A Muscle Tension Receptor in the Locust Leg

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Summary. The anatomy of the sensory nerve branches in the mesothoracic and prothoracic femur of *Schistocerca* is described. A single multipolar receptor cell on the cuticular end of the distal flexor tibiae muscle fibres is identified and examined. This cell is shown to be a tonic receptor for active and passive tension in the muscle fibres to which it is attached. It generally causes reflex excitation of flexor motoneurons and inhibition of the slow extensor neuron, although the sign of the reflexes can be reversed.

Introduction

In vertebrate limbs the Golgi tendon organs are well known as receptors for active muscle tension (e.g. Houk and Henneman, 1967). Tension receptors have also been found on the apodemes of leg muscles in *Cancer* (Macmillan and Dando, 1972) and *Limulus* (Eagles, 1978). However, no receptors directly sensitive to muscle tension have so far been identified in the legs of insects, although there is physiological evidence for their existence in the locust (Burrows and Horridge, 1974) and in the stick insect (Bässler, 1977). In addition to receptors for joint position and movement (Burns, 1974; Coillot and Boistel, 1968) the insect leg is well supplied with campaniform sensilla which detect cuticular stress (Pringle, 1938) and it has been suggested that the latter receptors also function indirectly as muscle tension receptors.

In this paper we describe the anatomy of sensory nerve branches in the femur and report a single receptor cell attached to the flexor tibiae muscle of the prothoracic and mesothoracic legs of the locust, which responds to passive and active tension in the

muscle, and which is capable of mediating reflexes in the femoral muscles.

Materials and Methods

The present work was performed on the mesothoracic leg of the adult female locust, *Schistocerca americana gregaria*. The leg was removed from the animal and mounted ventral side down on Tackiwax. In order to measure isometric tension in the flexor tibiae muscle the tibia was disarticulated, cut to a 1 mm stump and attached to a silicon strain gauge transducer (compliance 0.05 mm/g) which could be moved to stretch the muscle. In some experiments the tibia was left intact to ensure that the muscle length remained within its natural range and the femur-tibia angle was measured visually against a protractor scale. The dorsal cuticle of the femur and the extensor tibiae muscle were removed and the whole leg was immersed in circulated, oxygenated saline (Usherwood and Grundfest, 1965) at room temperature. Records of activity from the sensory nerves in the femur were made with a glass suction electrode, gold plated to increase the signal to noise ratio. Passive tension was produced in the flexor tibiae muscle by extending the tibia or by stretching the muscle directly with a lever on its apodeme which was attached to the armature of a small relay. Active tension in the flexor muscle was induced by stimulating the motor nerve (nerve 5B2). Neural activity was recorded on magnetic tape and either photographed from the oscilloscope screen or photographed from an instantaneous frequency display.

In order to study reflexes mediated by the tension receptor the leg was fixed and dissected in the same way, but was left attached to the locust. Nerve 5B2 was cut at the proximal end of the femur (see Fig. 1A) and motoneuron activity was recorded from the proximal side of the cut and from the extensor tibiae motor nerve. Tension was developed in the flexor tibiae muscle by stimulating nerve 5B2 distal to the cut. All branches of nerve 5 were cut except the one from the tension receptor which was monitored to check receptor function. In some experiments the femurtibia joint and nerves 5B1b and 5B1c were left intact. The tibia was then moved with a galvanometer motor driven by an electronic ramp generator so that the flexor muscle was both passively stretched and reflexly excited via the chordotonal organ.

The anatomy of the sensory nerve branches in the leg was determined by perfusing cobalt chloride peripherally down the nerves and precipitating it as cobalt sulphide. This was done by sucking the cut end of the nerve into a glass suction electrode filled with 0.5 M cobalt chloride.
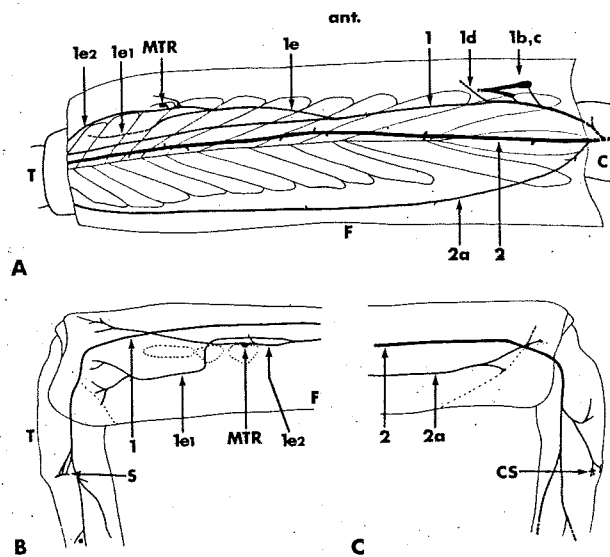
Fig. 1 A–C. Anatomy of sensory nerve branches of the mesothoracic leg of the locust. **A** Dorsal view of branches of nerve 5B in left femur; **B** Anterior view of branches of nerve 5B1 in right proximal tibia; **C** Posterior view of branches of nerve 5B2 in right proximal tibia. All nerves numbered are branches of nerve 5B. *MTR*, muscle tension receptor; *CS*, campaniform sensilla; *S*, subgenual organ; *C*, coxa; *F*, femur; *T* tibia

