I

THE EXOSKELETON AND INSECT PROPRIOCEPTION.
I. RESPONSES OF TIBIAL CAMPANIFORM SENSILLA
TO EXTERNAL AND MUSCLE-GENERATED FORCES IN
THE AMERICAN COCKROACH, *PERIPLANETA AMERICANA*

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SUMMARY

1. The tibial campaniform sensilla are a group of mechanoreceptors in the cockroach leg that respond to cuticular strain. Each sensillum consists of a single bipolar neurone whose dendrite inserts into an ovoid cuticular cap embedded in the exoskeleton.

2. The tibial campaniform sensilla are consistently separable into two subgroups with mutually perpendicular cap orientation: the long axis of the caps of proximal subgroups are oriented perpendicular to the tibial long axis; caps of the distal subgroup are parallel to the tibia.

3. The responses of individual, identified sensilla from both subgroups were tested to the following forces: bending forces (perpendicular to the leg long axis), axial forces (parallel to the leg axis), torques (twisting about the leg long axis) and forces generated by the tibial muscles.

4. The tibial campaniform sensilla respond vigorously to bending forces imposed in the plane of movement of the adjacent femorotibial joint. Individual sensilla exhibit orientation-dependent directional sensitivity in their response: the proximal sensilla respond only to dorsal bending; the distal sensilla respond only to ventral bending. Sensilla respond less vigorously to bending forces in other planes.

5. Responses are weak but directionally sensitive to axial forces: the proximal sensilla fire upon axial compression; the distal sensilla fire upon axial tension.

6. Both subgroups respond simultaneously but weakly to imposed torques.

7. Contractions of the tibial muscles produce strong orientation-dependent responses: the proximal sensilla respond only to flexor muscle contractions; the distal sensilla respond only to extensor muscle contractions.

8. These responses are accurately predicted from a simple model in which the tibia behaves as a cylinder under stress. The tibial campaniform sensilla respond as directionally sensitive strain gauges. Each individual sensillum responds only to compressions perpendicular to the long axis of its cuticular cap.

9. Tibial campaniform sensilla respond best to those forces that the animal can most effectively control.

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INTRODUCTION

The insect exoskeleton functions primarily as a rigid supportive structure that provides for muscle attachments (Locke, 1974). In addition, the exoskeleton serves as a sensory surface through which an insect detects its environment and, by proprioceptive sense organs, monitors its own behaviour. (Dethier, 1963). This paper is the first in a series examining one type of insect proprioceptor, the campaniform sensillum, which responds to mechanical strain in the exoskeleton (Pringle, 1938a). The goals of these investigations are twofold: (1) to determine how campaniform sensilla provide specific proprioceptive information to the insect, and (2) to determine how this sensory input modifies the animal's behaviour.

The morphology of cockroach campaniform sensilla is well understood (Pringle, 1938a; Moran, Chapman & Ellis, 1971; Moran & Rowley, 1975; Moran et al. 1976). Each sensillum consists of a single bipolar neuron whose dendrite bears a modified cilium that inserts into an ovoid cuticular cap at the surface of the exoskeleton. Strains in the surrounding cuticle deform the tip of the modified cilium and evoke sensillum discharge.

Previous accounts of the specific responses of cockroach campaniform sensilla are confusing. In early studies, Pringle (1938a, b) proposed that campaniform sensilla are directionally sensitive and respond only to compressions *parallel* to the long axis of the cuticular cap. This view has subsequently been held by other authors (Young, 1970; Heitler, 1977). In preliminary direct recordings from cockroach leg campaniform sensilla, however, Spinola & Chapman (1975) found these receptors respond to compressions *perpendicular* – not parallel – to the long cap axis. Pringle (1938b) also postulated that the response of a campaniform sensillum could be biased according to its orientation and position on the exoskeleton. Pringle noted, as have several other authors (Knyazeva, 1974; Knyazeva, Fudalewicz-Niemczyk & Rosciszewska, 1975), that groups of campaniform sensilla often occur near muscle insertions. The responses of these groups of sensilla to muscle contractions have not, as yet, been systematically tested.

