measurements (Circuit 1 in Huelsman, 1966);

8. careful alignment of the strain ring and vibrator shaft with the natural line of muscle pull. Unless otherwise stated initial muscle length was set to give a peak of active tension during an isometric twitch. Rack and Westbury (1969) have observed that in some cats the active twitch tension of soleus continued to rise with progressive extension of the muscle even beyond its maximal physiological length. We have observed this phenomenon in tibialis anterior and in such cases set initial length to yield 50 gms initial tension. At this length the maximum active tension was usually within 20—50 gms of the peak that could be obtained at longer lengths. In soleus, we regularly found a peak of active tension well within the physiological range for length. On a few occasions the peak of active tension was sustained over several millimeters of lengthening. In these latter cases initial length was set at the shortest length giving the peak tension;

9. a stimulus train of rather long (500 msec) duration to generate peak tetanic tension. Buller and Lewis (1965) found that the fast muscle flexor hallucis longus showed an abrupt plateau of tetanic tension while the slower soleus showed a slow rise of tension over several hundred milliseconds. We observed a similar difference in the profile of rising tension for isolated anterior tibial and soleus motor units but negligible increase in tension for soleus units after a 500 msec train. Stimulus rates of 100 p/sec for anterior tibial units and 50 p/sec for soleus units were used to elicit peak tetanic tension (Mosher *et al.*, 1972);

10. prevention of current spread from one ventral root filament to another. Ventral root filaments were split to the level of their emergence through the dura so that they were all separate from one another as they passed through the saline-mineral oil interface (Rack and Westbury, 1969). Each filament could then be laid on a bipolar stimulating electrode (4 mm wire separation) with the cathode at least 2 cm from the combined rootlets. Current spread, if still present, could be recognized by determining the relation between the stimulus strength and size of the resulting contraction (Brown and Matthews, 1960). Commonly there was a ×5 safety margin between the threshold stimulus and that larger stimulus producing a jump in the amplitude of contraction;

11. ruling out the possibility that functionally isolated "single" alpha axons are in reality two axons with almost identical thresholds and viabilities (Norris and Irwin, 1961). In practice one rarely finds a filament containing two axons of identical threshold. Its occurrence is readily checked by setting stimulus strength at threshold for twitch tension. If two axons are present the profiles of twitch tension show activation of sometimes one, sometimes the other and sometimes both axons. In such case a definitive electrical proof (i. e. isolated conduction velocity spike) was not available.

Finally, in view of the variety of in-parallel responses to be described, it is appropriate to comment specially on the identification of a functionally isolated Ib afferent. Houk and Henneman (1967) have listed the four following criteria for identifying a triceps surae tendon organ: 1. its discharge accelerates during the entire rising phase of a maximal muscle twitch; 2. this characteristic response persists for all values of initial tension; 3. it exhibits a passive force threshold (presumably generated by static stretch) of greater than 20 g; and, 4. it displays little adaptation in response to a sudden stretch. To our way of thinking criteria 1. and 3. are excessively restrictive but perhaps necessary in the original report of in-parallel tendon organ responses. Tendon organs with high dynamic sensitivity often cease firing before the peak of twitch tension, and a few of these receptors fire at zero initial tension (Alnaes, 1967; Stuart *et al.*, 1970a). For anterior tibial receptors Green and Kellerth (1967) found acceleration during the rising phase of twitch tension to be an unreliable index. They noted that spindle afferents also fire repetitively throughout the rising phase of twitch tension. Our experience indicates that the least equivocal classification for anterior tibial receptors is based on the response to tetanic contraction of the whole muscle. If the ventral roots are stimulated at 50 p/sec and stimulus strength is adjusted to fire the majority of alpha fibers and a minimum of gamma fibers (i. e. a 90% contraction), then sustained Ib firing is always produced while gamma-activated spindle discharge is either absent or intermittent. This procedure could still produce a beta-activated spindle discharge, but beta motor fibers are absent or at best rare (ca. 2%) in cat hind limb muscles (Boyd and Davey, 1968).

Results

Successful measurements were made on the responses of 19 Ib afferents to contraction of small groups of motor units (7 soleus experiments, 7 anterior tibial experiments) and of 21 Ib afferents to contraction of 1—16 of their exciting motor units (6 experiments on soleus, 7 experiments on tibialis anterior). Conduction velocities of the Ib afferents ranged from 84—126 m/sec. Static stretch thresholds ranged from 10—750 gms. In both muscles the receptors we studied were broadly distributed along musculotendinous junctions in each muscle.

Mechanical Arrangement of Tendon Organs

A schematic representation of Houk and Henneman's (1967) concept of the relation and responsiveness of a soleus tendon organ to the muscle fibers around it is given in Fig. 2. The model shows a tendon organ in-series with some muscle fibers but in-parallel with others. Tetanic stimulation of a motor unit or group of units contributing fibers in-series causes the receptor to fire even with development of very little tension. Conversely if the tendon organ is firing in response to passive stretch, tetanic contraction of motor units contributing fibers in-parallel can unload the receptor to the extent that it stops firing. If in-series fibers maintain their contraction while in-parallel fibers are also contracting, the receptor responds as it does to the in-series force alone.