Results

Anatomy

In the femur of the prothoracic and mesothoracic legs of the locust the extensor tibiae muscle lies under the dorsal cuticle while the larger flexor tibiae muscle lies in the lower half of the femur. In structure both muscles are a combination of pinnate and fusiform type and they are composed of a number of discrete muscle bundles or units (defined by Hoyle, 1955) attached to a common apodeme. The flexor tibiae muscle consists of 10–12 anterior muscle bundles attached to the cuticle in a row of approximately circular discrete insertions, the same number of posterior bundles with elongated insertions tending to merge into one another, and a single proximal bundle with a ventral insertion very close to the trochanter. There is no accessory flexor corresponding to that in the metathoracic leg.

A single large nerve trunk enters the femur from the coxa. It is formed by the fusion in the coxa of nerves 3B2 and 5B1 (Campbell, 1961) and divides into two major branches in the femur, nerve 5B1 and nerve 5B2 as shown in Fig. 1A.

Nerve 5B1. This nerve innervates the chordotonal organ (Burns, 1974) and then gives off two more branches in the femur before passing into the tibia

where it innervates sensory hairs near the joint, the subgenual organ and cuticular receptors a little further down the tibia (Fig. 1B). The first of the two major branches (n.5B1d) carries the only motor axons in the nerve and supplies the extensor muscle. The second branch (n.5B1e) separates from the main nerve half way along the femur and runs along the anterior dorsal surface of the flexor muscle for a short distance before dividing into two smaller nerves. The first of these (n.5B1e1) continues along the surface of the muscle and then dives down between two flexor muscle bundles to innervate hairs on the anterior face of the distal femur. The close association between the nerve and the muscle at this point suggested that there might be sensory receptors involved, but none could be identified. The second half of the nerve (n.5B1e2) gives rise to a small branch connected to the flexor tension receptor (Fig. 2) and one innervating a small field of cuticular hairs before passing along the anterior cuticle to innervate dorsal mechanosensory hairs including the very large ones immediately dorsal to the femur-tibia joint.

Nerve 5B2. This nerve contains the motor axons of the flexor tibiae, the retractor unguis and the tibial muscles. It gives rise to one sensory branch in the femur, the lateral nerve (n.5B2a) which innervates the multipolar joint receptors (Williamson and Burns, 1978) and sensory hairs on the posterior face of the femur. All the remaining sensory fibres in the nerve originate in tibial or tarsal receptors. Upon entering the tibia nerve 5B2 divides into three branches (Fig. 1C) the first of which supplies three groups of five campaniform sensilla and some sensory hairs. The remaining branches continue to the tarsus, forming the dorsal and ventral nerves (Kendall, 1970).

