J. Physiol. (1975), **248**, *pp.* 519–529
With 6 text-figures
Printed in Great Britain

RESPONSES OF TENDON ORGANS IN A LIZARD

BY J. E. GREGORY AND U. PROSKE
From the Department of Physiology, Monash University, Clayton, Victoria 3168, Australia

(*Received 13 November 1974*)

SUMMARY

1. In the lizard *Tiliqua* the tendons of the caudo-femoralis muscle are supplied by a nerve which runs separately from the muscle nerve.

2. Recordings of afferent discharges in the tendon nerve revealed the presence in the tendon of stretch-sensitive mechanoreceptors which responded to both passive changes in limb position and to muscle contraction.

3. A preparation of the tendon and its nerve were dissected free of surrounding tissue and studied in isolation while recording the activity of single functional units. The minimum tension in the tendon necessary for a maintained response from a receptor lay in the range 5–35 g (mean 16 g) and the firing rates at these tensions were in the range 5–14 impulses/sec (mean 9 impulses/sec).

4. Receptors showed a steep increase in firing rate with increase in tension up to about 120 g. The firing rate 30 sec after the onset of a tension change did not exceed 40 impulses/sec.

5. During the tension change the receptor responded with a burst of impulses whose frequency depended on the velocity of stretch. With large, rapidly rising tension steps peak firing rates of up to 300 impulses/sec were observed.

6. Tension and length changes recorded during rapid tendon-stretches were very similar, with little sag in tension at the new length. The response of all units however continued to fall throughout the stretch. Some of the possible causes of this adaptation have been discussed.

INTRODUCTION

Tendon organs are stretch-sensitive mechanoreceptors commonly located at the muscle-tendon junction. They are thought to signal muscle tension produced by passive stretch and active contraction.

Most studies of the physiological properties of tendon organs have been restricted to mammals, although it has been known for a long time that

similar receptors are found in the tendons of other vertebrates (Huber & De Witt, 1900; Regaud, 1907). In the lizard *Tiliqua* one of the tendons of the caudo-femoralis muscle contains a group of tendon organs. The feature which first attracted attention to these receptors is that they are supplied by a small nerve which leaves the main nerve trunk independently of the much larger muscle nerve (see Fig. 1). It has proved possible to dissect out the tendon with its nerve as an isolated preparation free of muscle tissue, and to study the responses of single receptors during stretch of the tendon at different rates and amplitudes. A preliminary report of this work has already been published (Gregory & Proske, 1974).

METHODS

The muscle and tendons with their respective innervation are shown in Fig. 1. Caudo-femoralis attaches proximally to lateral processes of caudal vertebrae and inserts by a tendon which branches into two portions. A short stout tendon attaches to the proximal end of the femur while a second thinner tendon extends along the length of the thigh to the popliteal fossa, where it attaches to ligaments and cartilages of the joint (Snyder, 1954). The nerve carrying the tendon organ afferent fibres leaves the nerve trunk separately from the muscle nerve. It then branches, supplying each of the two portions of the tendon.

The longer tendon was dissected free of surrounding tissue and, together with its nerve supply, removed from the animal and placed in a bath through which an aerated Ringer solution flowed. Afferent discharges were recorded from single functional units, prepared by splitting the nerve trunk into fine filaments. Each filament was tested for the presence of afferent activity by placing it over bipolar platinum electrodes and stretching the tendon. Action potentials were amplified and displayed on an oscilloscope. In most experiments the reciprocals of the intervals between successive action potentials were displayed rather than the action potentials themselves. This was done by means of a 'frequency meter', built from a design similar to that of Kay (1965). Responses were stored on tape (Hewlett Packard Model 3960 instrumentation recorder) or filmed using a Grass Kymograph camera.

The tendon was clamped at one end to an isometric tension transducer (built using Pye semiconductor strain gauges and having a compliance of 0·1 mm/kg). The other end was attached to an electromagnetic stretching device (Ling 406) supplied with feed-back. The tendon was stretched at a predetermined rate to different levels of tension and the discharge rate of receptors measured during the tension change. The total time of 'stretch and hold' was adjusted to be 40 sec, followed by a 50 sec test period.