Our evidence tends to confirm the Houk-Henneman model but indicates gradations in the extent to which muscle fibers are either in-series or in-parallel with a given receptor. It should be emphasized that interpretation of many of the arrangements implied in Figs. 2—8 must take into account that simultaneous

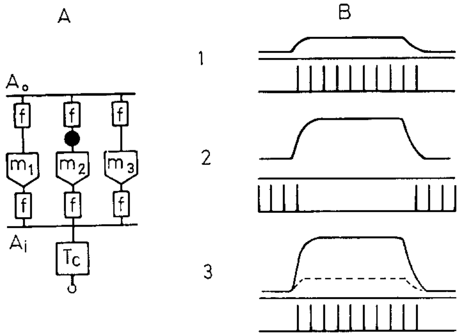

Fig. 2. *Houk and Henneman's (1967) concepts of the mechanical arrangement of tendon organs.* *A* shows the basic arrangement of a tendon organ (black dot) within a muscle with: A_0 and A_1, aponeuroses of origin and insertion; Tc, common tendon of insertion; f,tendinous fascicles; M_1, M_2 and M_3, groups of muscle fibers organized either in-series (M_2) or in-parallel (M_1 and M_3) with the receptor. This model incorporates the generally accepted viewpoint (Rack and Westbury, 1969) that each bundle of extrafusal fibers in cat soleus extend the whole distance between aponeuroses of origin and insertion. Not shown are the various non-contractile attachments that Houk and Henneman designated "extra-connective tissue", in-parallel with the muscle fibers and in series with the common tendon. *B* shows muscle tension (upper trace), zero tension (middle trace) and Ib firing pattern (lower trace) during contraction of: 1, a small portion of the muscle contributing fibers to the M_2 bundle; 2, a larger portion contributing fibers to M_1 and/or M_3 bundles, with the unit brought to sustained firing by increasing initial muscle tension; and, 3, both the small in-series portions and the larger in-parallel portion. The dotted line indicates the amount of tension contributed by contraction of the in-series portion

stimulation of more than one functionally isolated alpha axon may result unavoidably in co-contraction of both loading and unloading motor units. At the same time one must acknowledge that normal muscle activity necessarily involves the contraction of motor units in combination.

In-Parallel Responses

An in-parallel arrangement between certain motor units and tendon organs is implied when either the spontaneous or stretch-activated discharge of a receptor is suppressed by tetanic contraction of a group of these motor units (Figs. 4—6), or alternatively when a silent receptor is activated in the declining phase of a tetanus ("off" response, Fig. 3). For silent receptors proof that the exciting motor units are indeed organized in-parallel could be obtained by increasing initial tension of the muscle until a stretch-activated response ensued. In this situation the contraction suppressed the stretch-activated discharge and augmented the off response.

Unloading responses of varying degree are shown in Figs. 4 and 5. Receptors were subjected to tetanic contraction elicited by stimulation of different ventral root filaments. Responses range from barely detectable slowing to suppression of discharge for the duration of the tetanus (Fig. 4). In some cases the pause in receptor discharge extends 100—300 msec beyond termination of the contraction. This finding implies subtle shifts in the alignment of receptor and contracting muscle fibers, too minute to be reflected in the tension measurement.

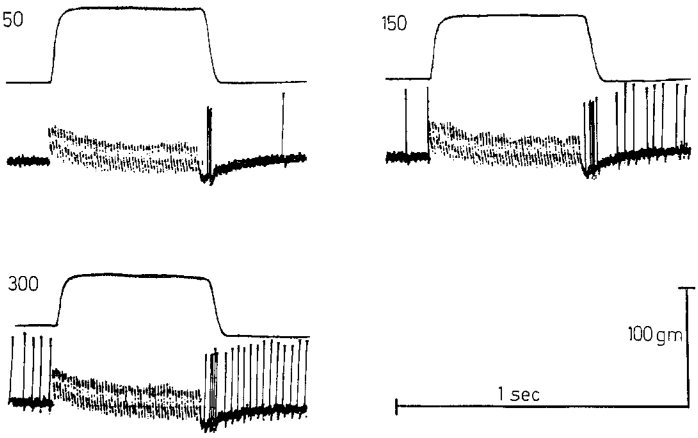

Fig. 3. *The off response.* An anterior tibial Ib afferent is shown responding on the declining phase of 3 tetanic contractions produced by stimulation of a ventral root filament. Active tension was reduced when initial muscle tension (shown in upper left corners) was raised from 50 gms to 150 gms and 300 gms. In these two latter cases initial tension was sufficient to produce a sustained discharge which was interrupted by the contraction

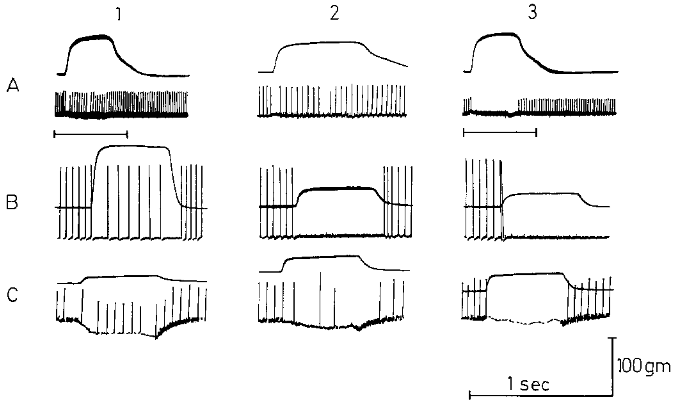

Fig. 4. *Patterns of unloading. A, B* and *C* show responses from 3 different experiments, of soleus (A) and anterior tibial (B and C) Ib afferents to stimulation of different ventral root filaments (1, 2 and 3). Unloading effects of increasing degree are seen. Initial tensions were 50, 50 and 300 gms for A, B and C respectively