The first study in this series was therefore undertaken to examine the responses of campaniform sensilla and to answer these questions: (1) Are campaniform sensilla directionally sensitive? (2) Does the position and orientation of an individual campaniform sensillum limit its response? To further characterize these receptors, succeeding studies examine the reflex action of campaniform sensilla upon motoneurons and the activity of these receptors in freely moving animals (S. N. Zill & D. T. Moran, in preparation).

We have, for several reasons, elected to study one group of campaniform sensilla, the tibial campaniform sensilla (Pringle's (1938b) Group 6) of the american cockroach *Periplaneta americana*. First, Group 6 is unique in its spatial arrangement. The receptors may be divided into two subgroups with cuticular caps of mutually perpendicular orientation. If campaniform sensilla are directionally sensitive, the responses of the two subgroups should be substantially different. Second, Group 6 is located on the tibia, a long cylindrical structure. The mechanics of strain in cylinders is relatively simple and well described (Timoshenko & MacCullough, 1935). The types of forces that can act upon cylinders are combinations of bending force

perpendicular to the long axis), axial forces (parallel to the long axis) and torques (twisting about the long axis). The responses of the tibial campaniform sensilla to each of these forces are tested in the following experiments and analyzed according to the strains that would result if the tibia has the properties of a simple cylinder.

The results of these tests show that campaniform sensilla are consistently directionally sensitive and strongly suggest the tibial campaniform sensilla respond best to those forces the animal can most effectively control.

MATERIALS AND METHODS

Morphology

After metathoracic legs of adult *Periplaneta americana* (anaesthetized with CO_2) were severed, pieces of tibial cuticle bearing group 6 sensilla were placed in Karnovsky's (1965) fixative overnight and rinsed in 0·2 M cacodylate buffer. Tissues to be examined as whole mounts by light microscopy were immersed overnight in 2 N potassium hydroxide, dehydrated in acetone, cleared in xylene and mounted in Harleco synthetic resin. Tissues to be examined by scanning electron microscopy were dehydrated in acetone, critical-point-dried in a Tousimis Sandri PVT-3 unit, and examined in a Cambridge Stereoscan Mark IV.

Physiology

Experimental animals were adult *Periplaneta americana* of both sexes, either reared in laboratory cultures at 30 °C or commercially obtained (Carolina Biological Supply). Prior to experimentation, animals were briefly anaesthetized with carbon dioxide and placed ventral surface up on a plastic block coated with Sylgard resin. The block was bolted to a steel plate mounted on a heavy marble table that was supported by four mini-bike tire tubes to dampen transmitted vibrations.

In most experiments the animal was positioned on the resin-coated block so that one metathoracic leg rested, anterior face up, on a plexiglass platform. The femur was attached to the platform with very small drops of sticky wax (L. D. Caulk, Co.) so the femoro-tibial joint projected over the edge of the block (Fig. 1). The tibial campaniform sensilla were viewed through a Wild dissecting microscope by placing a first surface mirror (Edmund Scientific Co.) below the femoro-tibial joint. The other legs of the animal were restrained by staples.

When complete immobilization of the femoro-tibial joint was required, one metathoracic leg was turned anteriorly and attached (by a small drop of wax on the anterior surface of the coxa) to an adjustable platform fixed vertically over the animal. Two small pins projecting from the platform held the distal femur. The femoro-tibial joint was immobilized with fast-setting epoxy resin placed at least 0·5 mm from the tibial campaniform sensilla. The other legs were again restrained by staples.

