J. Physiol. (1976), **261**, *pp.* 633–645
With 5 text-figures
Printed in Great Britain

FREQUENCY OF TENDON ORGAN DISCHARGES ELICITED BY THE CONTRACTION OF MOTOR UNITS IN CAT LEG MUSCLES

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(*Received 19 March 1976*)

SUMMARY

1. The responses elicited in individual tendon organs by the contraction of single motor units were studied in peroneus longus, peroneus brevis, tibialis anterior and soleus muscles.

2. No simple relation was found between the discharge frequency of a tendon organ and the tension produced in the muscle tendon by the contraction of individual motor units.

3. The sensitivity of a given tendon organ to contractile tension was not the same for each of the motor units which elicited its discharge. There was no correlation between the sensitivity of the receptor and the strength of the motor units.

4. Upon repetitive stimulation of a tendon-organ-activating motor unit at increasing rates, the frequency of the receptor sustained discharge reached a maximal value for rates of stimulation eliciting submaximal tetanic tension. Higher rates only produced an increase in the dynamic component of the tendon organ response.

5. These observations show that the contractile tension sensed by a tendon organ is not a simple fraction of the tension which appears at the muscle tendon. They might be accounted for as consequences of the fine structure of tendon organs and of variations in the number of muscle fibres contributed by different motor units to the bundle inserted on each receptor. The location of most tendon organs at musculo-aponeurotic junctions rather than in the tendon proper, could also be responsible for some of the observed discrepancies.

INTRODUCTION

Since early studies (Matthews, 1933; Hunt & Kuffler, 1951) Golgi tendon organs were known to be activated during muscle contraction; more recently, it was shown that their adequate stimulus is in fact the tension

produced by muscle contraction (Jansen & Rudjord, 1964; Alnaes, 1967). The threshold of tendon organs is very low since they will respond to the contraction of a single motor unit; several motor units, each on its own, can excite the same receptor (Houk & Henneman, 1967).

Reinking, Stephens & Stuart (1975) studied the physiological properties of tendon-organ-activating motor units in cat medial gastrocnemius muscle and found that the two to five motor units whose contraction elicited the discharge of the same tendon organ exhibited wide differences in twitch contraction time, tetanic tension and resistance to fatigue. In a previous report on tendon organs of four other muscles of the cat leg (peroneus longus and brevis, tibialis anterior and soleus) we showed that the motor units acting upon a given receptor have axonal conduction velocities and tetanic tensions dispersed over the same range as those of the whole muscle population, so that each individual tendon organ monitors a representative sample (Jami & Petit, 1976). Since a single tendon organ can be activated by the contraction of motor units producing different tensions, we examined in the course of the same investigation, whether these differences would be reflected in the discharge frequency of the receptor. This study shows, in agreement with Stauffer & Stephens (1975) and Reinking *et al.* (1975), that there is no simple relation between the discharge rate of a given tendon organ and the tension of individual motor units activating this receptor, as measured at the muscle tendon. It does not, however, provide support to these authors assumption of a preferential sensitivity of tendon organs for tension developed by the contraction of small slow-twitch motor units.

A preliminary account of these results has been presented (Jami & Petit, 1975).

METHODS

Experiments were performed on eighteen adult cats anaesthetized with pentobarbitone sodium (Nembutal, Abbott), 40 mg/kg. The preparation, recording arrangement and methods for identification of Ib afferents and single α motor axons have been previously described (Jami & Petit, 1976).

Four muscles of the leg were examined: four experiments were carried on the peroneus brevis muscle (fourteen Golgi tendon organs studied), five experiments on the peroneus longus (nineteen Golgi tendon organs studied), four experiments on the soleus (fifteen Golgi tendon organs studied) and five experiments on the tibialis anterior (fourteen Golgi tendon organs studied).