It would also appear that the degree of unloading produced by contraction of some in-parallel motor units depends upon initial muscle tension as illustrated in Fig. 5. Some receptors can be unloaded only when the initial tension is set at a critical level slightly above the static stretch threshold. In these receptors unloading did not occur at higher initial tension, implying a relatively loose relationship between many motor units and tendon organs. Other groups of motor units and receptors are arranged so that the initial tension has no effect on the unloading response. It was even observed that stimulation of some ventral root filaments had a weak accelerating effect at zero initial tension and a weak decelerating effect at higher initial tension. Taken together these responses suggest that un-

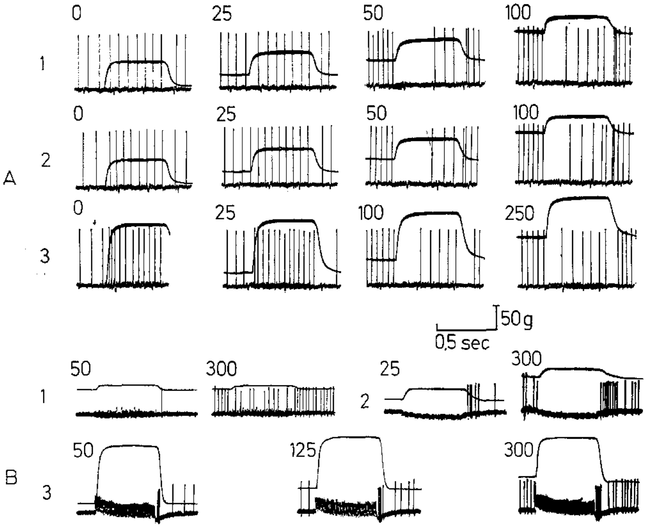

Fig. 5. *Unloading as a function of initial tension. A* shows the response of a Ib afferent to stimulation of 3 different ventral root filaments (1, 2 and 3) at the initial tensions shown in the upper left corners. The contraction evoked by stimulation of the first filament (1) evoked an unloading effect at 50 and 100 gms initial tension but not at 0 and 25 gms tension. Similar behavior was seen during stimulation of the second filament with suggestion of a loading (accelerating) effect at 0 and 25 gms tension. That opposite effects could be elicited at different tension settings was again shown by stimulation of the third filament (3). This receptor was firing spontaneously at 0 tension. *B* shows responses of three TA receptors (1—3) from 3 different experiments. In each case the unloading effect to stimulation of the same ventral root filament was seen over a wide range of initial tensions. Note in particular that the static stretch threshold of the third receptor was 125 gms

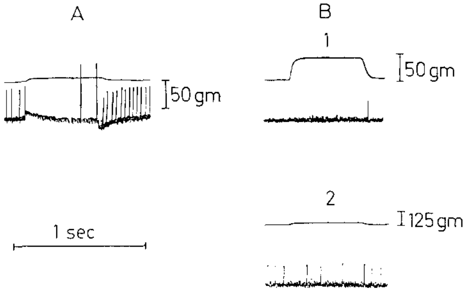

Fig. 6. *Examples of unloading produced by very low active tensions. A* and *B* from two different experiments on tibialis anterior. In *A* unloading of a Ib afferent was produced by a 5 gm contraction produced by stimulation of a ventral root filament. In *B* the response of a Ib afferent is shown to contraction of an isolated motor unit. At 50 gms initial tension (1), this unit produced 38 gm tension and an "off" response ensued. At an initial tension of 375 gms (2) the motor unit generated less tension (25 gms) but the contraction was still sufficient to retard the stretch-activated discharge

loading effects are not confined to a narrow range of initial tension within the muscle but may assume functional significance when groups of motor units are being recruited in a contraction of increasing force and when movements are initiated from limb positions involving different levels of muscle tension.

It should be emphasized that unloading can be produced by very small contractions of the muscle. Figure 6A shows the response of an anterior tibial Ib afferent to stimulation of a ventral root filament which produced only 5 gms of tension. It is likely that a single motor unit was being activated since the peak tensions of our isolated anterior tibial motor unit sample range from 4—65 gms (Mosher *et al.*, 1972). Figure 6B reveals that contraction of a functionally isolated motor unit is indeed sufficient to unload certain receptors even when the receptor has been brought to sustained firing well above its static stretch threshold.

In-Series Responses

A wide range of Ib firing patterns results from stimulation of the subdivided ventral rootlets. Figure 7A shows examples from an experiment in which an anterior tibial tendon organ responded to stimulation of 40 L_6 and L_7 ventral root filaments. Fifteen of these filaments evoked brisk, sustained discharge, 13 evoked feeble or intermittent discharge, while 9 gave "off" or unloading responses and 3 gave "on-off" responses consistent with co-activation of loading and unloading motor units. Clearly, as seen for both soleus and anterior tibial receptors, firing rate is not a function of the developing tension alone. For example one soleus Ib afferent (Fig. 7C) fires at 53 imp/sec to a 35 gm tetanus produced by stimulation of one ventral root filament and then at 38 imp/sec to a 575 gm tetanus produced by stimulation of another filament.