Mechanical stimulation. Forces were applied to the tibia by a short segment of heavy tungsten wire attached to a piezo-electric crystal (lead-zinc bimorph, Clevite Industries; kindly provided by Dr Kent Chapman). The crystal, mounted between two pieces of plexiglass and held in a micromanipulator, could be rotated about the axis of the wire. Forces could thus be exerted in different planes. The angle of deviation from the vertical was indicated by a small protractor.
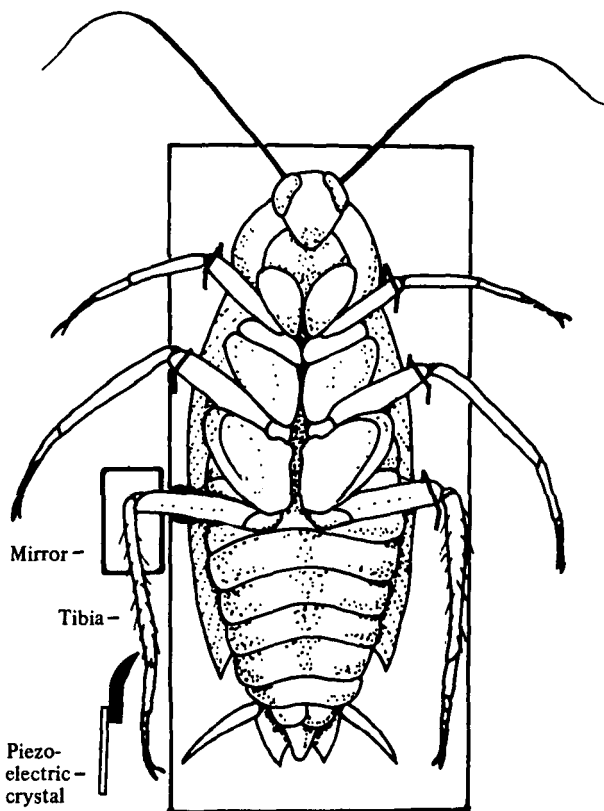
Fig. 1. Preparation for testing the responses of tibial campaniform sensilla. The animal was placed ventral surface up on a resin-coated block. One metathoracic leg was waxed in place so the femoro-tibial joint extended over the block's edge. Tibial campaniform sensilla were viewed through a small first-surface mirror placed below the joint. Bending forces were applied to the end of the tibia with a heavy tungsten wire mounted to a piezo-electric crystal. Recordings were taken from the femur as described (see Methods).

The piezo-electric crystal was driven by pulse voltages (up to 100 V) from a Phipps-Bird stimulator. A capacitor and potentiometer, placed in parallel with the crystal, slightly increased the rise time of the square wave voltage pulse; this dampened oscillatory vibrations that occur upon sudden displacement of the piezo-electric crystal.

The magnitudes of the forces generated by the piezo-electric crystal were determined by applying pulse voltages with the attached tungsten wire against a Grass force transducer (FTO3C). Since the force generated by a piezo-electric crystal varies according to load, the displacement of the wire tip was also determined by observation through a calibrated ocular on the dissecting microscope. Forces, when subsequently applied to the leg, were considered equal to those producing equivalent displacement.

Receptor cap stimulation. Individual campaniform sensilla were stimulated using a modification of the method of Chapman, Duckrow & Moran, (1973). A very fine tungsten wire, mounted to a piezo-electric crystal, was bent to 90 ° and electrochemically

ched to a tip diameter of about 1 μm. The wire was thin enough to permit direct observation of single sensillum stimulation, and pliable enough that no response was generated when it was pressed against the cuticle surrounding the sensillum cap. This ensured the stimulation of single, identified sensilla.

Recording of afferent activity. Extracellular records of action potentials of tibial campaniform sensilla were obtained from either the dorsal sensory nerve (nerve 5r8, Nijenhuis & Dresden, 1952, 1956) or the main femoral nerve (nerve 5) using chloridized 75 μ silver wire hook electrodes. The nerves were exposed through a very small window in the femoral wall, lifted clear of the haemolymph with the hook electrodes, and coated with a mixture of vaseline and paraffin oil to prevent desiccation. Extracellular action potentials from single sensory neurones were often several millivolts in peak-to-peak amplitude. These potentials were amplified, displayed and recorded conventionally. Spike counting and frequency analysis were aided by a Monsanto Programmable Timer-Counter.

Recordings of muscle activity. Myograms of extensor and flexor tibiae muscles were recorded with 50 μ copper wires inserted through small holes in the cuticle of the proximal femur (Krauthamer & Fourtner, 1978). These wires were insulated to their tips and placed less than 0·5 mm into the muscles. Myographic activity was recorded and analyzed by methods similar to those used for nerve recordings.