In each experiment the procedures involved functional isolation of single Ib afferent fibres in dorsal root filaments (usually four in each experiment) and preparation of single α motor axons (from twenty-four to ninety-five in each experiment). The effect of stimulation of each motor unit on each of the studied tendon organ afferents was investigated. The response of tendon organs to a single motor unit twitch could be either an isolate spike or a burst of variable frequency and duration; the timing of this response with respect to the onset of tension rise was also variable. Therefore, in order to standardize the results, a tendon organ was considered

activated by a given motor unit only when repetitive stimulation of this unit during 2 sec elicited a discharge (or an acceleration of the discharge) of the receptor which persisted throughout the muscle contraction. Each of the motor units which activated a given tendon organ was stimulated at 150/sec and the receptor discharge rate as well as motor unit tension were measured 1 sec after the onset of motor axon stimulation. In addition the motor units which activated sixteen tendon organs (eight from peroneus longus and eight from soleus) were systematically stimulated at increasing rates ranging from 10 to 150/sec. The tension developed and the frequencies of receptor discharges were simultaneously recorded 1 sec after the onset of motor axon stimulation.

For each unit, the axonal conduction time was noted and, at the end of the experiment, the distance between stimulating and recording electrodes was measured in order to calculate the motor axon conduction velocity.

RESULTS

Each of the motor units whose contraction activated a given tendon organ (four to eight on average, see Jami & Petit, 1976) elicited a different rate of the receptor discharge. However, no clear relation between the receptor discharge frequency and the tension produced in the tendon by individual motor units was observed. Fig. 1 shows four typical examples, each taken from a different muscle. The peroneus brevis tendon organ was activated by six motor units, which developed tetanic tensions ranging from 2·5 to 60 g and elicited discharges ranging from 20 to 105 impulses/sec. The absence of correspondence between motor unit tension and frequency of tendon organ response appears in the fact that the discharge frequency of this receptor during the contraction of the motor unit which produced 5 g tension was higher (50 impulses/sec) than the frequency elicited by the contraction of the unit producing 50 g tension (30 impulses/sec). The tibialis anterior tendon organ was excited by five motor units and its discharge rate reached 60 impulses/sec under the influence of the motor unit which developed 11 g tension, whereas it did not exceed 45 impulses/sec under that of a stronger unit developing 40 g tension. The peroneus longus example shows similar discrepancies: this receptor fired 50 impulses/sec in response to the contraction of a motor unit which produced 4·5 g maximal tension and 110 impulses/sec for another unit producing 9 g tension but only 32 and 75 impulses/sec during the contraction of two other units which developed, respectively, 14 and 25 g tension. The soleus tendon organ was activated by six motor units, two of which developed similar tensions (18 and 20 g) but elicited quite different rates of discharge (respectively 90 and 25 impulses/sec), whereas two other units with different tensions (12 and 50 g) activated the receptor at the same rate (65 impulses/sec).

Repetitive stimulation of a tendon-organ-activating motor unit at frequencies below those eliciting unfused tetanus produced discontinuous

firing of the receptor. The level of unfused tetanus tension from which a tendon organ started discharging continuously was not the same for the different motor units acting upon this receptor, a fact which appears consistent with previous statements that the tension threshold of a given