Tight and loose in-series coupling was also evident from the responses to stimulation of isolated motor units. Sustained discharge during graded repetitive stimulation (shown in Fig. 11) is indicative of tight in-series coupling between motor unit and tendon organ. Loose in-series coupling is suggested by the weak responses in Fig. 7B and D, in which the receptors fire even more feebly at peak tetanic contraction than during unfused tetanus. We would conclude that an exciting motor unit need not be aligned directly in-series with a given receptor, but may be off line from it. Moreover it is possible that the mechanical arrangement between a tendon organ and some motor units may be in-series at one level of activity and in-parallel at another.

Houk and Henneman (1967) would maintain that only motor units contributing fibers directly in series with a receptor are capable of driving it. They searched systematically for the total number of motor units which could drive a single tendon organ. Their data suggested that the number of motor units capable of driving a receptor (4—15) would always be less than the number of muscle fibers for which it provided insertion (5—25, according to the histological studies of Barker, 1967, and Bridgman — personal communication). We have performed similar experiments, noting the responses of tendon organs to stimulation of natural subdivisions of the ventral rootlets. To avoid deterioration of filaments, division was not necessarily continued until an individual alpha axon had been functionally isolated. Under these conditions it is not known if a given filament might contain more than one potentially exciting motor unit, nor if co-contraction of one exciting motor unit with several in-parallel motor units might obviate the response to the exciting unit. Therefore estimations of the number of motor units driving a receptor are almost certainly conservative. The minimum number of motor units capable of exciting soleus

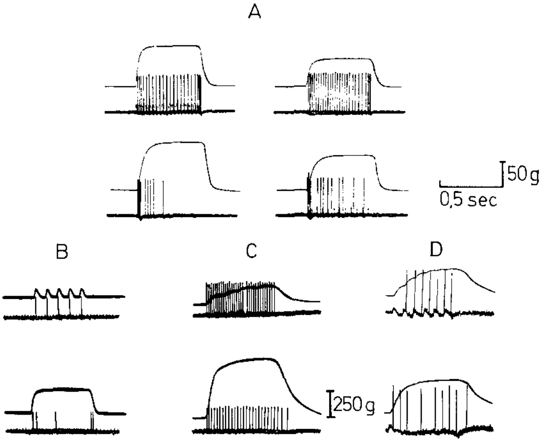

Fig. 7. *Patterns of loading. A* shows responses of an anterior tibial Ib afferent to stimulation of various ventral root filaments, some of which evoked sustained discharge (upper traces) indicative of tight "in-series" coupling and some of which evoked feeble and intermittent discharge (lower traces) indicative of loose "in-series" coupling. *B* shows another anterior tibial Ib afferent responding to stimulation of an isolated motor unit at two different frequencies (upper trace at 10 pps and lower trace at 60 pps). The response to the lower stimulus frequency indicates a tighter "in-series" relation than the response to the higher stimulus frequency. *C* shows a soleus Ib afferent responding to stimulation of two different ventral root filaments. The response is not simply a function of the amount of tension developing and suggests that either the motor units activated by stimulation of the second filament (lower trace) were coupled more loosely than those connected to the first filament or alternatively that there was co-activation of both loading and unloading units. *D* shows response of another soleus Ib afferent to stimulation of a functionally isolated motor unit first at 10 pps (upper trace) and second at 30 pps (lower trace). Loose "in-series" coupling is suggested by the lack of sustained discharge at the fusion frequency

tendon organs was 0—12, mean 7, for 8 receptors; 10 anterior tibial receptors were driven by a minimum of 7—36 motor units (mean 18). The tendon organ for which no exciting motor unit could be found had an active force threshold of 250 gms and presumably was located in the tendon proper. Though inconclusive in themselves these data do suggest that at least some anterior tibial tendon organs may be activated by more units than there are muscle fibers making direct in-series insertions.

Our visual observations suggest that tetanic contraction of groups of motor units or even a single motor unit can excite a receptor located at some distance (up to 4 cm) from the contraction. At first glance this observation may be of dubious merit since the extent of intermingling and average territories of anterior tibial and soleus motor units are not known (cf. Ekstedt, 1964). It was our experience, however, that stimulation of the natural subdivisions of the ventral rootlets resulted consistently in overlapping but restricted dimpling of the surface muscle in both soleus and tibialis anterior. In a careful study on cat medial gastrocnemius by Swett *et al.* (1970) there was also evidence of a distinct though imprecise somatopic organization of nerve supply and muscle. The territory of a motor unit can now be examined directly with development of a technique for histochemical "marking" of all the unit's muscle fibers after depletion of their fiber glycogen by repetitive stimulation (Edstrom and Kugelberg, 1967). Extensive intermingling of muscle fibers from different motor units has been established. Anterior tibial units of the rat have been shown to occupy a territory approximately 12 % of the cross-sectional area of the muscle (Brandstater and Lambert, 1971).