RESULTS

Anatomy

Location and orientation. The Group 6 campaniform sensilla of *Periplaneta americana* are 9–14 (mean 11·5 ± 1·4 S.E. *n* = 12) receptors located in the proximal tibia 1 mm distal to the femoro-tibial joint (Fig. 13). The cuticular caps of these receptors lie on the dorsal surface of the tibia 10–15 ° posterior to its plane of movement. The caps of the sensilla exhibit a consistent, mutually perpendicular orientation that permits division of this group into two subgroups: a distal subgroup of 3–5 receptors (mean 3·6 ± 0·7) oriented parallel (± 5 °) to the long axis of the tibia, and a proximal subgroup of 6–10 receptors (mean 7·7 ± 1·2) oriented perpendicular (± 5–10 °) to the tibial axis. These two subgroups are typically separated from each other by approximately 50 μ, although an occasional single small distal sensillum may be found closer to the posterior part of the proximal subgroup. This spatial separation simplifies reliable stimulation of single sensilla in each subgroup.

Innervation. The tibia and femur contain two nerves closely applied against a large central trachea. The larger of these, the main leg nerve (n5 of Nijenhuis & Dresden, 1952), is located in the posterior half of the tibia and moves to occupy a ventral position in the femur. Nerve 5 contains many sensory axons from the tibia and tarsus and supplies the motor innervation for the tibial flexor and tarsal muscles. The smaller nerve (n5r8 of Nijenhuis & Dresden, 1952) is located in the anterior half of the tibia. It moves to a dorsal position in the femur. This nerve is purely sensory and receives axons from the tibial spines and subgenual organ (Dresden & Nijenhuis, 1958).

The axons of the tibial campaniform sensilla vary in their projections through these nerves to the central nervous system. As judged from extracellular recordings,
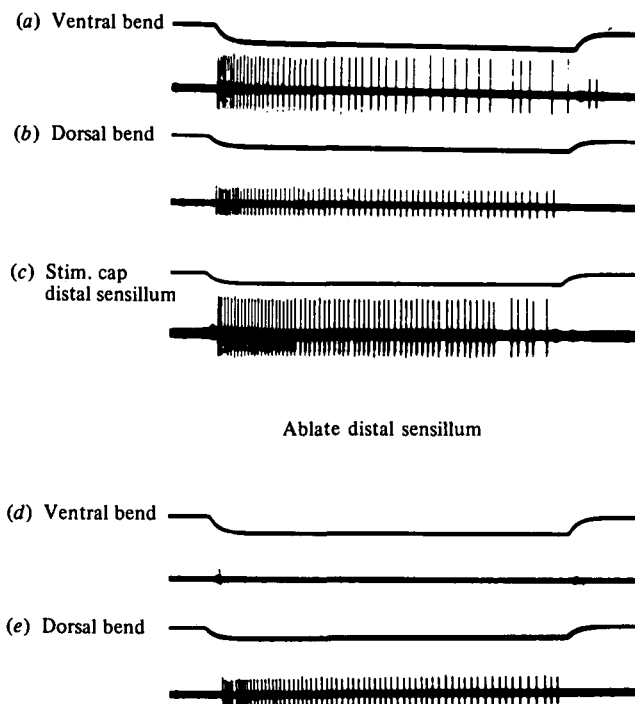
Fig. 2. Response of the tibial campaniform sensilla to bending in the plane of movement of the femoro-tibial joint: joint immobilized with epoxy. (a) Bending the tibia ventrally produces excitation of a single large unit. (b) A smaller unit responds to dorsal bending. (c) The discharge to ventral bending is mimicked by punctate stimulation of a distal campaniform sensillum. (d) Ablation of the cap of this sensillum eliminates the response to ventral bending. (e) The response to dorsal bending is unaffected by distal sensillum ablation. Stimulus duration = 400 ms.

axons of the more anterior of the Group 6 sensilla are found in nerve 5r8, and those more posterior are in nerve 5. Typically, axon spikes produced by stimulation of 2–3 proximal and 1–2 distal sensilla were recorded in nerve 5r8; occasionally only single proximal or distal sensilla were recorded. This distribution is more variable than the limited, anatomical descriptions of Nijenhuis and Dresden (1952) or Schnorbus (1971) suggest.