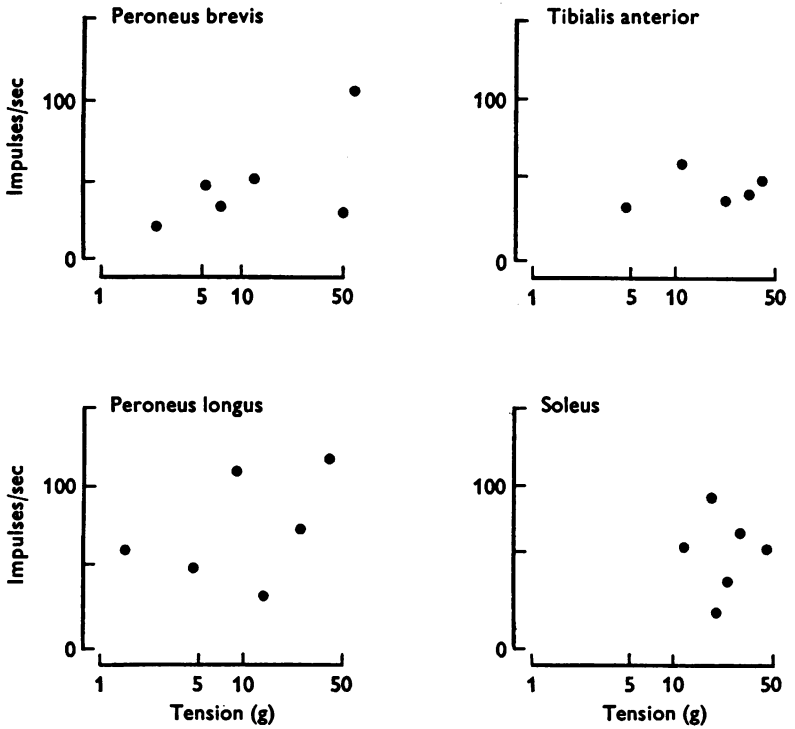

Fig. 1. Absence of correspondence between the discharge frequency of a tendon organ and the tension developed by individual motor units activating this receptor. In each graph, the dots represent the responses of a Golgi tendon organ to the maximal contraction of its activating motor units. The peroneus brevis tendon organ (conduction velocity of the Ib afferent: 100 m/sec) was activated by six motor units, the tibialis anterior tendon organ (conduction velocity of the Ib afferent: 97 m/sec) by five motor units and each of the peroneus longus (conduction velocity of the Ib afferent: 102 m/sec) and soleus (conduction velocity of the Ib afferent: 89 m/sec) tendon organs by six motor units. The discharge frequency of the receptor is plotted against the logarithm of the tension developed by each motor unit upon stimulation of its motor axon at 150/sec.

tendon organ can be different for each of its activating motor units (Stuart, Mosher, Gerlach & Reinking, 1972; Jami & Petit, 1976). In keeping with the above reported observations (cf. Fig. 1), the frequency of the minimal continuous discharge elicited in a tendon organ by the

different motor units whose contraction influenced this receptor also varied from one unit to another, apparently without relation to the developed tension.

When a tendon-organ-activating motor unit was repetitively stimulated at increasing rates above those producing unfused tetanus, the frequency of the receptor discharge rose with the tension developed by the motor unit but reached a maximal value for rates producing submaximal tetanic tension. A typical example of the relation between the discharge frequency of a peroneus longus tendon organ and the tension developed by a motor unit which excited this receptor is illustrated by Fig. 2. For stimulation rates above 40/sec, the receptor discharge increased, at first, with the motor

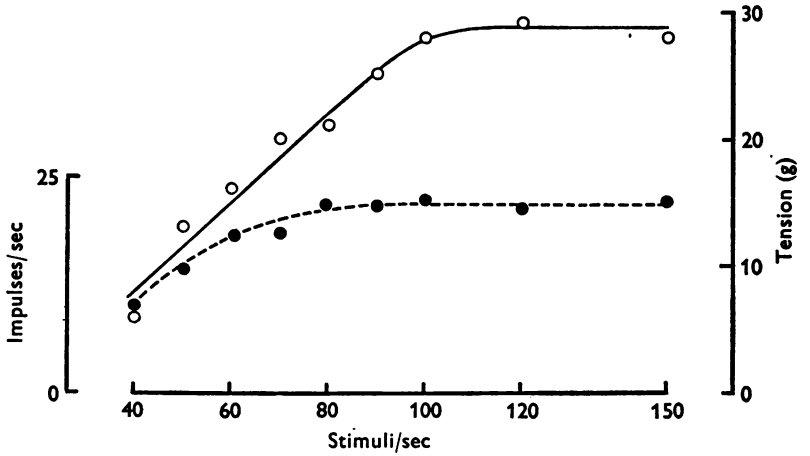

Fig. 2. Limited influence of increases in contractile tension developed by a motor unit on the response of an activated tendon organ. Comparison of the discharge frequency (●) of a peroneus longus tendon organ (conduction velocity of the Ib afferent: 102 m/sec) and of the tension (○) developed by one of its activating motor unit (conduction velocity of the motor axon: 90 m/sec) for increasing rates of stimulation of this unit.