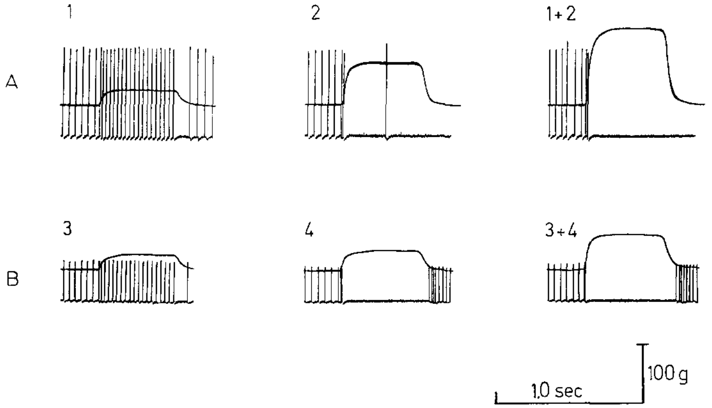

Fig. 8. *Response of an anterior tibial tendon organ to concomitant stimulation of loading and unloading motor units.* This Ib afferent (gain reduced in *B*) fired steadily at 50 gms initial tension. Stimulation of different ventral root filaments produced either a loading (1, 3) or an unloading (2, 4) effect. Paired stimulation of filaments 1 and 2 and of 3 and 4 resulted in a summing of individual tensions with the unloading effect prevailing

These findings support the view that intermingling of fibers from different motor units takes place within a generally limited territory. We would suggest that with such an arrangement motor units can deliver force essentially in-series with a tendon organ without contributing muscle cells to it directly.

Co-Contraction of Loading and Unloading Groups of Muscle Fibers

In general agreement with Houk and Henneman (1967) was the finding that Ib afferents usually fired in response to co-contraction of loading and unloading portions of the muscle. An exception is shown in Fig. 8 where co-activation resulted in a predominance of the unloading effect. It is well to remember that in an arrangement where there are varying degrees of in-series and in-parallel alignment, co-activation of a weakly in-series motor unit or units and a strongly in-parallel group would favor an unloading effect. Such is probably the case for the receptor shown in Fig. 8 in that the loading contraction of 30 gms increased firing only to 37 imp/sec, whereas other 30 gm contractions produced by stimulation of other ventral root filaments brought the firing rate to 57 imp/sec. Conversely the unloading effects were pronounced, which implies a strong in-parallel relationship. Unlike Houk and Henneman (1967), we found that the firing rate to contraction of an in-series portion was usually slowed to some extent by co-contraction of an unloading portion.

Relative Sensitivity of Tendon Organs to Active and Passive Inputs

For 10 soleus and 10 anterior tibial receptors measurements were made of the relative sensitivity to active force produced by twitch contraction of isolated motor units and to passive force developed by dynamic stretch, initial tension being the same in both cases (Figs. 9 and 10). Active and passive force thresholds are here defined as the increment of tension above initial tension at the moment of first sensory response. For active force thresholds this response had to occur with greater than 2.5 msec latency from start of the twitch contraction. This

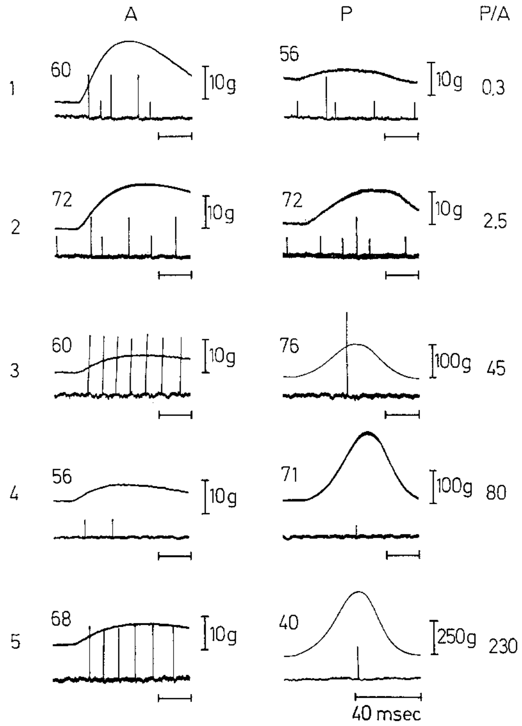

Fig. 9. *Relative sensitivity of soleus tendon organs to active and passive forces.* Column *A* shows response of 5 different receptors (1 to 5) to twitch contraction of the most powerful excitatory motor unit. Contraction times (in msec) for these motor units shown above tension profiles. Column *P* shows response of same receptor to a dynamic stretch delivered from the same initial tension as used in *A* and with tension rise time approximately as for the twitch. The tension at the moment of first sensory response to stretch divided by a similar value for the twitch gives a P/A ratio indicating relative sensitivity of the receptor to active and passive force. Time calibration, 40 msec

rule eliminates potential interference from early discharge spikes (Hunt and Kuffler, 1951; Granit *et al.*, 1959) which can appear on rare occasions even during twitch contraction of single motor units. A receptor had a separate threshold to each one of its exciting motor units, the difference between minimum and maximum values usually varying by less than 5 gms. Minimum active force thresholds for soleus and anterior tibial receptors were similar (mean 2.4 gms for soleus; 1.5 gms for tibialis anterior), and ranged, for 16 of the 20 afferents, from 0.5 to 3 gms. Only 2 receptors had thresholds as high as 12 gms and both responses occurred after the peak of twitch tension. In these unusual cases it is not known if the high threshold is a true reflection of the receptor's capabilities or if: a) more effectively exciting motor units were lost in subdivision of the ventral rootlets; or, b) the exciting motor unit was located off-line or at some distance from the receptor. We consider the latter arrangement a possibility since we have seen a Ib afferent display a low (2 gm) threshold to twitch of a motor unit located at some distance from the receptor. It must also be remembered that some tendon organs are not fired by twitch or tetanic contraction of single motor units. Non-