Flexor Tension Receptor. This receptor is a single large multipolar cell located at the base of the second or third most distal anterior bundle of the flexor tibiae muscle. It is about 60 μm long and 20 μm in diameter (Fig. 2) and has four major dendrites which branch profusely to connect with more than 7 muscle fibres over a distance of about 600 μm. Some of the fine processes of the dendrites attach to the surface of the outermost flexor muscle fibres within 20 μm of their attachment to the cuticle, while most of them pass between the fibres at the same level so that their sites of attachment are within the muscle. No direct connections between the cell and the cuticle were found. From its shape the receptor cell can be classified as a type II mechanosensory neuron (Zarwarzin, 1912) or a multiterminal cell (Finlayson, 1968). It is similar in shape to those found in the abdomen of Orthoptera (Slifer and Finlayson, 1956)
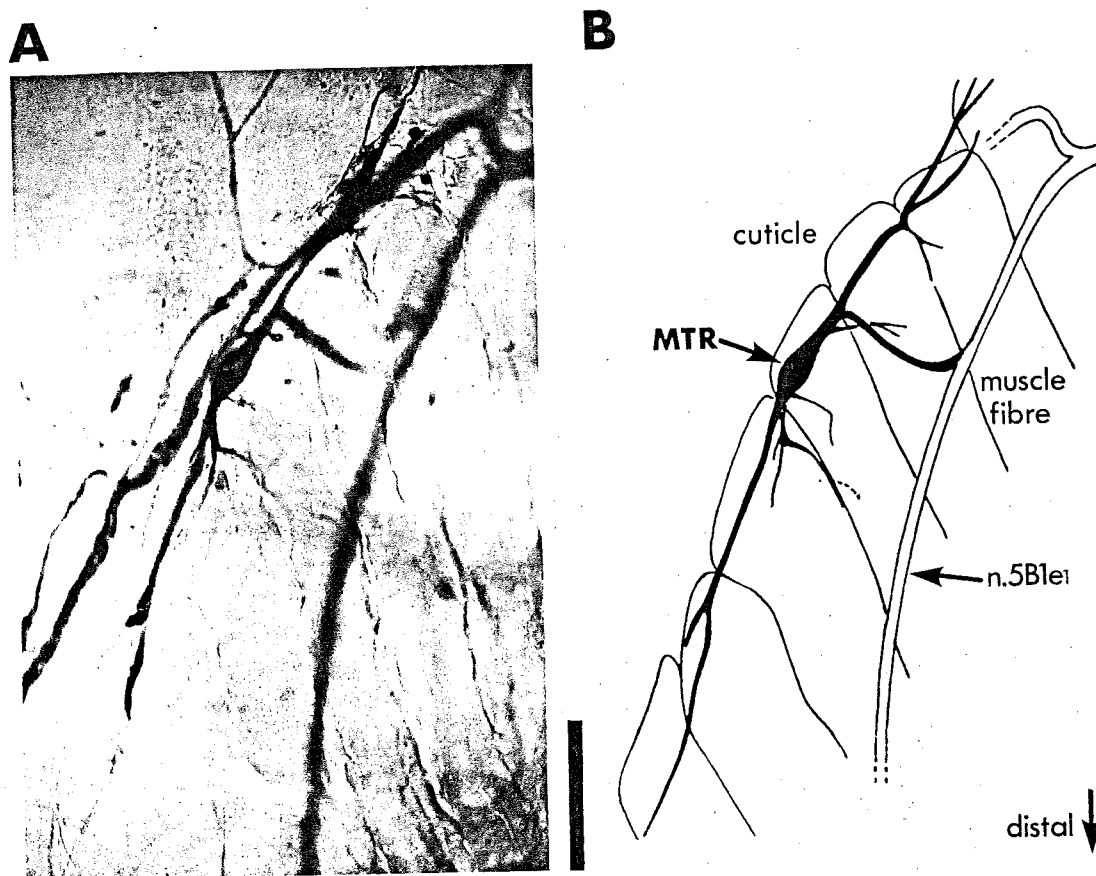
A

B

cuticle

MTR→

muscle fibre

←n.5B1e₁

distal ↓

Fig. 2A and B. Morphology of flexor muscle tension receptor (MTR). **A** Branches of nerve 5B1e filled with cobalt sulphide; **B** Diagram of the same preparation. Scale bar = 100 μm

but unlike them it is not attached to a single specialised muscle fibre.

The anatomical features described above are almost identical in the prothoracic and mesothoracic legs of the locust, but are different from those of the metathoracic leg. In the latter, the chordotonal organ is distal in position, Brunner's organ is present, the proximal tibia has a specialised buckling region and fewer campaniform sensilla (Heitler and Burrows, 1977) and nerve branch 5B1e is absent. No structure corresponding to the mesothoracic flexor tension receptor could be found.

Physiology

In order to evaluate the sensory contributions of the nerve branches described above, their activity was monitored in the femur of an isolated leg while the tibia was passively flexed and extended over the 90–120° range used in walking (Burns, 1973). Recordings from the distal parts of nerve 5B1 (Fig. 3E) and 5B2 (Fig. 3D) show activity from tibial receptors which may be responding to vibration (subgenual or-

gan) and cuticular stress (campaniform sensilla). Activity in nerve 5B2a, the only sensory branch of nerve 5B2, comes from the multipolar joint receptors responding directly to tibial position (Williamson and Burns, 1978). Nerve 5B1 shows the highest level of activity (Fig. 3A), most of which comes from the chordotonal organ in response to tibial position (Burns, 1974). However, after cutting nerves 5B1b, 5B1c and 5B1 to the tibia, some sensory activity can be seen coming from nerve 5B1e (Fig. 3C). This activity comes from a single small axon with a spike amplitude only 3–5 times the noise level and some 30 times smaller than the spike from the large sensory hair afferents running in nerve 5B1e. It persists when all the branches of nerve 5B1e are cut distal to the multipolar cell but ceases when the nerve is cut proximal to the cell. It is also greatly increased by any mechanical disturbance to the flexor muscle near to the cell. Thus the axon almost certainly originates in the multipolar cell.