unit tension but the maximal response (22 impulses/sec) was obtained with 21 g tension for stimulation at 80/sec, that is below the rate which produced the maximal tetanic tension. Increase in the motor unit tension from 21 to 28 g did not significantly accelerate the tendon organ discharge any further, as if the sensory endings activated by this unit were saturated. Actual saturation of this receptor did not occur since upon stimulation of a coarse ventral root filament containing several motor units, whose simultaneous contraction developed about 100 g tension, the same tendon organ fired at higher frequencies (not shown) and its maximal response then reached 75 impulses/sec. Fig. 3 shows another

example of this apparent saturation effect on two tendon organs from soleus, activated by the same motor unit. For the contraction of this unit the maximal responses of these receptors, respectively 32 and 45 impulses/sec, were reached upon stimulation of the motor unit at 25/sec producing 12 g tension, whereas the maximal tetanic tension was 14 g. Comparison of Figs. 2 and 3 shows that the rate of motor unit stimulation which elicited the tendon organ maximal response was lower for slow motor units (25/sec in the soleus) than for fast units (80/sec in the peroneus longus) as could be expected from the known difference between fusion frequencies for both types of units (Burke, 1967).

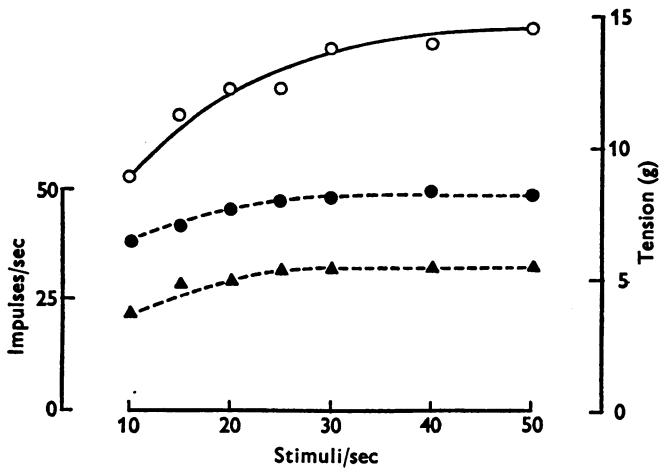

Fig. 3. The discharge of two soleus tendon organs activated by the same motor unit reach a maximal frequency for stimulation rates producing submaximal tetanic tension. The filled circles and triangles represent the discharge frequencies of the two receptors (conduction velocities of the Ib afferent: 81 m/sec for ● and 74 m/sec for ▲) during stimulation of the motor unit at increasing rates (conduction velocity of motor axon: 80 m/sec).

The maximal frequency response was not the same for all the motor units activating an individual receptor, nor was it reached for the same tension. Fig. 4 shows the response of a soleus tendon organ to gradually increasing tetanus of two different motor units. Unit *A* produced 10 g tension when stimulated at 10/sec, thus eliciting a sustained receptor discharge of 35 impulses/sec. With an increase of only 1 g tension, the discharge rose to 55 impulses/sec and that was the maximal response of the tendon organ to contraction of this motor unit, whatever the further increases in tension. By contrast, motor unit *B*, which developed a tension twofold that of *A*, elicited a slower discharge of the receptor, with a maximal frequency of 35 impulses/sec only, for 26 g tension.

In summary, variations in the contractile tension produced by an individual motor unit activating a tendon organ appear to influence the receptor discharge frequency within a limited range only, that is from unfused tetanus eliciting the minimal continuous firing of the receptor to the maximal response level. Between these limits, the ratio of the increase in receptor discharge frequency to the increase in tension can be considered