Physiology

Characteristics of afferent activity. The action potentials of Group 6 campaniform sensilla exhibited several consistent characteristics in extracellular recordings. First, within a subgroup the largest action potentials were derived from sensilla with the largest cuticular caps. Sensilla with large cuticular caps (greater than 10 μ) routinely produced extracellular action potentials of over 0·5 mV (range 0·52–2·75 mV), whereas receptors with smaller cuticular caps produced spikes that rarely exceeded 50 μV. Consequently, reliable recordings from identified sensilla were limited, in these experiments, to the larger sensilla. Typically, one distal and one or two proximal sensilla were recorded and identified in nerve 5r8, although as many as two distal

Table 1. *Directional sensitivity of tibial campaniform sensilla to imposed bending in the plane of movement of the femoro-tibial joint. Group 6 exhibited perfect directional sensitivity to forces imposed in the joint plane*

	Proximal sensilla	Distal sensilla
Respond to dorsal bending	16	0
Respond to ventral bending	0	11

$n = 12$ animals

and four proximal sensilla have been recorded in a single preparation. Also, the largest distal campaniform sensilla always exhibited a greater spike height than any proximal sensilla. This difference in action potential heights facilitated rapid identification of individual campaniform sensilla.

Response to externally imposed forces with movement resisted.

(1) *Bending forces in the plane of joint movement.* The response of the tibial campaniform sensilla to bending forces applied at the distal end of the tibia in the plane of movement of the femoro-tibial joint were examined in two types of preparation: those with the femoro-tibial joint immobilized with epoxy and others with the joint pushed to full extension. The first type of preparation permitted tests of the directional sensitivity of Group 6 sensilla to both dorsal and ventral bending. The second type of preparation was free of possible artifacts from the application of epoxy.

In preparations with the femoro-tibial joint completely immobilized by epoxy, vigorous discharges were recorded upon application of either dorsal or ventral bending forces (Fig. 2a, b). The receptors responsible for these discharges were positively identified by the following sequences of tests. After the activities in response to dorsal and ventral bending were recorded, the caps of individual campaniform sensilla were mechanically stimulated (see Methods). Single campaniform sensilla were located whose discharge to punctate stimulation was identical in extracellular action potential height and waveform to the activity seen in response to applied bending (Fig. 2c). The cuticular caps of these campaniform sensilla were then ablated using a very sharp, heavy tungsten wire and the bending response was retested (Figs. 2d, e). These ablations led to the absence of response of single identified units. In experiments where the activity of few sensilla were recorded in the dorsal nerve (n5r8), the entire response to bending in one direction could be eliminated by ablation of a single sensillum (Fig. 2d).

The tibial campaniform sensilla responded with absolute directional sensitivity to bending forces in the plane of joint movement. This directional sensitivity depended upon sensillum cap orientation. The proximal sensilla, whose caps are oriented perpendicular to the tibial axis, responded only to dorsal bending. The distal sensilla, whose caps are parallel to the tibial axis, responded only to ventral bending (Table 1).