In another series of experiments, the caudo-femoralis muscle and its tendons were left in place in the animal. Recordings of tendon organ discharges were made from the whole nerve supplying the longer tendon during passive limb movement or during muscle contraction. In some of these experiments, the tendon was cut distally and its end attached to a strain gauge, so that tension could be measured.

All experiments were performed at room temperature, which was between 21° and 26° C.

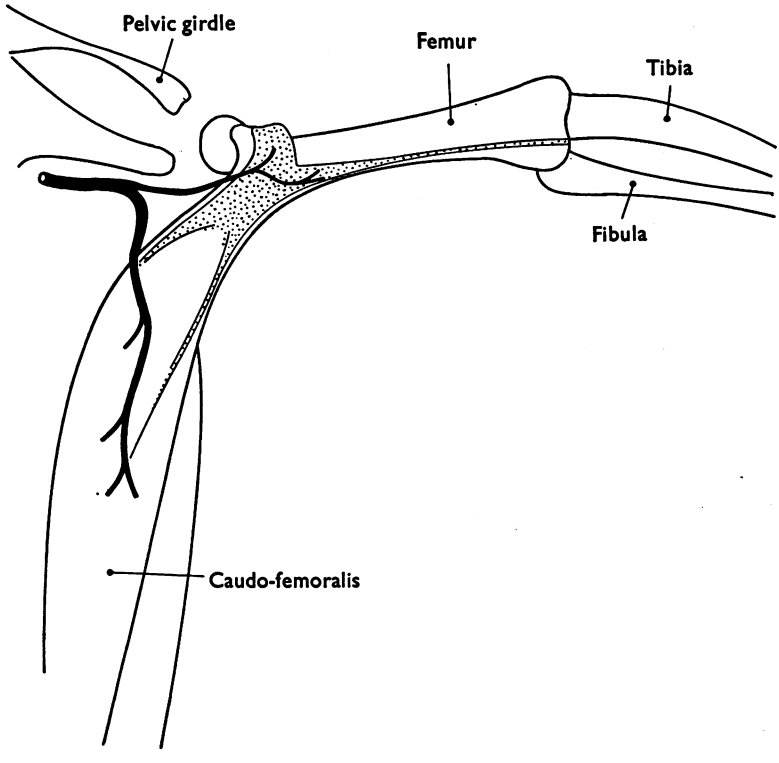

Fig. 1. Diagrammatic representation of ventral aspect of hind limb of *Tiliqua*, showing the arrangement of m. caudo-femoralis, its tendons of insertion (stippled) and the nerve supply (thick lines) to tendon and muscle.

RESULTS

Identification of receptors

Preliminary histological observations of silver stained preparations of the tendon revealed branching nerve endings typical of tendon organs. Sections of the nerve stained for myelin gave counts of sixteen to twenty axons, which had diameters of approximately 10 μm. Some attempt was also made to measure conduction velocities, but the short length of nerve made this difficult. Values obtained were in the range 30–40 m/sec.

Gross nerve recordings showed that the tendon contained stretch-sensitive mechanoreceptors. Vibration and local tactile stimuli were also effective in producing a response. Recordings during passive limb movement showed that receptors began firing when the limb was approximately at right angles to the body. When the limb was fully flexed, the tendon was quite slack and the receptors silent. If the caudo-femoralis muscle was contracted tetanically, receptors would begin firing at limb positions for

which they had previously remained silent. However, with the limb in the fully flexed position even a maximal tetanic contraction of the muscle did not produce sufficient tension in the tendon to produce a receptor discharge. Measurements of tension in the tendon with different amounts of passive tension (corresponding to various limb positions) gave, during maximal contraction of the muscle, peak tensions of 250 g with maximum rates of rise of tension in excess of 2000 g/sec.