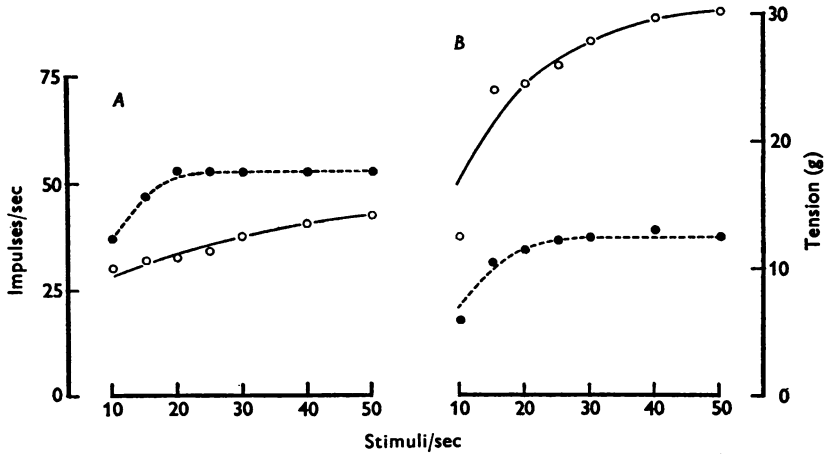

Fig. 4. Differences in the responses of a soleus tendon organ to graded tetanus of two of its activating motor units. *A*, discharge frequency of the receptor (filled circles; conduction velocity of the Ib afferent: 84 m/sec) during stimulation of a motor unit (conduction velocity of the motor axon: 74 m/sec) at increasing rates. The tension developed by this unit is represented by open circles. *B*, discharge frequency of the same receptor during stimulation of another motor unit. (Same conventions as in *A*; conduction velocity of the motor axon: 85 m/sec.)

as an approximate expression of the tendon organ sensitivity for contractile tension (i.e. the sensitivity of a linear equivalent tension transducer) expressed in impulses/sec per gram. Fig. 4 further illustrates the fact that an individual receptor displayed differences in sensitivity for tension produced by the different motor units whose contraction elicited its discharge; this soleus tendon organ had a much higher sensitivity for the tension developed by contraction of motor unit *A* (20 impulses/sec per gram) than for motor unit *B* (1·5 impulses/sec per gram). The sensitivities of six soleus tendon organs for eighteen activating motor units (range of tetanic tensions: 2–30 g) and of five peroneus longus tendon organs for seventeen motor units (tensions: 1–44 g) ranged from 1 to 25 impulses/sec per gram in our experimental conditions. In this sample the sensitivity of the receptors appeared equally low (1–5 impulses/sec

per gram) for motor units producing either less than 10 g or more than 30 g tetanic tension. For motor units developing tensions intermediate between 10 and 30 g, the activated tendon organs displayed a wide range of sensitivities and no correlation emerged between these and the strength of the motor units. Thus, for five peroneus longus motor units whose tetanic tensions were 10, 16, 19, 25 and 28 g the sensitivities of the activated tendon organs were respectively 1, 6, 1·5, 10 and 1 impulses/sec per gram.

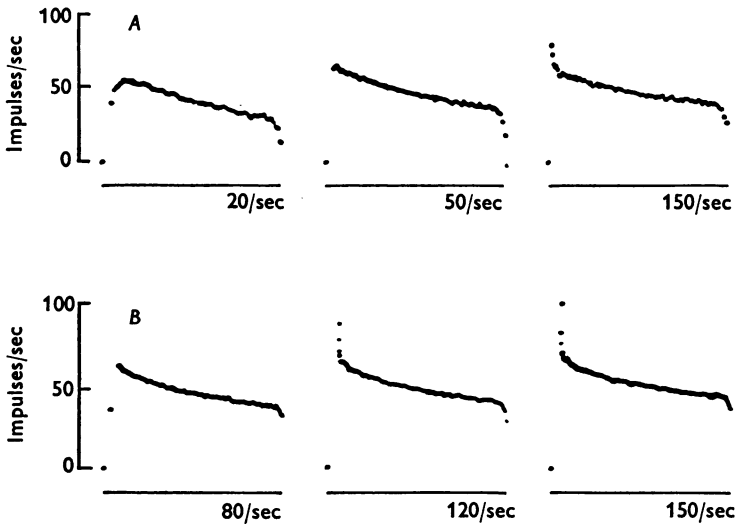

Fig. 5. Increase in the transient overshoot of tendon organ discharge frequency upon stimulation of its activating motor unit at rates above those eliciting the receptor maximal sustained response.