The responses of Group 6 sensilla to dorsal bending forces of long duration and different magnitude were further examined in animals with the femoro-tibial joint
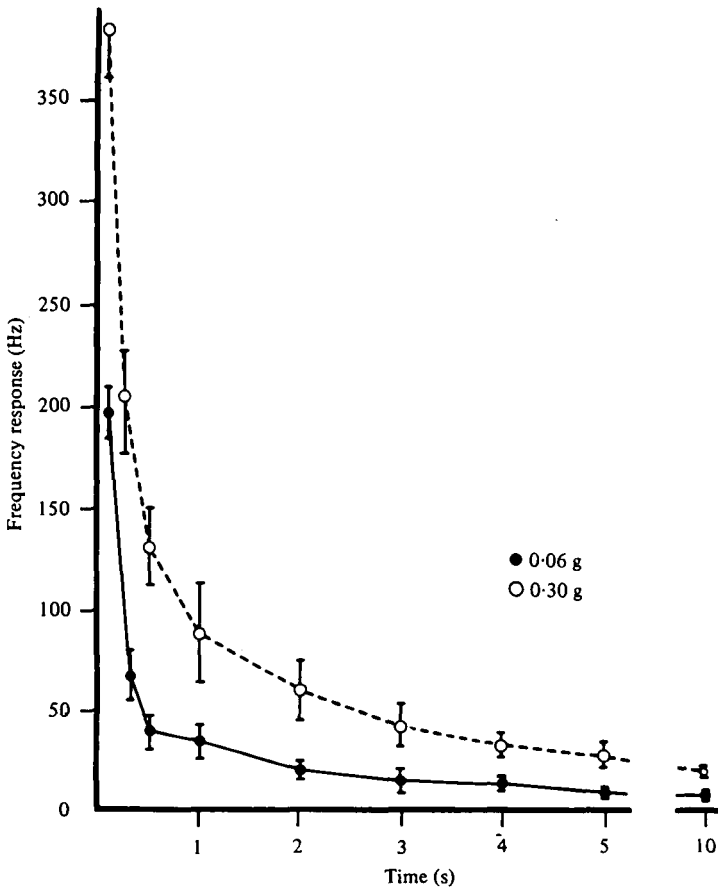
Fig. 3. Discharge of a proximal sensillum to sustained dorsal bending at different levels of force. Bending force was applied at $t = 0$ as plotted on the abscissa. The response frequency of a proximal sensillum is plotted on the ordinate. Each point represents the mean firing frequency during the preceding interval. The first second was divided into bins of 0·1, 0·2, and 0·5 s successively. At low levels of force (0·06 g) the sensillum fired intensely at first but rapidly adapted. At high levels of force (0·30 g) the sensillum fired more intensely and its response was prolonged. By 10 s, sensillum firing at all levels of force was small. Bar indicates $\pm 1 \times$ S.E.

fully extended. Only the proximal sensilla responded to dorsal bending in agreement with their determined directional sensitivity. Two characteristics of their response to forces applied as step functions were noted.

Response adaptation. The response of the proximal campaniform sensilla consisted of intense initial firing that showed considerable adaptation at all levels of applied force (Fig. 3). The response to small bending forces (15 mg) ceased completely within 100 msec. At higher levels of force, adaptation was delayed and less complete; a low level of activity (approximately 20 Hz) was maintained after 10 s of continuous force application.

A

(a) 90° ant.

(b) 45° ant.
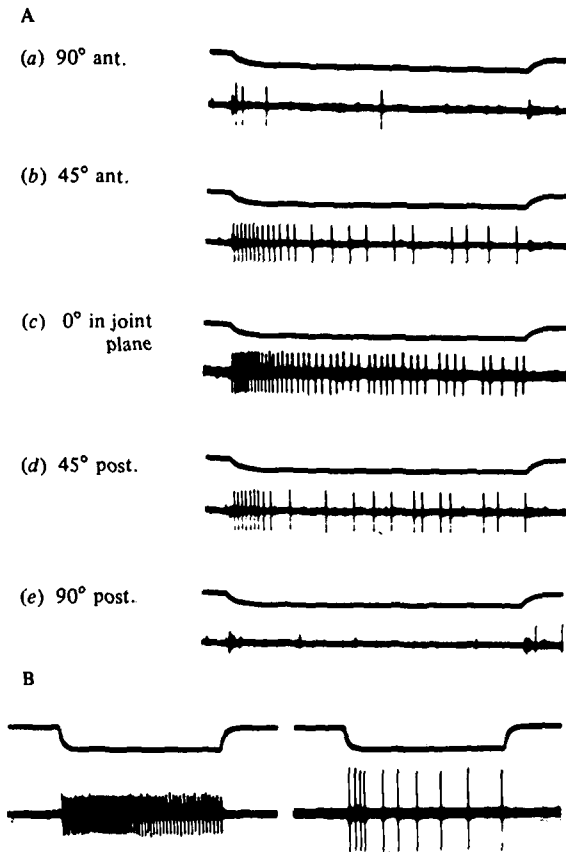
(c) 0° in joint
plane

(d) 45° post.

