THE EXOSKELETON AND INSECT PROPRIOCEPTION

II. REFLEX EFFECTS OF TIBIAL CAMPANIFORM SENSILLA IN THE AMERICAN COCKROACH, *PERIPLANETA AMERICANA*

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SUMMARY

1. Mechanical stimulation of individual tibial campaniform sensilla produces specific reflex effects upon motoneurones to leg muscles.

2. The reflex effects of a campaniform sensillum depend upon the orientation of its cuticular cap. The proximal sensilla, oriented perpendicular to the long axis of the tibia, excite slow motoneurones to the extensor tibiae and extensor trochanteris muscles and inhibit slow motoneurones to the flexor tibiae and flexor trochanteris muscles. The distal sensilla, oriented parallel to the tibia, exhibit reflexes of opposite sign, inhibiting the extensors and exciting the flexors.

3. These reflexes constitute a negative feedback system. Individual sensilla specifically excite motoneurones which innervate muscles whose resultant tensions decrease the firing of those sensilla.

4. It is postulated that individual campaniform sensilla can detect loading of the leg in various postures and can excite appropriate motoneurones in compensation. These receptors can also detect strains caused by large, resisted contractions of the antagonist muscles and inhibit the corresponding motoneurones.

INTRODUCTION

Rapid compensation for variation in load is essential to ensure co-ordination in many behavioural patterns (Sherrington, 1947). Loading of an appendage is most frequently detected by proprioceptive sense organs that reflexly excite motoneurones (Henneman, 1974; Mill, 1976). However, excitation of motoneurones, whether of central or reflex origin, must be limited to prevent unco-ordinated or excessive and damaging muscle contractions (Granit, 1970).

In vertebrates these two functional requirements, load compensation and limitation of muscle tension, are thought to be fulfilled by reflex input from at least two kinds of proprioceptive sense organs – muscle spindles and Golgi tendon organs. Muscle spindles detect loads as changes in muscle length and monosynaptically excite motoneurones in compensation (Matthews, 1964). Golgi tendon organs monitor

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muscle tensions and inhibit motoneurones to prevent overcontractions (Henneman, 1974). The stability of these systems is further ensured by negative feedback: reflex inputs to motoneurones result in changes of muscle lengths and tensions that decrease afferent activity.

In insects it is still unclear which sense organs provide for load compensation or tension regulation. Several different systems have been proposed as follows.

(1) *Sense organs that monitor joint angle.* Insect chordotonal organs and most multipolar receptors monitor joint angle (Dethier, 1963; Young, 1970; Burns, 1974; Moran, Varela & Rowley, 1977). Leg chordotonal organs can mediate 'resistance' reflexes that generate muscle contractions opposing forced joint movement (Usherwood, Runion & Campbell, 1968; Bassler, 1972). These reflexes could function in load compensation if increased weight produced deviations in joint angle. However, in some insects resistance reflexes produce only weak muscle contractions, and their compensatory function has been questioned (Burrows & Horridge, 1974). Also, reversal of the sign of these reflexes has been reported (Bassler, 1976), producing positive feedback of unknown function.

Multipolar receptors may contribute to load compensation (Guthrie, 1967), but the specific function of these receptors in most insects remains unclear (Coillot & Boistel, 1968, 1969). In sum, no single monitor of joint angle has been shown unequivocally to mediate load compensation. Furthermore, receptors that monitor muscle length, as do vertebrate muscle spindles, have not been demonstrated in insect legs (Hoyle, 1974).

(2) *Sense organs that monitor muscle tension.* A multipolar receptor has recently been found (Theophilidis & Burns, 1979) in the fibres of the prothoracic and mesothoracic flexor tibia muscles of the locust leg that responds to active and passive tensions in the muscle fibres. Stimulation of the multipolar receptor generally produces re-excitation of flexor motoneurones and inhibition of the antagonist slow extensor motoneurone, although reflexes of opposite signs were also elicited. Unknown factors preventing continuous positive feedback would be necessary if these receptors were to function in load compensation.