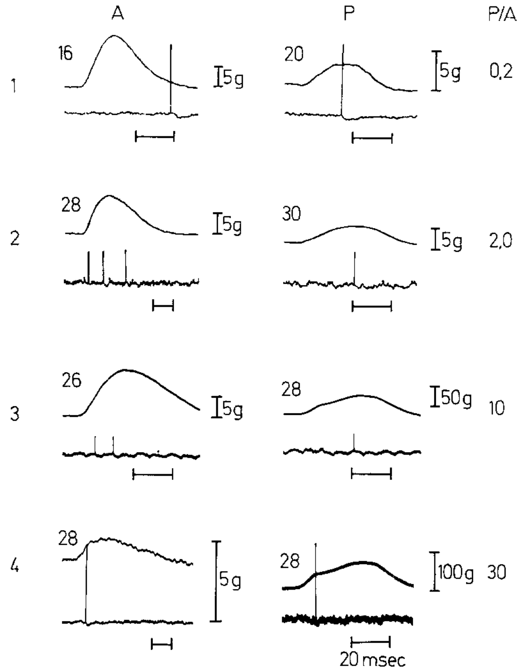

Fig. 10. *Relative sensitivity of anterior tibial tendon organs to active and passive forces.* Figure shows similar procedures to those outlined for Fig. 10. Acceleration artifact in tension profiles was accounted for when measuring the threshold tension. Time calibration, 20 msec

etheless, accepting all these qualifications, it is obvious that tendon organs in both soleus and tibialis anterior have a very low active force threshold.

Dynamic stretch thresholds were determined by use of sine wave stretches with rise times of tension closely matching the range of contraction times for isolated motor units. For soleus this procedure involved use of stretches ranging in rise time from 40—80 msec and for tibialis anterior from 15—40 msec. Under these conditions the dynamic stretch threshold of the anterior tibial receptors (24 ± 21 gms) was considerably lower than that of the soleus receptors (67 ± 50 gms). While direct measurements were not made, measurements of threshold as a function of tension rise time suggested that, even at identical stretch rates, dynamic stretch thresholds would be considerably lower for the anterior tibial receptors.

Division of the dynamic stretch threshold by the minimum active force threshold provides an index of the extent to which tendon organs are more sensitive to active than passive inputs. For soleus receptors the numbers obtained were: 0.3, 3, 16, 25, 30, 35, 45, 45, 80 and 230. For anterior tibial receptors the numbers were: 0.2, 4, 4, 5, 10, 12, 20, 20, 40 and 40. The lower values generally obtained for anterior tibial tendon organs are principally a reflection of low dynamic stretch thresholds in these receptors. We cannot exclude the physiological significance of responses to passive stretch, therefore, particularly when due consideration is given to the rates and extents of muscle extension in natural locomotor activity (Stuart *et al.*, 1971).

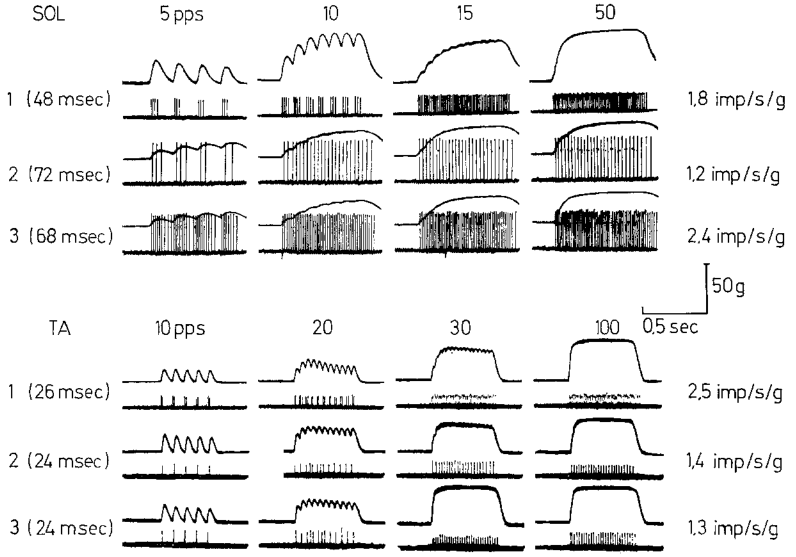

Fig. 11. *Responses of a soleus and an anterior tibial tendon organ to graded repetitive stimulation of 3 different motor units,* the contraction times of which are shown to the left of each row of recordings. Sensitivity values in imp/sec/gm calculated by dividing the mean firing rate during peak tetanic contraction by the peak tension achieved. Tension calibration for the first soleus motor unit at 5 and 10 pps is half that shown for all other tensions

Responses to Graded Tetanus of Isolated Motor Units

For 9 soleus and 11 anterior tibial receptors, responses were noted to stimulation of single exciting motor units at increasing frequencies up to that eliciting a peak tetanic contraction. For soleus this test involved stimulus frequencies of 5, 10, 15, 20, 50 and 100 pps and for tibialis anterior, 10, 20, 30, 40, 50, 100 and 200 pps. Results now to be described are restricted to the vigorous responses of tendon organs to contraction of strictly in-series motor units. Typical data are shown in Fig. 11.