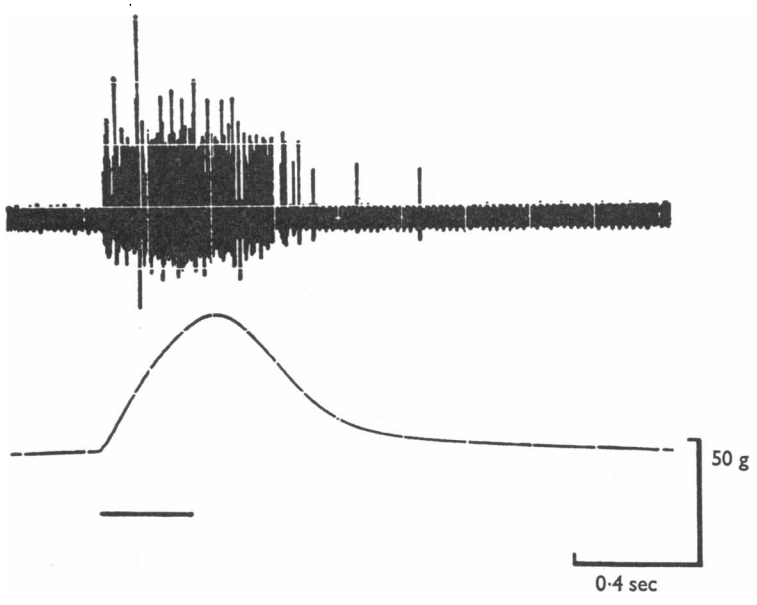

Fig. 2. Mass discharge from tendon organs (upper trace) recorded from tendon nerve during brief tetanic stimulation (40 impulses/sec) of the nerve to m. caudo-femoralis. Muscle tension shown on lower trace. Horizontal bar beneath lower trace indicates duration of stimulation.

An example of discharges recorded in the nerve, with the tendon under moderate passive tension, during a brief tetanic contraction of the muscle is shown in Fig. 2. The discharge is at its most intense during the rising phase of the contraction, falling off rapidly except for one unit during the falling phase. This sort of behaviour, typical of tendon organs, was characteristic of all units tested.

A detailed analysis was made of responses from fifteen receptors. None showed a resting discharge in the absence of applied tension. For each unit, measurements were made of the threshold tension for a minimal response and for a response sustained for 1 min. The tension necessary for the minimal response varied between 1 and 20 g (mean 7 g) while for the

sustained response it lay in the range 5–35 g (mean 16 g). The firing rate at threshold varied between 5 and 14 impulses/sec (mean 9 impulses/sec).

The impulse-frequency: tension relation

The response of a receptor to different levels of tension was measured by using rapidly rising tension steps of different amplitude and measuring the response after it had adapted to an approximately steady level. Examples of the responses of a single receptor to tension steps of different amplitudes are shown in Fig. 3. The tension changes very closely resembled the length changes, indicating that the tendon behaves as an almost purely elastic structure with very little viscosity. The responses however did not closely follow the shape of the tension step. An initial burst of impulses at a frequency of up to 300 impulses/sec associated with the rising phase of the step was followed by a gradual decline in firing throughout the period of stretch. The important conclusion from these records is that the adaptation of receptor discharge is not reflected by gross tension changes in the tendon as measured by the transducer.

The firing rate was compared with the tension 30 sec after the onset of the tension step. Although at this time the firing rate was still falling, its value appeared to be independent of the rate of the initial tension change and therefore was chosen as a measure of the static component of the receptor's response. An example of the relation between firing frequency and tension for one unit is shown in Fig. 4. The features which were typical of all of the responses recorded were a steep increase in firing rate with increase in tension up to 120 g and a peak firing rate which did not exceed 40 impulses/sec. For tensions above 120 g the adapted firing rate remained approximately constant or began to fall, although the initial transient response at the onset of tension became progressively larger.

In an attempt to explore further the relation between firing rate and tension, the above points were replotted on a double logarithmic scale. This produced a curve of which the initial points (up to 120 g) were well fitted by a straight line. The range of slopes measured varied between 0·24 and 0·59 (mean 0·42). The double logarithmic plot represents a power relation (see (Alnaes, 1967), with a mean value for the exponent of 0·42.

Responses to the rate of change of tension

The size of the initial peak in the response at the onset of a tension step depended not only on the size of the step but on the velocity of the tension change. An example of response during each of three stretches of identical amplitude but at different rates is shown in Fig. 5. The peak rate of firing during the stretch is seen to depend on the velocity of stretch. It reaches only 80 impulses/sec at the lowest rate while at the highest rate it exceeds

130 impulses/sec. One unexplained feature of the response seen with the lower stretch rates is that the firing rate reaches its peak value well before the end of the dynamic component of stretch and then begins to fall slightly. This is clearly seen with the low and intermediate stretch rates. It cannot represent saturation of the impulse generating mechanism since with the more rapid stretches higher firing rates are reached. One possibility could be that not all of the tension changes recorded by the transducer are being transmitted right to the receptor terminals.