The receptor axon is continuously active at 5–10 spikes per second when the flexor tibiae muscle is fully relaxed, but when the muscle is stretched by rapidly extending the tibia the firing frequency in-
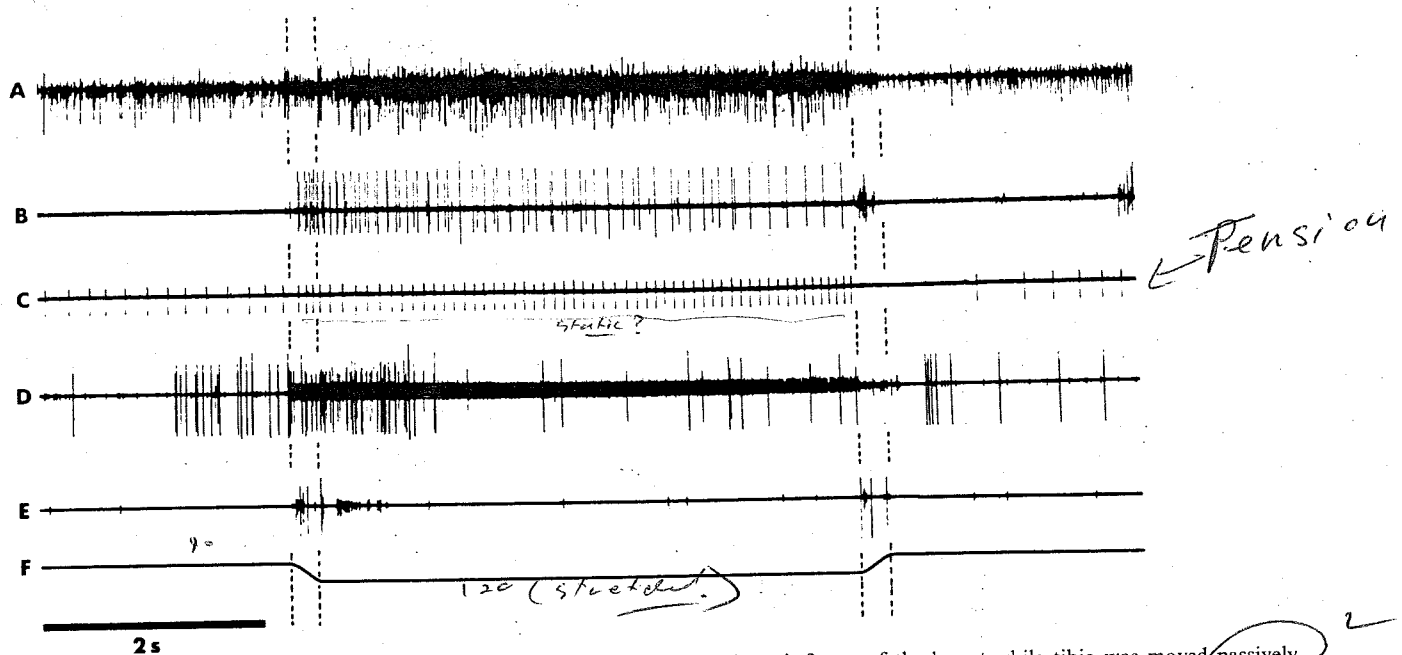
Fig. 3A–F. Records made from sensory nerve branches in the isolated mesothoracic femur of the locust while tibia was moved passively. Records are from: **A** Nerve 5B1 proximal (chordotonal organ); **B** Nerve 5B2a (multipolar joint receptors); **C** Nerve 5B1e (flexor tension receptor); **D** Nerve 5B2 distal (tibial receptors); **E** Nerve 5B1 distal (tibial receptors). **F** Movements of tibia between a femur-tibia angle of 90° (trace up) and 120° (trace down). Gain was different for each trace