A, discharges of a soleus tendon organ (conduction velocity of the Ib afferent: 99 m/sec) recorded with an instantaneous frequency-meter during stimulation of a motor unit (conduction velocity of the motor axon: 81 m/sec; maximal tetanic tension: 13 g) at various rates. The horizontal bar indicates the duration of the stimulation and gives the time scale: 2 sec.

B, discharges of a peroneus longus tendon organ (conduction velocity of the Ib afferent: 117 m/sec) during stimulation of a motor unit (conduction velocity of the motor axon: 92 m/sec; maximal tetanic tension: 35 g) at various rates. Same conventions as in *A*.

For a group of twelve soleus motor units whose tetanic tensions ranged between 13 and 15 g (according to McPhedran, Wuerker & Henneman (1965) the mean tetanic tension of motor units in cat soleus is 14·8 g) the sensitivities of the activated tendon organs were evenly dispersed from 2·5 to 20 impulses/sec per gram. Two examples are illustrated by Fig. 3: for this motor unit contraction, the sensitivity of the receptor represented by a filled circle was 3·3 impulses/sec per gram and that of the receptor

represented by a triangle was 4 impulses/sec per gram. A third example is given by Fig. 4*A*.

Golgi tendon organs are known to be sensitive to the rate of change in muscle tension as well as to the tension itself (Jansen & Rudjord, 1964; Houk & Henneman, 1967). This velocity component of tendon organ sensitivity is demonstrated by the transient overshoot of the receptor discharge frequency during a rapid increase in muscle tension (Gregory & Proske, 1975). When a muscle is tetanized, the rate of tension development augments with increases of stimulation frequency well above the apparent fusion frequency (Buller & Lewis, 1965). Similarly, increases in stimulation frequency of a single motor unit will accelerate the rate of its tension development and, consequently, the tendon organs activated by this unit will exhibit larger overshoots of their discharge frequency during the period of muscle tension rise. The dynamic component of a tendon organ response is not affected by the apparent saturation of the receptor. Fig. 5 shows the examples of a soleus (*A*) and a peroneus longus tendon organ (*B*) each of which was activated by a motor unit developing maximal tetanic tension when stimulated respectively at 50/sec for *A* and 120/sec for *B*. In *A* the firing frequency of the tendon organ was maximal for contraction of the motor unit at 20/sec but the receptor discharge nevertheless displayed a larger overshoot when the motor unit was stimulated at 150/sec than at 20/sec. Similarly, in *B*, stimulation of the motor unit at 120 and 150/sec produced increasing overshoots of the receptor discharge despite the fact that its maintained discharge frequency was already maximal when the motor unit was stimulated at 80/sec.

DISCUSSION

It is now currently accepted that Golgi tendon organs function essentially as contractile tension receptors (Houk & Henneman, 1967; Houk, Singer & Henneman, 1971). However, their transducer properties appear difficult to appreciate because the tension sensed by the receptor is not related in a simple manner to the tension measured at the muscle tendon, as shown by the characteristics of the responses of individual tendon organs to the contraction of different motor units: (i) the firing threshold is not the same for all the units (Stuart *et al.* 1972; Jami & Petit, 1976); (ii) there is no simple relation between the tension developed by a motor unit and the frequency of the discharge it elicits (cf. Fig. 1). (Stuart *et al.* 1972; Stauffer & Stephens, 1975; Reinking *et al.* 1975); (iii) the maximal response of the receptor is reached at a different level of tension for each unit (cf. Fig. 4); (iv) the receptor sensitivity is different for contractile tension developed by the different units (cf. Fig. 4).

Moreover, as recently noted by Stauffer & Stephens (1975), the tendon organ sensitivity is higher when contractile tension is produced by single motor units (1–25 impulses/sec per gram in the present study; see also Houk & Henneman, 1967 and Stuart *et al.* 1972) than when it is developed by the whole muscle contraction (8 ± 3 impulses/sec per 100 gram in Jansen & Rudjord, 1964; see also Alnaes, 1967).