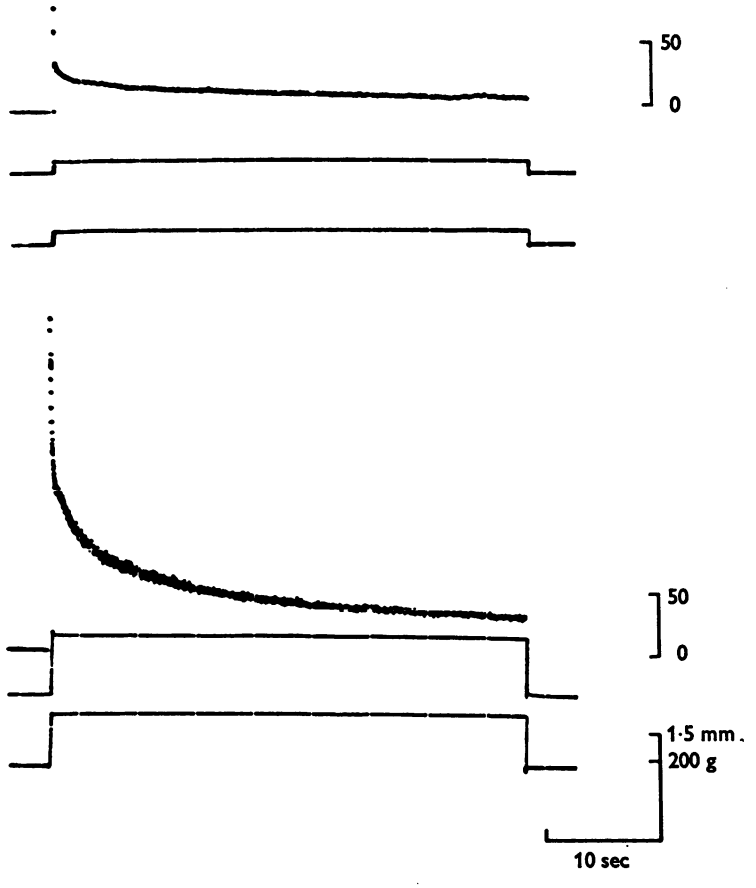

Fig. 3. Response of one unit to two rapid tendon-stretches of different amplitude. Response (top trace in each record) shown as reciprocals of successive spike intervals; calibration to the right of each trace is instantaneous frequency of firing in impulses/sec. Bottom trace in each record shows amplitude of stretch; upward deflexion indicates increase in length of the tendon. Middle trace represents tension in the tendon; tension prior to stretch about 2 g. Length and tension calibrations apply to both records.

The responses of other receptors conformed with this general pattern although the tension at which the firing rate began to level out differed between units. On several occasions the rate of increase in firing just prior to the peak was rather steeper than during the initial period of stretch. This would again suggest that tension changes at the receptor were different from those measured in the whole tendon.