creases in a response which has both phasic and tonic components (Fig. 4D). The phasic response is confined to the first 0.5 s after the muscle is stretched and also appears as a transient reduction in firing frequency below the rest level when the muscle is relaxed. If the muscle is stretched to different lengths within its physiological range by increasing the femur-tibia angle (FTA), both the tonic activity in the receptor axon and the activity in the first 10 s after the movement increase non-linearly (Fig. 4E). The relationship between muscle length and FTA is almost linear (Fig. 4C) showing that the non-linearity in the response must reside in the muscle fibres or the receptor. It also suggests that the apodeme of the flexor muscle is fairly stiff where it attaches to the tibia since a completely flexible apodeme would result in a sinusoidal relationship between length and FTA. From the responses to passive extension of the muscle it is not possible to show that the effective stimulus is muscle tension rather than length, although the firing frequency in the receptor axon (Fig. 4E) appears to be very closely related to the passive tension in the muscle (Fig. 4B). The close similarity between the instantaneous frequency in the receptor axon (Fig. 4D) and the passive muscle tension during a quick stretch (Fig. 4A) also suggests that the phasic component of the response may be entirely due to the mechanical properties of the muscle.

The responses of the receptor to active contractions of the flexor muscle do show that it is primarily sensitive to muscle tension. If the muscle is made to twitch isometrically by stimulating the excitatory axons in nerve 5B2 after cutting the nerve branches to the rest of the muscle, the receptor activity increases (Fig. 5A), but if the tibia is free to move so that conditions are isotonic, the receptor does not respond (Fig. 5C). When the region of the muscle containing the receptor twitches under isometric conditions the frequency in the receptor nerve accurately follows the tension, with a lag of about 40 ms (Fig. 5D, E). The response frequency increases with increasing rest tension in the muscle (Fig. 6) when the muscle is passively stretched, although this reduces the amplitude of the muscle fibre movement. The receptor also responds to the reduction in tension induced by stimulating the inhibitory fibres in the flexor motor nerve (Fig. 5B).

Like the chordotonal organ (Burns, 1974) the responsiveness of the tension receptor depends on its environment during the experiment. It is most responsive in haemolymph with the tracheal system functioning and its sensitivity is similar in circulated, oxygenated saline. However, if the saline is still, or is not oxygenated the responses of the receptor to isometric twitches disappear, leaving only the responses to passive tension. This may be the result of a loss of phasic responsiveness.

Reflexes Mediated by the Tension Receptor

If the tension receptor normally participates in the coordination of leg muscles it should be possible to

A

B

C

D

E
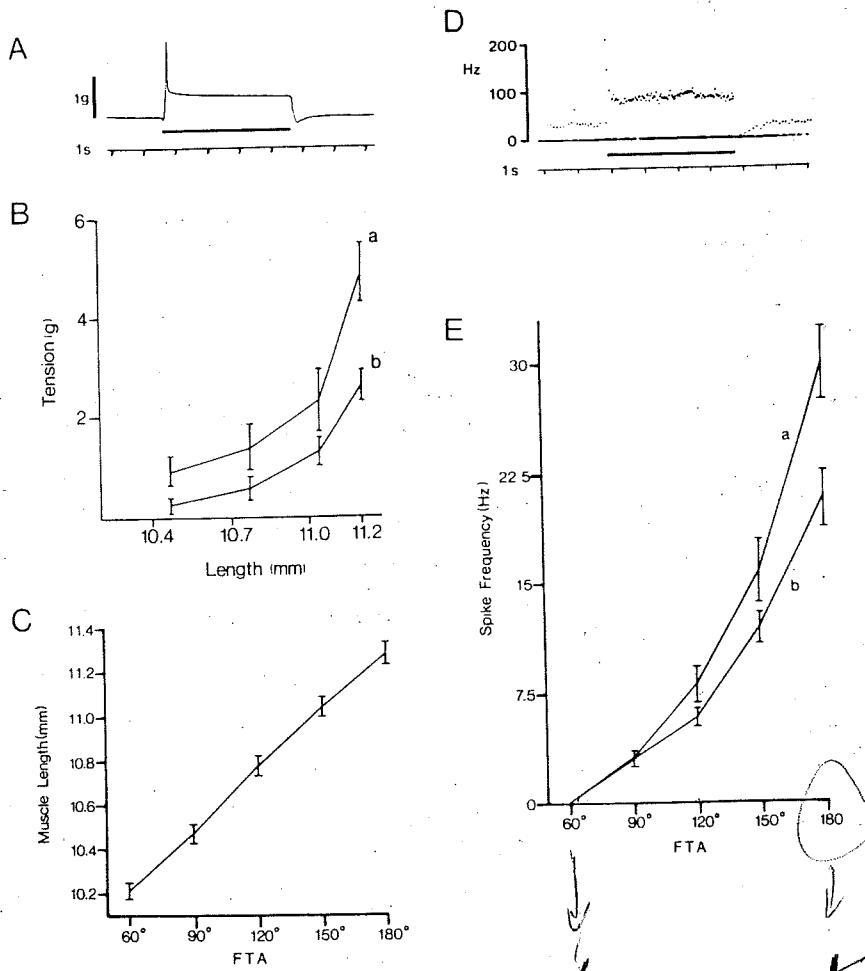
Fig. 4. A Passive tension in the flexor tibiae muscle when muscle was stretched from 10.5 to 10.8 mm length for duration of the bar;
B Peak (a) and plateau (b) passive tension in the muscle when stretched to different lengths at 1.4 cm/s;
C Relationship between muscle length and femur-tibia angle (FTA);
D Instantaneous frequency display of tension receptor response when muscle was stretched from 10 to 11.5 mm length for duration of the bar;
E Spike frequency in the receptor axon in the first 10 s after extending tibia to the angle shown (a) and in subsequent 100 s. All experiments were done on legs of same size