(3) *Sense organs that monitor cuticular strain.* Cuticular strain is detected by campaniform sensilla (Pringle, 1938b). Pringle (1940) demonstrated that these sensilla reflexly excite motoneurones to leg muscles. He postulated that these reflexes operate in load compensation: weight upon the leg would produce strains in the exoskeleton and elicit campaniform sensillum discharges that would excite motoneurones opposing load. However, Pringle (1961) envisaged these reflexes as part of a positive feedback system in that muscle contractions alone would also excite the same sensilla. Such a function has been proposed in the legs of a cockroach (Pearson, 1972) and locust (Burrows & Horridge, 1974). In neither case have mechanisms been proposed for limiting potentially damaging positive feedback (Bennet-Clark, 1975), nor were the responses of campaniform sensilla to muscle contractions directly recorded. In contrast, Seath (1977) has proposed that campaniform sensilla of locust mandibles inhibit motor output when closer muscle tensions become too high. Thus, a role for campaniform sensilla in load compensation and tension regulation remains equivocal.

The preceding study (Zill & Moran, 1981) showed that the tibial campaniform sensilla are activated by compressions perpendicular to the cap long axis and specifi-

ally respond to muscle contractions according to sensillum cap orientation: the distal campaniform sensilla, lying parallel to the leg's long axis, respond to extensor muscle contractions; the proximal sensilla, lying perpendicular to the leg's long axis, respond to flexor muscle contractions. If these sense organs are part of a positive feedback system for load compensation, stimulation of individual campaniform sensilla should excite motoneurones to muscles whose contractions, in turn, excite these sensilla. If, however, these receptors are part of a negative feedback system, motoneurones to antagonist muscles should be excited. These two consequent hypotheses are tested in the following experiments.

METHODS

Preparation

Adult American cockroaches, *Periplaneta americana*, of both sexes were briefly anaesthetized with carbon dioxide, and attached by small staples through the pronotum and edge of the abdomen to a Sylgard resin-coated plastic block for ventral dissection. Most experiments were performed on metathoracic legs, but similar reflexes were also elicited in mesothoracic legs. The animal's other legs were left as free to move as possible and were generally restrained only by small staples.

Myograms of the extensor and flexor tibiae were taken according to the method of Krauthamer & Fourtner (1978) as previously described (Zill & Moran, 1981). Recordings of the axons of extensor tibiae motoneurones were taken from the trunk of nerve 3 B (Nijenhuis & Dresden, 1956) in the distal coxa. Nerve 3 B was exposed by carefully removing the ventral cuticle in the mid-coxa and tracing it distally. While the nerve, at this point, also contains axons of motoneurones to the reductor femoris muscle (Dresden & Nijenhuis, 1958), activity of the extensor tibiae motoneurones could be unequivocally identified by a $1:1$ correspondence with the myogram that was simultaneously recorded.

The nerves to the extensor and flexor trochanteris muscles were dissected according to the methods of Pearson & Bergman (1969) and Pearson & Iles (1971).

Stimulation and recording

Individual campaniform sensilla were stimulated with a fine-etched tungsten wire probe affixed to a piezo-electrical crystal. Nerve recordings were taken with chloridized $75 \mu m$ silver wire hook electrodes. All recordings were amplified and stored on tape as has been described (Zill & Moran, 1981).

RESULTS

Reflex effects were studied in the motoneurones innervating four leg muscles, the extensor and flexor tibiae and the more proximal extensor and flexor trochanteris (Fig. 1). When the distal leg segments grasp a walking surface, both the extensor tibiae and the extensor trochanteris muscles act to raise the animal and serve as anti-gravity and propulsive muscles in upright posture and locomotion (Pearson, 1972; Krauthamer & Fourtner, 1978). The flexor tibiae and flexor trochanteris muscles have been shown to lift the leg in walking (Pearson, 1972; Krauthamer & Fourtner, 1978). Myo-
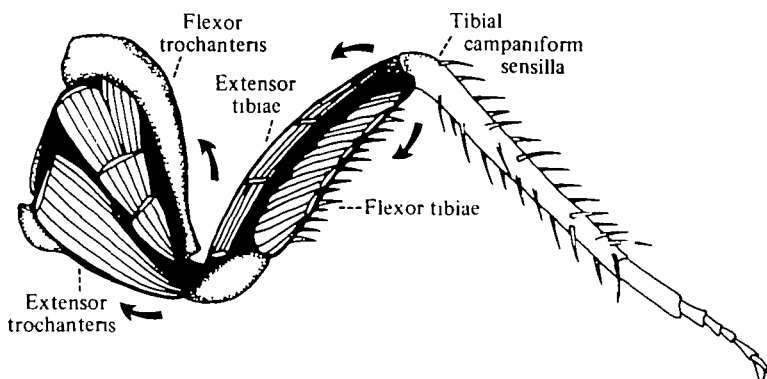
Fig. 1. Location and action of tibial and trochanteral muscles. Both the coxo-trochanteral and femoro-tibial joints are hinged, and move only in the plane of the diagram. A pair of antagonist muscles operates at each joint.