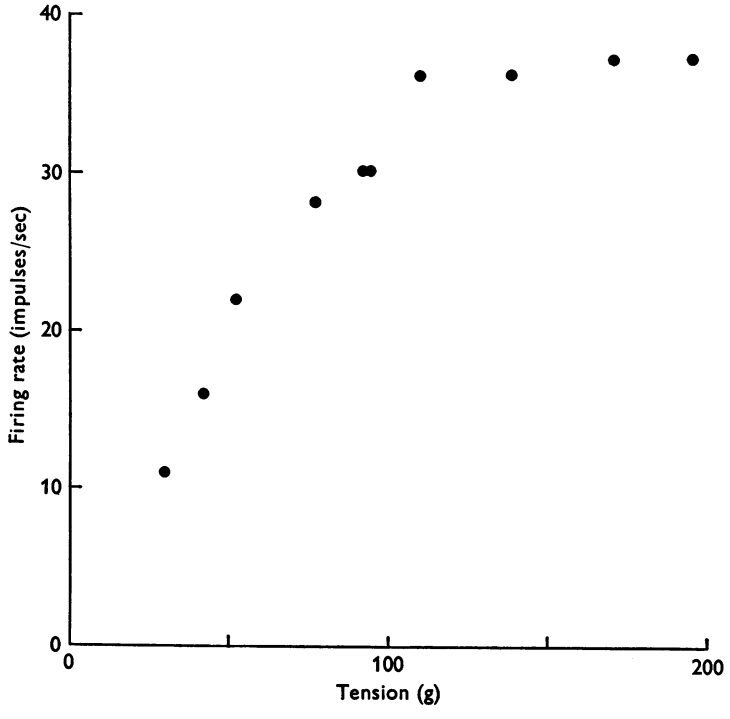

Fig. 4. Relation for one unit between tension in the tendon and rate of firing 30 sec after the onset of a rapid stretch.

As a convenient measure of the velocity component of a response, the dynamic index was calculated (Jansen & Matthews, 1962). This represents the difference between the peak firing rate and that 0·5 sec after the end of the tension change. In our experiments, however, it was decided to measure the rate, not 0·5 sec, but 5 sec after the tension change. A plot of the dynamic index against rate of increase of tension is shown in Fig. 6. The dynamic index increases gradually up to tension changes of 200 g/sec and beyond this much more steeply. Since preliminary measurements of the maximum rates of rise of tension in the tendon during contraction of its muscle (see earlier) exceeded 2000 g/sec the large velocity responses plotted in Fig. 6 may not be entirely unphysiological. What actual tension changes occur during a step cycle remains, of course, unknown.

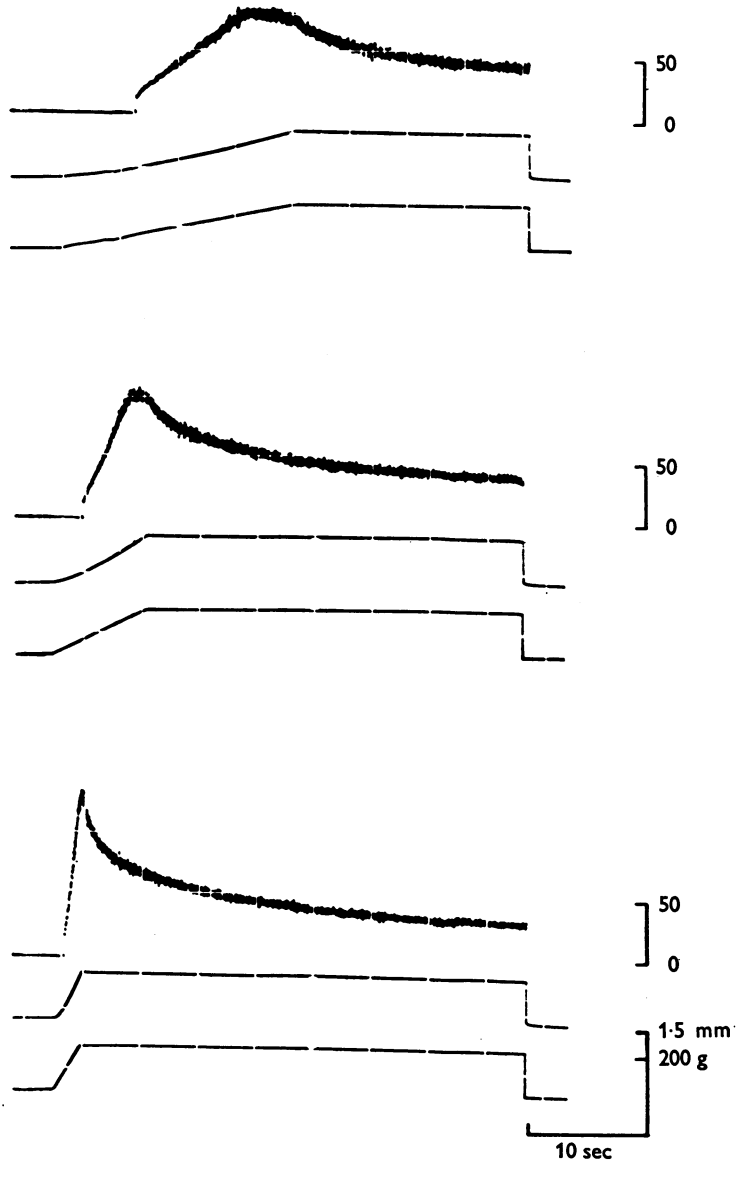

Fig. 5. Response of one unit to three tendon-stretches at different rates but of the same final amplitude. Response (top trace in each record) shown as instantaneous frequency of firing; calibration in impulses/sec to the right of each trace. Bottom trace in each record represents amplitude of stretch. Tension in the tendon is shown in the middle trace.