A

B

C

D

E
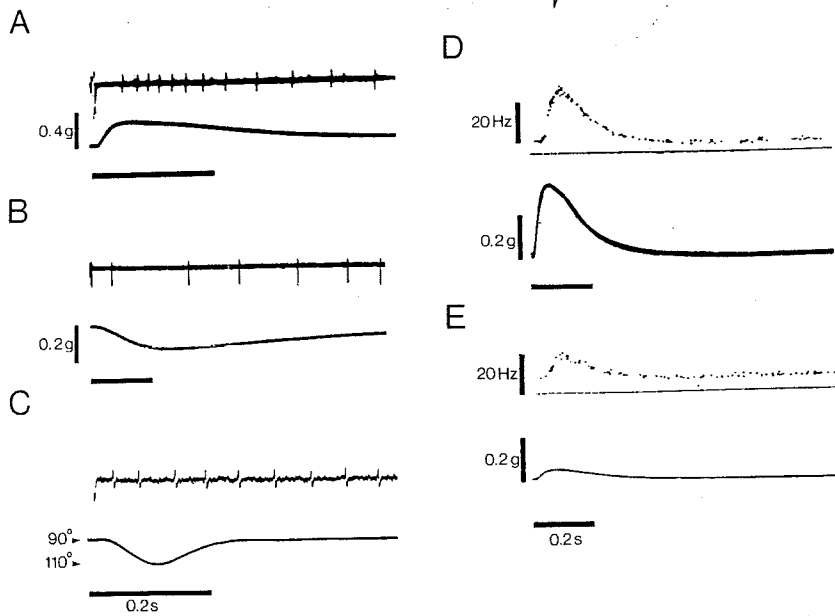
Fig. 5A–E. Responses of tension receptor to twitch contractions of flexor tibiae muscle.
A Maximal isometric twitch of whole muscle;
B Isometric relaxation due to single stimulus to the inhibitory axons;
C Near isotonic twitch of muscle with the femur-tibia angle recorded;
D and **E** Instantaneous frequency plots of responses to isometric twitches of two different strengths in the part of muscle to which the receptor is attached. Time calibrations the same for all records
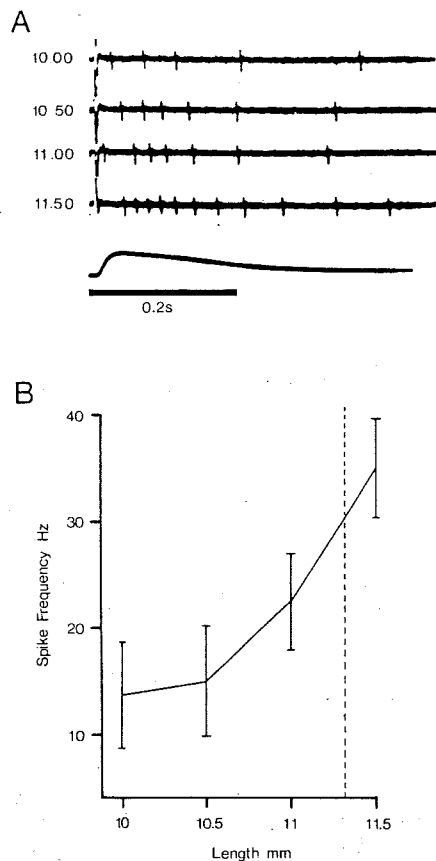
A