graphic recordings of flexor activity in freely moving preparations also indicate that the flexors can act as anti-gravity muscles when the animal is climbing or standing on an inverted surface (S. N. Zill, unpublished observations).

Extensor tibiae

The extensor tibiae muscle is innervated by two excitatory motoneurones, one fast and one slow, and at least one inhibitory neurone (Atwood, Smyth & Johnston, 1969). Activity of these motoneurones was recorded by electromyography (11 animals) and by extracellular recordings from nerve 3B in the distal coxa (7 animals). In pinned-down preparations activity of the slow extensor was typically low in the resting state (less than 10 Hz) and accelerated during extension movements. The fast axon usually fired only when slow axon activity was extremely high (over 400 Hz).

Punctate stimulation of single tibial campaniform sensilla produced repeatable reflex effects upon the activity of the slow extensor tibiae motoneurone that depended upon sensillum cap orientation. Stimulation of proximal sensilla increased activity in the slow extensor motoneurone; stimulation of the distal campaniform sensilla inhibited its activity (Fig. 2a(i), (ii)).

The magnitude of reflex accelerations from proximal sensillum stimulation usually varied according to the baseline levels of firing in the slow motoneurone. Often, in the absence of background activity, the slow extensor fired at a low rate (10–20 Hz) only during the time of proximal sensillum stimulation. When background activity was somewhat higher (approximately 10–30 Hz) the slow extensor fired more vigorously (50–100 Hz) in reflex response. Discrete bursts coincident with sensillum stimulation could be elicited repeatedly over long periods. At very high levels of motoneurone activity, the reflex response declined in relative magnitude and only a small acceleration could be noted. These findings suggest that proximal sensilla could best modulate firing at moderate rates of motoneurone activity. The latency from initial afferent firing of these reflex effects was quite short in nerve recordings (mean 7·4 ms ± S.E. 1·1).
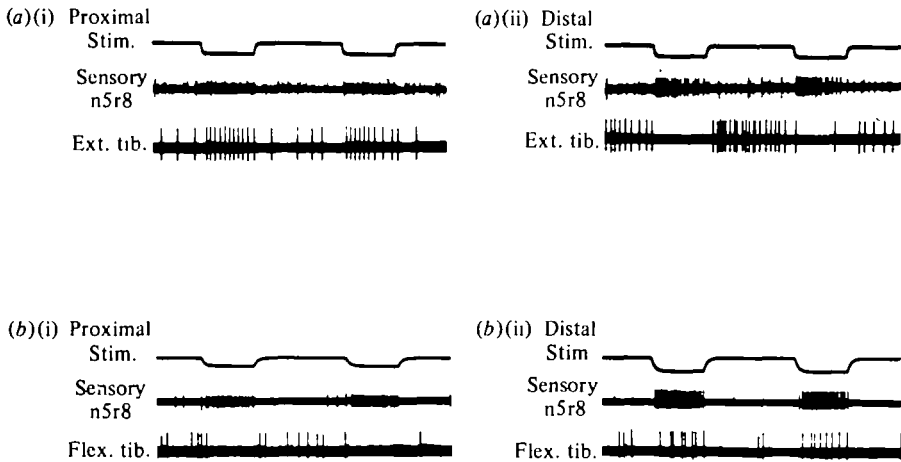
Fig. 2. Reflex effects of the tibial campaniform sensilla on tibial motoneurones. Individual campaniform sensilla were stimulated with a fine tungsten wire mounted on a piezo-electric crystal that was driven by smoothed square wave voltages indicated in the first trace. In the second trace sensillum activity was recorded by a small wire placed near the dorsal nerve in the femur (n5r8). (*a*) Extensor tibiae activity was recorded myographically. Junctional potentials produced by the single slow extensor tibiae motoneurone are shown. The extensor was excited by the proximal sensilla (i) and inhibited by the distal sensilla (ii). (*b*) Flexor tibiae activity was also recorded myographically. The proximal sensillum inhibited the low levels of background activity of at least one flexor tibiae motoneurone. Motoneurone activity was enhanced by distal sensillum stimulation. Stimulus duration = 400 ms.