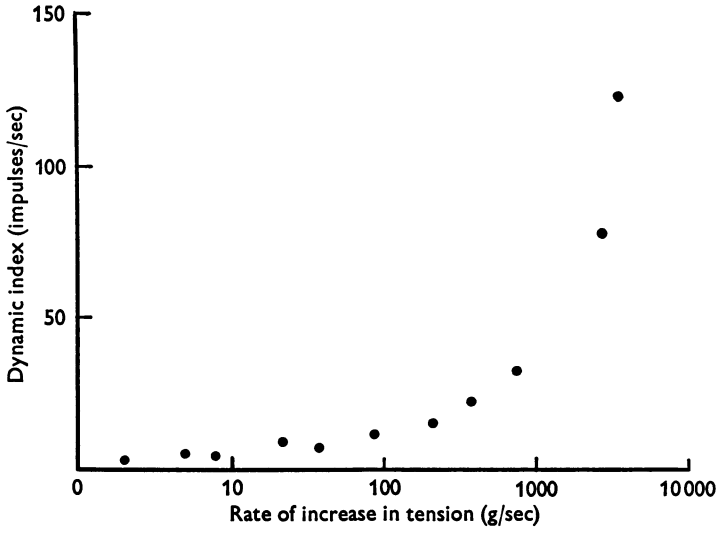

Fig. 6. Relation for one unit between stretch rate and dynamic index, using stretches of constant final amplitude. Values on the ordinate represent the difference between the peak firing rate during the stretch and the rate 5 sec after the end of the rising phase of the stretch.

DISCUSSION

Mammalian tendon organs are encapsulated nerve endings, located at the muscle–tendon junction. The nerve endings studied here do not appear to be enclosed within a capsule and they are located out in the tendon at some distance from the region of attachment to muscle fibres. Perhaps it would be more appropriate then, to compare the lizard endings with the 'Ruffini' endings of mammals. There is also a physiological basis for such a comparison. Ruffini endings are slowly adapting mechanoreceptors located in the connective tissue of joint capsules. They respond both to change and rate of change of joint position (Skoglund, 1956; Boyd, 1954). The frequency:tension relation of Ruffini endings (Eklund & Skoglund, 1960) resembles in several respects that for the tensions in excess of 250 g. Responses from the receptors in the lizard reached a peak of 40 impulses/sec for 120 g tension. However, in making this sort of comparison it should be kept in mind that the two sets of results were obtained under very different experimental conditions, Eklund & Skoglund making their measurements during a constantly rising (5 g/sec) tension.

A comparison with tendon organs in mammals encounters similar difficulties. The measurements which resemble ours most closely are those made by Houk & Simon (1967) on the cat soleus muscle. They determined

the relation between tension and the adapted response, allowing 60 sec of adaptation (cf. 30 sec used here). The slope of their plot was 3 impulses/sec per 100 g tension and peak firing rates of 20–30 impulses/sec for tensions in excess of 0·5 kg were reported. Alnaes (1967), using tibialis anterior of the cat and measuring the response 0·3 sec after a tension change, obtained a range of slopes of 4–15 impulses/sec per 100 gram. Alnaes also replotted his data on double logarithmic co-ordinates and from this obtained a power relation with a mean exponent of 0·49 (cf. 0·42 for the lizard endings).

The above comparisons suggest that the endings in lizard tendon respond at lower tensions than the mammalian receptors and increase their firing rate rather more steeply with increasing tensions. It should be kept in mind, however, that all of the responses in the lizard were obtained with an isolated segment of tendon. Stretch of a preparation comprising both muscle and tendon may give a very different distribution of tension, relative to the receptor endings, especially if these are located at the muscle–tendon junction. The fact that the lizard endings are positioned well out in the tendon must also mean that they signal mean tension in the tendon and not only that produced by one or a few selected motor units (cf. Houk & Henneman, 1967).