B

Fig. 6A and B. Responses of tension receptor to isometric twitch contractions of flexor tibiae muscle at different rest lengths. A Typical records at rest lengths marked; B Increase in receptor firing frequency above resting rate. Dotted line shows maximum natural length of muscle
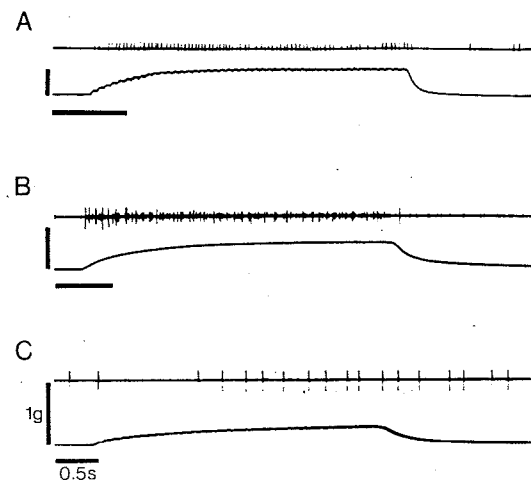
A

B

C

Fig. 7. A Activity in tension receptor axon during a maintained flexor muscle contraction; B and C Reflexes evoked by receptor in flexor motor nerve (B) and slow extensor tibiae (SETi) motoneuron (C) in response to active tension in distal part of flexor muscle (lower traces). Flexor motor nerve cut half way along the femur and stimulated distal to the cut to induce a contraction in the part of muscle containing the receptor. The cut prevented flexor reflex from affecting the receptor. Calibrations the same for all records
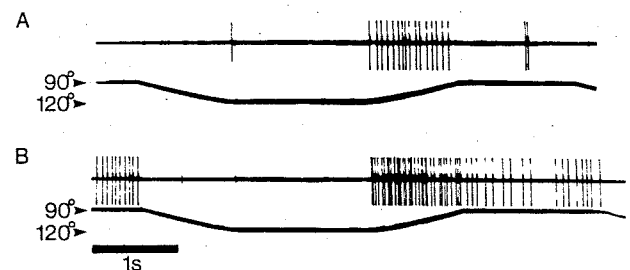
A

B

Fig. 8A and B. Influence of flexor tension receptor on resistance reflex in slow extensor tibiae (SETi) motoneuron. A Resistance reflex in intact leg; B Resistance reflex with tension receptor axon cut. Lower traces show imposed movement of the tibia

demonstrate that its activity has an influence on motoneuron firing patterns. This was attempted by developing tension in the part of the muscle connected to the receptor and looking for reflex responses in the flexor and extensor motoneurons. Typical results are shown in Fig. 7. This demonstrates firstly that the receptor responds well to maintained contraction of the muscle (Fig. 7A), which is more like the natural behaviour of the muscle in the intact locust, and secondly, that this pattern of receptor activity causes a reflex activation of a number of slow flexor motoneurons (Fig. 7B) and a transient inhibition of the slow extensor motoneuron (SETi) (Fig. 7C). These positive feedback reflexes onto the flexor neurons were found in 18 out of 20 cases, while the inhibition of the SETi occurred in 6 out of 7 cases. In the remaining animals the signs were reversed, so that the flexor reflex became negative and the SETi was excited by the receptor.

The reflex onto the SETi is less clear than the flexor reflex and can be demonstrated more convinc-

ingly by looking at its effect on the normal resistance reflex of the intact leg. With all the sensory systems in the leg intact the SETi is usually activated when the tibia is passively flexed and its firing frequency depends on the velocity of the movement (Fig. 8A). When the flexor tension receptor axon is cut the resistance reflex is considerably enhanced (Fig. 8B), suggesting the removal of an inhibitory input. When the chordotonal organ is also removed, the resistance reflex disappears altogether.

Discussion

The results show conclusively that the prothoracic and mesothoracic femurs of the locust contain a single neuron whose axon runs in nerve 5B1e2 and which

is a tonic receptor for tension in one of the distal bundles of the flexor tibiae muscle. There seems little doubt that this muscle tension receptor (MTR) is the large multipolar neuron located at the base of one of these bundles. The properties of the receptor are very similar to those of the single unit investigated by Bässler (1977) in the stick insect. Bässler was unable to identify the neuron responsible, but comparison with the locust leg suggests that the large nucleus he found on stick insect nerve F121 is the correct choice. The locust muscle tension receptor may be analogous to the large multipolar neurons found at both ends of the tibial flexor muscle of *Limulus polyphemus* (Eagles, 1978; Eagles and Gregg, 1978). However, in this animal the cells at the insertion of the muscle are reported to be receptors for muscle length rather than tension.