The decrease of motoneurone firing frequency produced by distal sensillum stimulation was somewhat more variable. At moderate frequencies of motoneurone firing, this inhibition was often complete, even with low levels of sensillum activity. Periods of inhibition were, in many cases, followed by slight rebound accelerations in motoneurone activity.

In most preparations the magnitude of inhibition declined at high levels of motoneurone activity but in some animals total inhibition of firing could still be produced; an effect that was quite dramatic as only a single sensory neurone was being stimulated. This complete inhibition occurred most often with stimulation of the largest distal sensillum. The latencies of distal sensillum effects were also quite short (mean 8·0 ms ± S.E. 1·6).

Effects of both larger (greater than 10 μm in cap diameter) and smaller sensilla have been tested. Afferent spikes of small sensilla, often no larger than 10 μV, could still be detected. The small sensilla produced orientation-dependent reflex effects similar to those of the larger sensilla. As many as four proximal and three distal sensilla have been tested in a single preparation.

Although effects upon the *slow* motoneurone were pronounced, no change in activity of the *fast* or inhibitory extensor tibiae motoneurone was observed during sensillum stimulation. The fast motoneurone fired only intermittently and at high frequencies of slow motoneurone activity, so that its possible reflex modulation could not be extensively examined.
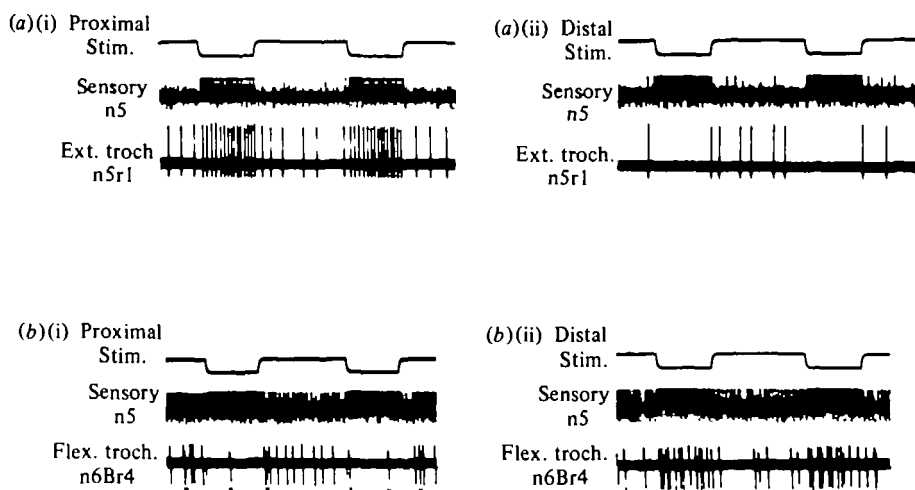
Fig. 3. Reflex effects of the tibial campaniform sensilla on trochanteral motoneurones. Sensory activity recorded in the main sensory nerve (n5) in the coxa. (*a*) Activity of the slow extensor motoneurone was recorded with hook electrodes from the nerve to the trochanteral extensor muscle (n5r1). Stimulation of the proximal sensilla (i) enhanced extensor activity while the distal sensilla (ii) produced inhibition. (*b*) Activity of the flexor trochanteris motoneurones was recorded from the nerve to the flexor muscle. Activity of two motoneurones is apparent. The smaller motoneurone (marked with ■) is a branch of the common inhibitory neurone, as was confirmed by simultaneous recording of the nerve to the extensor trochanteris. The larger flexor axon was affected by campaniform sensillum stimulation. Activity of this motoneurone was increased by distal sensillum stimulation and decreased by proximal sensillum firing. Stimulus duration = 400 ms.