In their study of the tendon organs of medial gastrocnemius muscle, Reinking *et al.* (1975) similarly found a lack of relationship between the receptors firing rates and the tension developed by their activating motor units. However, they reported that the apparent sensitivity of the receptor during a motor unit contraction is inversely related to the strength of this unit but this statement is a mere implication of the definition they chose for the tendon organ apparent sensitivity (i.e. the ratio of the receptor maximal response frequency to the tetanic tension of the unit). The present results do not point to a relation, either direct or reverse, between a tendon organ sensitivity and the strength of its activating motor units, since the studied receptors displayed equally low sensitivities for weak and strong motor units.

The absence of simple relation between the tension produced by a motor unit and the characteristics of the tendon organ discharge it elicits might be partly accounted for as a consequence of the structure and location of tendon organs within the muscle. Some motor units may contribute more than a single fibre to the bundle of three to twenty-five muscle fibres inserted on a tendon organ (Bridgman, 1970; Barker, 1974). If a slow motor unit has more muscle fibres connected to a given tendon organ than a fast unit, its pull on this receptor can be more effective than the pull of the fast unit, despite the fact that the latter produces in total a larger amount of tension.

If one assumes, as did Reinking *et al.* (1975), that each motor unit whose contraction excites a given tendon organ contributes only one muscle fibre to the bundle inserted on the receptor, variations of innervation ratios from one unit to another might provide a clue for the observed discrepancies. Burke & Tsairis (1973) calculated the innervation ratios of three different gastrocnemius motor units: the larger comprised 750 fibres and produced 120 g tetanic tension and the two others, which contained 300 and 500 fibres developed respectively 35 and 39 g tension. Assuming linear addition of tensions of individual muscle fibres, such innervation ratios give mean tensions of 0·16 g per fibre for the 120 g unit, 0·12 g per fibre for the 35 g unit and 0·07 g per fibre for the 39 g unit. In soleus muscle, the same authors (Burke, Levine, Salcman & Tsairis 1974) found innervation ratios of 50 for a motor unit producing 4·2 g tetanic tension and of 427 for another unit developing 35·2 g tension; the

mean tension per individual fibre is the same, 0·08 g for both units. These figures indicate that the tension developed by a single muscle fibre is a variable fraction of its parent unit total tension.

The majority of tendon organs are located at musculo-aponeurotic junctions rather than in the tendon proper (Swett & Eldred, 1960; Barker, 1967) and this can further complicate the relation between the total tension measured at the tendon and the fraction of this tension which is actually applied to a receptor. For instance, it may happen that the orientation of the line of pull of a motor unit with respect to the main axis of the muscle tendon results in a loss of vectorial tension at the tendon (Rack & Westbury, 1969), whereas a tendon organ is always directly pulled upon by the muscle fibres inserted on it.

However, since muscle control could hardly take place without the central nervous system being informed about the over-all muscle tension and since Golgi tendon organs appear to be the most sensitive receptors for this parameter, it seems difficult to admit that their discharge would not contain the relevant information. A most likely assumption would be that the summed activities of all the tendon organs from a muscle (Reinking *et al.* 1975; see also Fig. 2 in Gregory & Proske, 1975) might be the statistically significant factor in this respect.

The tendency of tendon organ discharge frequency to 'saturate' when the stimulus strength is increased above a given level has been mentioned in several reports (Houk & Simon, 1967; Green & Kellerth, 1967; Stuart *et al.* 1972; Stauffer & Stephens, 1975). This effect does not seem to depend on a characteristic of the receptor itself since its frequency and tension parameters are different for different motor units and it does not interfere with the dynamic sensitivity of the Golgi tendon organ (cf. Fig. 5). Morphological studies (Bridgman, 1968; Schoultz & Swett, 1972; Swett & Schoultz, 1975) indicate that the mechanical events leading to the tendon organ excitation occur in two steps. Contraction of muscle fibres inserted on the receptor increase the tensile force of the tendon organ collagen bundles which in turn squeeze the afferent nerve terminals interwoven among them. The apparent saturation of the receptor discharge might be related to features of the linkage between the muscle fibres and collagen bundles, or of the linkage between the collagen bundles and the nerve sensory terminals, or of both.

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