Mean twitch contraction time of soleus motor units (60 ± 7 msec) was much slower than that of anterior tibial motor units (24 ± 4 msec), and mean fusion frequency for the soleus sample (24 ± 6 pps) was almost half that for the anterior tibial sample (43 ± 9 pps). These differences are easily seen in the relation between tendon organ discharge and the profile of developing tension from unfused tetanus to peak tetanic contraction. At low stimulus rates the phasic tension profiles of excited motor units are clearly reflected in the intermittent response of the receptor. Considerably less Ib input is generated by anterior tibial than soleus receptors at frequencies of stimulation below 20 pps. Peak tetanic contraction drove soleus receptors at sensitivities ranging from 0.6—6.7 imp/sec/gm (mean 2.6) and anterior tibial receptors at sensitivities ranging from 0.6—6.0 imp/sec/gm (mean 1.7). The comparable sensitivities revealed by the responses to tetanic contraction of motor units suggest that soleus and anterior tibial tendon organs are capable of transducing active force to a similar extent and that differences in their firing patterns to unfused tetanic contractions are determined by the different mechanical properties of these two muscles and their motor units.

Repetitive stimulation of isolated motor units could also be related to the rate of receptor discharge. The following generalizations were drawn: 1) above low rates of stimulation (5 pps for soleus motor units and 10 pps for anterior tibial motor units) discharge of the receptors increased approximately 2—5 times, up to 95 imp/sec; 2) receptor discharge reached a peak at rates below fusion frequency for the motor unit being stimulated. For soleus receptors this rate was usually around 10 pps. With higher rates of stimulation, tension continued to increase toward a peak tetanic level, but the rate of receptor discharge changed very little. It is interesting to note that Roberts (1967) has found the preferred firing index of soleus motor units in the decerebrate cat to be around 10/sec. The preferred firing frequency of anterior tibial motor units is not known.

Discussion

Structural Considerations

This report calls attention to those structural and functional factors which determine the responses of an individual tendon organ. Certain anatomical considerations are fundamental. The typical tendon organ is surrounded by a capsule one end of which encloses collagen fascicles extending from the aponeurosis of origin or insertion, while the other end receives a cluster of 5—25 muscle fibers (Barker, 1967). Clearly seen in the reconstructive drawings of Bridgman (1968), these fibers are directly in-series with the receptor while adjacent muscle fibers are in-parallel. As tension is directed in the long axis of the musculotendinous junction, it is proposed by Bridgman that the collagen bundles will straighten out, allowing for graded compression of the nerve endings. At this structural level there is no evidence that the receptor can distinguish between traction upon the collagen fascicles produced by muscle contraction and stretch.

In the cat soleus there are approximately 45 musculotendinous tendon organs (Swett and Eldred, 1960) and 150 motor units (Boyd and Davey, 1968) with an average innervation ratio of 180:1 (McPhedran *et al.*, 1965). From these figures a total muscle fiber count of 27,000 (i. e. 150 × 180) can be derived. Thus, the number of muscle fibers inserting directly onto the 45 musculotendinous receptors is only a small proportion of the total fiber content of the muscle (ca. 2—3%). It is evident that tendon organs monitor contractile tension by sampling small fractions of the total force being generated whether or not they are responsive only to muscle fibers connected with them directly. Likewise, even if all the sites of insertion onto one tendon organ capsule were occupied by fibers from a single motor unit, there is strong indication that the receptor would detect only a small amount of the force that that particular motor unit could develop. At the other extreme we have presented evidence that receptors may also respond to motor units located off-line or in some distant portion of the muscle.

Sensitivity to Active In-Series Force

Responses to Single Motor Units

By reason of their structure and situation, then, tendon organs detect more readily force applied in-series with the receptor. This feature is emphasized in Houk and Henneman's (1967) schematic model relating a tendon organ to the muscle fibers and tendinous fascicles around it (see Fig. 2). Our results confirm the overall validity of Houk and Henneman's concept for both tibialis anterior and soleus. While in agreement regarding the low threshold of tendon organs to active contractile force, we propose that the in-series relations between a receptor and its exciting motor units may be more variable than previously described. Examples have been given in which: 1. a receptor fires briskly in response to stimulation of one or more motor units and weakly in response to stimulation of other motor units; 2. a receptor fires briskly at one level of initial muscle tension and weakly or not at all when the initial tension changes; 3. a receptor fires more briskly during unfused repetitive motor unit stimulation than during the peak tetanic contraction. In each case the receptor's capacity for vigorous discharge is demonstrated. These abbreviated or feeble responses, therefore, must signify that certain motor units are never directly in line with the receptor and that other motor units are in line with it under limited conditions of muscle activity. Further, there is evidence that tendon organs may be activated by contraction of some distant motor units. While the functional importance of these off-line responses is uncertain it must be conceded that the number of muscle fibers lying off-line, yet in a position to influence the receptor's firing pattern at some level of activity, is potentially very large.