Flexor tibiae

The flexor tibiae muscle is innervated by at least eight different motoneurones (Nijenhuis & Dresden, 1956) whose post-synaptic actions have not been characterized. Activity of these motoneurones was monitored solely by electromyography (14 animals).

Flexor myograms showed several small (50–75 μV) junctional potentials and one or two of intermediate size (100–150 μV). Stimulation of the distal campaniform sensilla regularly elicited reflex effects in one motoneurone that produced junctional potentials of intermediate size. The sign of these effects was opposite to that seen for the extensor tibiae: the distal campaniform sensilla increased flexor motoneurone activity (Fig. 2*b* (ii)). Stimulation of the proximal sensilla produced inhibition of flexor motoneurone activity in some preparations (Fig. 2*b* (i)) but observation of these reflex effects was limited by the irregular levels of activity shown by flexor tibiae motoneurones. At rest, firing frequency was often very low; during active flexions high levels of activity and extensive recruitment occurred. This connection should, therefore, be viewed as tentatively established. In no case was proximal campaniform sensillum stimulation followed by flexor excitation. The latencies of both these reflex effects are somewhat longer than those of the extensor tibiae (distal sensilla mean 11·1 ms ± S.E. 2·7; proximal sensilla mean 14·5 ± S.E. 3·6).

(a) Adequate stimuli

External forces

    Dorsal bending ⟶ Proximal

    Ventral bending ⟶ Distal

Muscle forces

    Flexor tib. ⟶ Proximal

    Extensor tib. ⟶ Distal

(b) Reflex effects

Proximal ⟶ Ext. tib.
            Ext. troch.

Distal ⟶ Flex. tib.
           Flex. troch.

⟶ Excitation
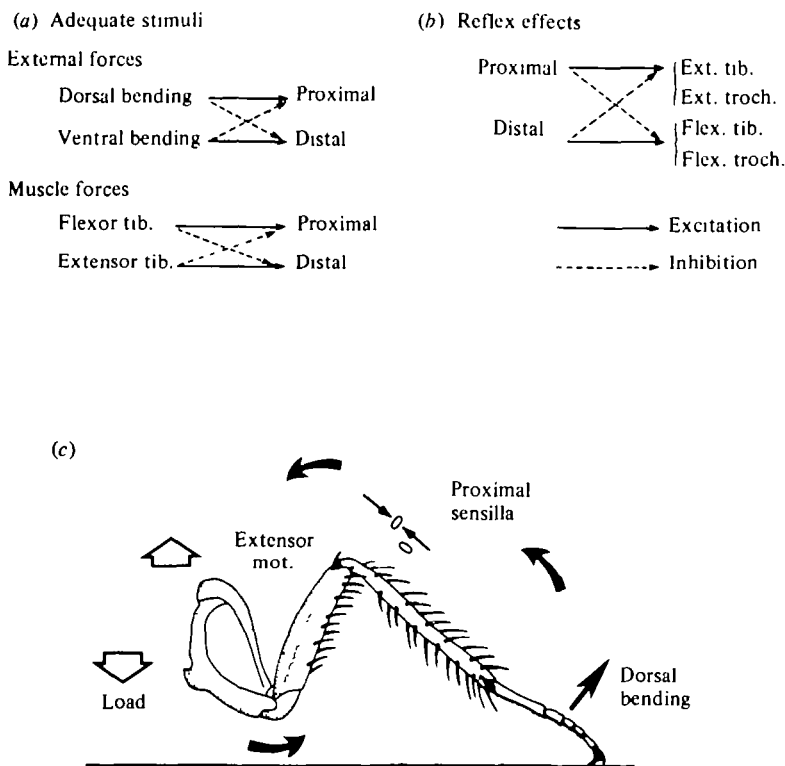
----------► Inhibition

(c)