The muscle tension receptor is morphologically very similar to the multiterminal stretch receptors attached to abdominal muscle fibres in many species of insect, in centipedes and in scorpions (Finlayson, 1976). In *Rhodnius* (Hemiptera) the abdominal receptors resemble the locust muscle tension receptor in that their dendrites are attached to a number of muscle fibres (Anwyl, 1972), but in most insects so far examined each receptor is connected to only one muscle fibre. If the muscle fibres concerned are part of the main segmental muscle the receptors could function similarly to the femoral muscle tension receptor and monitor muscle tension, but if they are innervated separately the receptors may function as segment length detectors.

The locust muscle tension receptor differs from tension receptors on the leg muscles of crustaceans and vertebrates in that it is a single cell located in a contractile region near the fixed end of the muscle rather than a multicellular organ located on the tendon. Although this means that it can only monitor tension in a small region of the muscle this is also true of a single neuron in the vertebrate Golgi tendon organ which usually monitors the tension in a restricted number of muscle fibres (Barker, 1967) all of which may be separately innervated (Reinking et al., 1975). In both receptors the sensitivity to active tension is greater than to passive force applied to the tendon because much of the passive tension is developed in connective tissue or muscle fibres not connected to the receptors (Houk, 1967). There is currently no evidence that the neurons of the crustacean tendon organ are differentially sensitive to different parts of the muscle although the fact that the neurons are distributed along the length of the apodeme in a pinnate muscle (Macmillan and Dando, 1972) would seem to place them in a good position to do so.

Since the locust flexor tibiae muscle is also pinnate in form it is not clear why the muscle tension receptor is located on the muscle fibres rather than the tendon. It may be that this position confers a special sensitivity to local contraction of the associated fibres, although there was no indication that these fibres are innervated differently from others in the same region. This region of the muscle is more tonic than the more proximal parts so that sensory feedback of flexor muscle activity may be divided between the muscle tension receptor responding to tension in the tonic distal fibres, the cuticular campaniform sensilla responding to stress from the more powerful phasic fibres and the chordotonal organ monitoring movements of the phasic proximal part of the flexor (Burns, 1974).

In spite of the fact that the muscle tension receptor is only a single cell it mediates a strong positive excitatory reflex onto the flexor motoneurons and an inhibition of the slow extensor motoneuron powerful enough to interfere with the reflex from the much larger chordotonal organ. Similar positive reflexes have also been found in the abdomen of the caterpillar (Weevers, 1966) where the single celled MRO receptor excites parallel muscles. The locust muscle tension receptor reflexes are opposite in sign to the equivalent reflexes in the stick insect (Bässler, 1977), the crab (Clarac and Dando, 1973) and in mammals (Granit and Ström, 1951). However, the sign of such reflexes may change with the behavioural state of the animal. Thus Macmillan (1976) reports that the crab tension receptor reflex is sometimes reversed when the animal is active and chordotonal reflexes in the stick insect femur change sign with changes in the state of arousal of the insect (Bässler, 1976). In a few locusts negative feedback reflexes from the muscle tension receptor were found.

The positive feedback may be part of a load compensation reflex similar to that mediated by campaniform sensilla in the cockroach (Pearson, 1972). A similar load sensitive reflex has been reported in the metathoracic leg of the locust (Burrows and Horridge, 1974) and was ascribed to muscle tension receptors which were not identified. In the mesothoracic leg it is possible that the muscle tension receptor excitation of the flexor motoneurons is also a mechanism for distributing loads over the whole muscle. Unlike the extensor motoneurons, most of the flexor neurons innervate only restricted areas of the muscle (Theophilidis and Burns, in preparation). The muscle bundle containing the muscle tension receptor does not appear to have its own unique motor supply, but it lies in the distal part of the muscle which shares few of its motor axons with the more phasic proximal parts. Thus tension developed in the distal muscle

fibres may cause the muscle tension receptor to reflexly excite motoneurons supplying other parts of the muscle, producing a contraction which will reduce the load on the distal fibres. In this connection it is interesting that it is the distal part of the flexor muscle which is most used in posture and in walking (Theophilidis and Burns, in preparation), so the muscle tension receptor reflex may be able to provide additional tension when it is needed.

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