The responsiveness of an individual tendon organ to active force has limits defined not only by the sensitivity of the receptor itself but also by its mechanical arrangement at any moment with surrounding muscle fibers. Increasing frequencies of motor unit stimulation drive the receptor toward a maximum rate of discharge beyond which it cannot signal efficiently any additional rise in tension. Houk and Henneman have recognized a saturation effect in the tendon organ responses to increasing tension in that responses of soleus receptors to simultaneous stimulation of two or more motor units did not sum algebraically (1967).

Responses to Combinations of Motor Units

While the responses of single tendon organs to active inputs may reveal the functional organization of a tension control system at a unitary level, they do not necessarily determine how that system would operate during natural muscle activity. Houk and Henneman (1967) contended that contraction of portions of the muscle that can unload a receptor do not influence its rate of discharge so long as it is firing in response to an in-series motor unit. This observation implies that in-series force delivered to a receptor is not attenuated by force delivered in-parallel. In contrast we have shown that the response of a tendon organ to in-series muscle fibers can be reduced or even abolished by concomitant stimulation of in-parallel groups of fibers. With recruitment of large numbers of motor units many contracting fibers will be brought into both in-series and in-parallel arrangement with tendon organs. These interactions impose a restriction upon the tension control system as a whole. Together with other factors which modify tendon organ responses to in-series force alone, they may account for the low active force sensitivity to contraction of the total muscle. It has been reported that the sensitivity of soleus receptors ranges from 0.02—0.14 imp/sec/gm (Jansen and Rudjord, 1964), and the sensitivity of anterior tibial receptors from 0.04—0.2 imp/sec/gm (Alnaes, 1967) for contractions of the total muscle. In contrast, from the responses to isolated motor units, we have given active force sensitivities ranging from 0.6—6.7 imp/sec/gm for the individual receptors. This disparity in sensitivities makes it clear that the responsiveness of tendon organs to active force cannot be gauged in relation to contraction of the muscle as a whole. Rather we must consider that, apart from their absolute rate of discharge, the distribution of tendon organs and the pattern by which they are recruited are also important in the moment to moment regulation of tension within a muscle.

Passive Force Responsiveness

Thresholds to dynamic stretch were considerably lower for anterior tibial receptors than for those of soleus, even though responses to active in-series force were quite similar. Since a tendon organ should give an identical response to force delivered at either end of the capsule, it follows that differences in passive force threshold relate more to the distribution and coupling of passive force than to the process of transduction itself. Soleus is a unipennate muscle whose contractile and non-contractile elements show a high degree of in-parallel organization. As a result only a small percentage of the total passive tension in soleus is applied directly in series with any of its tendon organs. Tibialis anterior is multipennate and its muscle fibers are relatively short. In addition its tendon organs are oriented more directly to the line of muscle pull, an arrangement which favors the coupling of passive tension to each receptor.

Lengthening Contractions and Functional Role of Tendon Organs

With recognition of their responsiveness to both active and passive forces, one might expect discharge from tendon organs to be prominent during activities in which intramuscular forces are developed by both contraction and stretch. Houk and Henneman originally noted acceleration in tendon organ discharge, paralleling an increase in the force of contraction, when the soleus muscle was stretched in the presence of a steady motor unit contraction (1967, see their Fig. 6). We have also made preliminary attempts to reproduce a lengthening contraction by subjecting soleus receptors to triangular wave stretches while the muscle was being tetanized. The firing rate of one tendon organ rose from 87 to 130 imp/sec (Stuart *et al.*, 1970a, see Fig. 5). Additional experiments will be necessary to determine, under conditions of co-incident contraction and muscle extension, to what extent tendon organs are responding to the passive stimulus per se or to an increment of active tension conferred by a shift along the length-tension curve.

Lengthening or eccentric contractions are less well understood than other forms of muscle activity such as passive stretch, isotonic and isometric contraction. Yet they play an important role in posture and locomotion. In the stance phase of the cat step cycle (cf. Engberg and Lundberg, 1969) knee and ankle joints initially yield under the weight of the body before extending to thrust the animal forward. During the yield electrical activity in leg extensors actually builds to a peak. Lundberg (1969) has suggested that the yield of the stance phase must be regulated by powerful inhibitory Ib connections among muscles operating at knee and ankle joints. The central connections of Ib afferents are widespread and allow for patterned and sequential engagement of synergists and antagonists as integrated movements evolve across one or more joints (cf. Stuart *et al.*, 1971). While autogenetic inhibition and its companion synaptic actions are the dominant spinal effects of Ib activation, there is likelihood that alternative pathways may serve to widen, restrict or even reverse the Ib influence (cf. Hongo *et al.*, 1969). Taking into account this lability of central effect along with the responsiveness of tendon organs to stretch as well as contraction and recalling the variety of movements which involve a blending of both active and passive inputs, there remains little doubt that the tendon organ has a far more significant role in the reflex regulation of muscle than has been previously appreciated.

Acknowledgements: This investigation was supported by USPHS grants NB 07888 and FR 05457. We would like to thank Mrs. Nancy Jensen and Mrs. Mary Louise Oslund for their preparation of the figures. Dr. James Houk read a draft of the manuscript and we thank him for his interest and thoughtful criticisms.

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