Fig. 4. Load compensation and limitation of muscle tension by cuticular strain receptors. (a) Summary of the adequate stimuli of the tibial campaniform sensilla (from Zill & Moran, 1981). External forces – Tibial campaniform sensilla respond best to bending forces. Dorsal bending excites proximal sensilla and inhibits distal sensilla; ventral bending excites distal and inhibits proximal sensilla. Muscle tensions – Flexor muscle contractions produce strains that excite proximal sensilla and inhibit distal sensilla. Extensor muscle contractions have opposite effects and excite distal and inhibit proximal sensilla. (b) Summary of reflex effects of the tibial campaniform sensilla. Proximal sensilla reflexly excite slow extensor tibiae and extensor trochanteris motoneurones and may inhibit both flexor tibiae and flexor trochanteris motoneurones. Distal sensilla excite both groups of flexor motoneurones and strongly inhibit slow extensor motoneurones. (c) Model of load compensation and limitation of muscle tension in upright walking. Increased load from the animal's weight upon the leg should produce dorsal bending that excites proximal sensilla. These sensilla reflexly excite extensor motoneurones whose muscles depress the leg, counter the load and straighten the tibia. Excessive extensor muscle contractions would produce a ventral bending and excite the distal campaniform sensilla that inhibit extensor motoneurones.

Extensor trochanteris

Recordings from the nerve to the trochanteral extensor (n5rl, Pearson & Iles, 1971) closely resembled those from the tibial extensor: the single slow motoneurone exhibited a low rate of background activity that accelerated during extension movements; the fast motoneurone generally did not fire except at high rates of slow motoneurone activity.

Stimulation of individual tibial campaniform sensilla elicited reflex effects from the trochanteral extensor (12 animals) equivalent to those seen in the tibial extensor. Proximal sensilla firing increased slow extensor motoneurone activity; distal sensilla

inhibited its firing (Fig. 3a (i), (ii)). These interjoint reflex effects were of longer latency (proximal sensilla mean 9·0 ms ± S.E. 1·2; distal sensilla mean 10·1 ms ± S.E. 0·8) than those seen in the slow motoneurone innervating the extensor muscle of the tibia. The effects on the trochanteral extensor were, however, qualitatively similar; reflex effects were again greatest at moderate rates of motoneurone activity.

Posterior flexor trochanteris

In contrast to the flexor tibiae, the innervation of the posterior flexor trochanteris has been well characterized. The trochanteral flexor receives twelve axons through a long branch of the sixth nerve of the metathoracic ganglion (n6Br4, Nijenhuis & Dresden, 1956). These axons can be readily identified by spike height in extracellular recordings from the flexor nerve and have been numbered according to increasing spike size. The postsynaptic actions of some of these motoneurones have also been characterized: axons 4, 5, 6 are slow excitatory motoneurones (Pearson & Bergman, 1969). Axon 3 is a branch of the common inhibitory neurone. Its identity was confirmed by simultaneous recording of another nerve (n4r2A, Pearson & Bergman, 1969) that contains an additional axonal branch of the common inhibitor and showed 1 : 1 firing with axon 3.

Stimulation of the tibial campaniform sensilla produced reflex effects in a single slow flexor motoneurone (axon 4) that were opposite in sign from the extensor reflex effects. The distal campaniform sensilla regularly excited this motoneurone while its activity was inhibited by proximal sensillum stimulation (Fig. 3b (i), (ii). The latencies of these reflex effects were comparable to those seen in the slow extensor trochanteris motoneurone (distal sensilla mean 9·4 ± S.E. 0·6; proximal sensilla mean 11·0 ± S.E. 1·3).

No reflex effects were elicited from other flexor excitatory motoneurones. The activity of the common inhibitory neurone, and all other inhibitory neurones examined in this study, seemed unaffected by sensillum stimulation.