(e) 90° post.

B

Fig. 4. Response of a proximal sensillum to bending forces in different planes. (A) The femoro-tibial joint was held fully extended and bending forces were applied to the distal end of the tibia. (a) 90 ° anterior to the plane of joint movement, (b) 45 ° anterior, (c) 0 ° (in the joint plane), (d) 45 ° posterior, (e) 90 ° posterior. The response is maximal in the plane of the joint and declines in other planes. (B) Punctate stimulation of the cuticular caps of Group 6. Two sensilla were recordable in nerve 5r8: one, a proximal sensillum matches the spike height recorded in A; the second, a distal sensillum, did not respond to any dorsal bending force.

Range compression. The proximal sensilla substantially increased their initial firing frequency when applied bending was increased from low levels of force (Fig. 3, 5c). As force intensity was further increased, however, the rate of increase of sensillum firing declined. This phenomenon, known as range compression, is also exhibited by many other receptors (e.g. Golgi tendon organs; Alnaes, 1967).

These characteristics confirm the predictions of Mann & Chapman (1975), who calculated transfer functions from the responses of tibial campaniform sensilla of the cockroach *Blaberus discoidalis* to sinusoidal punctate stimulation and predicted both considerable response adaptation and substantial range compression. The campaniform sensilla of *Blaberus* and *Periplaneta* are, therefore, extremely sensitive to low levels of applied bending force but rapidly adapt to maintained stress.
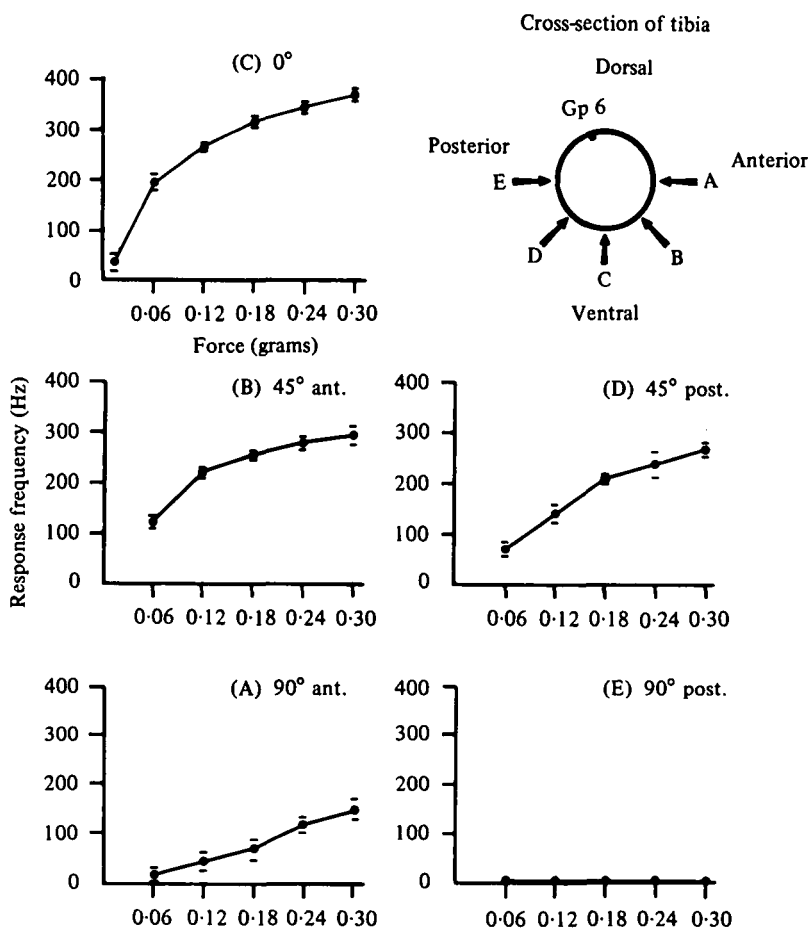
Fig. 5. Responses of a proximal sensillum to varied levels of bending forces in different planes. Responses at all levels of force were maximal in the joint plane. The responses to anterior bending forces were somewhat greater than to posterior bending. Each point is the mean firing rate during the first 100 ms after force application; data were calculated at each point from three sets of 20 consecutive responses of a single preparation. Bar indicates ± 1X s.e.