The velocity-sensitivity of the lizard endings compares with responses of Ruffini endings to velocity of movement of the joint (Skoglund, 1956), and the dynamic sensitivity of tendon organs (Houk & Simon, 1967; Alnaes, 1967; Anderson, 1974). Unlike the situation for muscle spindles, no simple structural feature can account for the velocity sensitivity of tendon organs. Certainly the mechanism proposed by Schoultz & Swett (1972) that nerve endings of tendon organs are stimulated by lateral compression from collagen bundles, provides no satisfactory explanation.

During tension changes a tendon behaves as an almost purely elastic structure, provided the tension does not exceed certain limits (Rigby, Hirai, Spikes & Eyring, 1959). This is reflected in the tension records of Figs. 3 and 5. The initial 'overshoot' following rapidly rising tension steps is relatively small and the new level of tension is held with little subsequent 'sag'. The response of the receptors, on the other hand, after reaching a peak at the end of the tension change, falls over the whole period during which the new tension is maintained. Such adaptation may be attributed to one or more of several causes: mechanical adaptation which cannot be detected by the tension recorder (localized changes in tension at the receptor terminals), accommodation at the site of impulse initiation or adaptation of the generator potential itself. There is no simple way of distinguishing between these possibilities. However, histological examination revealed no obvious specialization of the tendon's structure within the

sensory region. This suggests that at least a part of the observed adaptation may be contributed at the level of the transduction process. It is hoped in future experiments to explore this possibility further.

The authors would like to thank Professor A. K. McIntyre for help with the manuscript. Financial assistance was provided by the National Health and Medical Research Council of Australia.

REFERENCES

ALNAES, E. (1967). Static and dynamic properties of Golgi tendon organs in the anterior tibial and soleus muscles of the cat. *Acta physiol. scand.* **70**, 176–187.

ANDERSON, J. H. (1974). Dynamic characteristics of Golgi tendon organs. *Brain Res.* **67**, 531–537.

BOYD, I. A. (1954). The histological structure of the receptors in the knee-joint of the cat correlated with their physiological response. *J. Physiol.* **124**, 476–488.

EKLUND, G. & SKOGLUND, S. (1960). On the specificity of the Ruffini-like joint receptors. *Acta physiol. scand.* **49**, 184–191.

GREGORY, J. E. & PROSKE, U. (1974). Tendon organs in a lizard. *Proc. Aust. Physiol. Pharmac. Soc.* **5**, 73–74.

HOUK, J. & HENNEMAN, E. (1967). Responses of Golgi tendon organs to active contractions of the soleus muscle of the cat. *J. Neurophysiol.* **30**, 466–481.

HOUK, J. & SIMON, W. (1967). Responses of Golgi tendon organs to forces applied to muscle tendon. *J. Neurophysiol.* **30**, 1466–1481.

HUBER, G. C. & DE WITT, K. (1900). A contribution on the nerve terminations in neuro-tendinous end organs. *J. comp. Neurol.* **7**, 169–230.

JANSEN, J. K. S. & MATTHEWS, P. B. C. (1962). The central control of the dynamic response of muscle spindle receptors. *J. Physiol.* **161**, 357–378.

KAY, R. H. (1965). A reciprocal time-interval display using transistor circuits. *Electron. Engng* **37**, 543–545.

REGAUD, C. (1907). Les terminations nerveuses et les organes nerveux sensitifs de l'appareil locomoteur. II. *Revue gén. Histol.* **1**, 587–689.

RIGBY, B. J., HIRAI, N., SPIKES, J. D. & EYRING, H. (1959). The mechanical properties of rat tail tendon. *J. gen. Physiol.* **43**, 265–283.

SCHOULTZ, T. W. & SWETT, J. E. (1972). The fine structure of the Golgi tendon organ. *J. Neurocytol.* **1**, 1–26.

SKOGLUND, S. (1956). Anatomical and physiological studies of knee-joint innervation in the cat. *Acta physiol. scand.* **36**, suppl. 124, 1–101.

SNYDER, R. C. (1954). The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *Am. J. Anat.* **96**, 1–45.