DISCUSSION

Reflex effects of the tibial campaniform sensilla

Stimulation of individual tibial campaniform sensilla repeatedly elicits reflex effects in slow excitatory motoneurones that innervate the tibial and trochanteral muscles (Fig. 4a). The sign of these effects depends strictly upon sensillum cap orientation: the *distal* sensilla, whose caps are *parallel* to the axis of the leg, *excite flexor* motoneurones and *inhibit extensor* motoneurones; the *proximal* sensilla, that are *perpendicular* to the leg axis in orientation, *excite extensors* and *may inhibit* both tibial and trochanteral *flexor* motoneurones. Reversal of the signs of these reflexes did not occur in any preparations.

Effects of proximal sensilla stimulation are similar, in many respects, to previous accounts of reflexes elicited by stimulation of the trochanteral campaniform sensilla. Pringle (1940) found that pressure on the trochanter produced a strong discharge in the trochanteral extensor muscle. This finding was confirmed by Pearson (1972), who also produced inhibition of bursting activity of the trochanteral flexor motoneurones by squeezing the trochanter with forceps. In the present study, the proximal tibia

campaniform sensilla excited the slow trochanteral extensor and inhibited at least one motoneurone to the trochanteral flexor.

Effects of campaniform sensilla stimulation that produce flexor motoneurone excitation have not previously been reported. The distal tibial campaniform sensilla excite at least one flexor tibiae motoneurone and discretely enhance the activity of the same trochanteral flexor motoneurone that was inhibited by the proximal sensilla. While these connexions have not previously been demonstrated, several authors have speculated upon their existence (Pringle, 1961; Pearson, Fourtner & Wong, 1973) to potentially fulfil load compensation in postural use of flexor muscles. Also, reflex excitation of flexor tibiae motoneurones resulting from cuticular strain has been observed in the locust (Heitler & Burrows, 1977, p. 234) but the receptors mediating this excitation were not identified.

Despite general agreement in the literature on the implicit existence of these reflexes, the type of feedback system they form has remained unclear. Many authors (Pringle, 1961; Pearson, 1972; Burrows & Horridge, 1974; Mill, 1976) have considered campaniform sensilla as part of a positive feedback system.

The reflexes elicited by stimulation of the tibial campaniform sensilla, when viewed in conjunction with the response of these receptors to muscle contractions (Zill & Moran, 1981), clearly form a negative feedback system (Fig. 4a, b). Discharges of the proximal sensilla that excite the slow extensor tibiae motoneurone are decreased by contractions of the extensor muscles; activity of the distal sensilla excites flexor motoneurones that in turn reduce afferent firing.

Functions of the tibial campaniform sensilla

(a) *Load compensation.* The adequate stimuli and reflex connexions of the proximal tibial campaniform sensilla could readily comprise a system for load compensation in an upright posture (Fig. 4c). When standing or walking upright the tibia is typically held inclined away from the animal's centre of gravity (Hughes, 1952). In this position weight upon the leg should produce a dorsal bending of the tibia. Dorsal bending, as has been shown in the previous study, excites the proximal tibial campaniform sensilla. The present study has shown that activity of these sensilla reflexly excites the tibial and trochanteral extensor motoneurones. Contractions of the extensor muscles innervated by these motoneurones would effectively resist loading. The bending force exerted by the tibial extensor would then decrease the discharge of the proximal sensilla.

Could the distal campaniform sensilla also function in load compensation? The previous study (Zill & Moran, 1981) indicated that these sensilla are stimulated by ventral bending of the tibia. Ventral bending could be produced when the animal stands on an inverted surface. The distal sensillum activity produced by this bending would excite flexor motoneurones. Flexor muscle contractions could potentially resist this loading by pulling the animal up toward the walking surface.

Thus the connexions of both the proximal and distal campaniform sensilla could provide rapid load compensation in a variety of postures assumed by the animal under natural conditions.

There are several inherent limitations to this system. First, effective bending of the

leg by the weight of the animal requires resistance to movement. This resistance would have to be provided by existing tension in the tibial muscles. These tensions, however, could result from parallel reflexes dependent upon joint angle or by a centrally generated setting of initial posture. Resistance tensions could also be set by pre-existing equilibria established by the reflexes of the campaniform sensilla. Second, the large tibial campaniform sensilla show substantial adaptation, so that effective load compensation would have to occur rapidly. Subsequent fine adjustment of motoneurone rate and muscle tension could, however, still be accomplished by these receptors. In addition, the response adaptation of the smaller campaniform sensilla is not known; these receptors may have a substantial tonic discharge, as has been demonstrated for campaniform sensilla of the maxillary palps (Pringle, 1938a) or those associated with the tibial spines (Pringle & Wilson, 1952). Other proprioceptors have been shown to possess parallel phasic and tonic elements (Young, 1970; Kuffler, 1954).

(b) *Limitation of muscle tension.* Stimulation of the tibial campaniform sensilla produced inhibitory as well as excitatory reflex effects upon motoneurones. These effects were best demonstrated for the distal campaniform sensilla that potently inhibited activity of the slow excitatory motoneurones of the tibial and trochanteral extensors. The previous study (Zill & Moran, 1981) showed that resisted contractions of the tibial extensor muscle produced distal sensillum excitation. These receptors could, therefore, function to inhibit excessive extensor muscle contractions. The proximal sensilla may fulfil the same functional requirement for flexor muscle contractions.

Receptors that can limit muscle tension have not previously been identified in insect legs although their existence has been implied (Pringle, 1961). Recurrent reflex inhibition following resisted contractions of the locust extensor tibiae has been demonstrated (Heitler & Burrows, 1977) but the specific receptors were not identified. The proximal tibia of the metathoracic leg of the locust possesses campaniform sensilla that are positioned on the dorsal surface and oriented parallel to the leg axis (Heitler, 1977), as are the distal campaniform sensilla of the cockroach. In the locust, cutting the nerve containing the axons of these sensilla reduces the magnitude of recurrent inhibition of motoneurones innervating the extensor tibiae (Heitler & Burrows, 1977).

In Crustacea, at least one receptor that monitors cuticular strain has been shown to reflexly limit muscle tension. The cuticular stress detector (CSD_1) is a group of sensory neurones located on the basi-ischiopodite segment of the crustacean leg (Wales, Clarac & Laverack, 1971). Its position on the segment is close to the point of limb fracture in autotomy (Wood & Wood, 1932). Findlay has recently shown that stimulation of the CSD_1 inhibits firing in a group of leg motoneurones (Findlay, 1978). These motoneurones innervate a leg muscle that produces cuticular strains that excite the CSD_1. Strong contractions of this muscle also produce limb autotomy (Clarac, 1976). Thus the crustaean cuticular stress detector apparently functions to limit developed muscle tensions and prevent accidental autotomy. Its function is therefore, in many respects, similar to that postulated for the distal tibial campaniform sensilla.

Advantages of monitoring load as cuticular strain

The adequate stimuli and reflex connexions of the tibial campaniform sensilla suggest that they both: (1) compensate for loads applied to the leg, and (2) limit muscle contractions. In vertebrates, these functions are considered to be fulfilled by two separate receptors, muscle spindles located in the body of the muscle (Matthews, 1964) and Golgi tendon organs situated at the junction of muscle fibres and their tendons (Henneman, 1968).

What advantages are gained by insects in monitoring load and tension in the exoskeleton?

First, the insect can efficiently monitor both variables with a single receptor. Both external loads and muscles must act upon the same substrate, the exoskeleton. This efficiency may, however, impose limitations upon the adaptability of this system since, unlike vertebrate muscle spindles, load compensation cannot be adjusted for differences in muscle length.

Secondly, the cuticle is not static in its properties. Many insects shed their exoskeleton in repeated moults before reaching an adult form (Wigglesworth, 1965). During the period immediately after moulting the cuticle is extremely compliant. Strain receptors that monitor muscle tensions could prevent damage to the soft and fragile exoskeleton.

Last, these receptors ensure the structural integrity of the tibia. Many insects possess legs that are composed of jointed, long, thin tubes (Snodgrass, 1952). Increased length and segmentation of a leg permits traverse of longer distances in a single step (Manton, 1952). However, long leg segments are also subject to much greater bending moments. By monitoring load and muscle contractions as the strain these bending forces produce, the insect ensures that the legs can be used rapidly and freely but with inherent structural stability.

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