(2) *Bending forces applied in other planes.* Bending forces in directions outside of the plane of joint movement were applied to preparations with the femoro-tibial joint fully extended. In these experiments, the directional nature of the responses of tibial campaniform sensilla was perfectly maintained. Only the proximal sensilla responded to forces with a dorsal vectoral component (Fig. 4a). Although the activity of distal campaniform sensilla could be elicited by punctate stimulation (Fig. 4b), these receptors did not respond to any dorsal bending forces.

The responses of the proximal sensilla were maximal in the plane of joint movement and declined as force was applied in a more anterior or posterior direction (Fig. 4a). A very low level of discharge occurred when posterior bending force was applied but in an anterior direction no response was obtained and an inhibition of the background discharge of the proximal sensilla was seen.
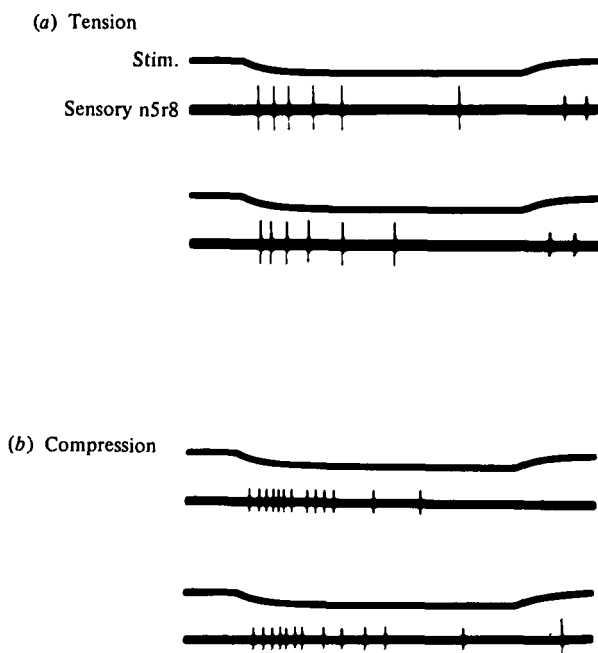
(a) Tension

(b) Compression

Fig. 6. Response of the tibial campaniform sensilla to axial forces applied at the distal end of the tibia. A large axial force (1·0 g) was applied by a long heavy tungsten wire attached to a piezo-electric crystal and arranged as a lever arm. (a) A distal sensillum responds weakly to axial tension. (b) A proximal sensillum exhibits a low level of discharge to axial compression. Sensilla were again identified by cap stimulation and ablation. Stimulus duration = 400 msec.

Curves of afferent firing frequency in response to increasing levels of applied force were generated for each plane (Fig. 5). Graphs of response frequency had the highest slope, that is, the greatest sensitivity, to low levels of force for most planes. Bending forces applied in intermediate planes produced responses that had lower initial slopes but lacked as great upper range compression. These findings support the conclusion that the proximal campaniform sensilla respond only to the dorsal vectoral component of the applied force.

(3) *Axial forces.* Axial forces produced only low frequency (less than 50 Hz) discharges from Group 6 campaniform sensilla ($n = 11$). At high levels of applied axial force (over 1 g) the proximal campaniform sensilla discharged upon axial compressions, while the distal sensilla responded slightly to axial tensions (Fig. 6).

These observations were limited by two factors. First, tibiae are rarely perfectly straight; applied axial forces could have been accompanied by slight bending. Forces were accepted as axial when no lateral displacement of the tibia was observed in the dissecting microscope. Second, the compliance of the tibia was very low to axial forces (Jensen & Weis-Fogh, 1962) and the piezo-electric crystal generated only small displacement at maximum voltages. This low compliance implies that, in its normal use, axial forces greater than the animal's weight would probably have to be applied to the tibia for the campaniform sensilla to respond.

(4) *Torques.* Torques were generated by applying force to a small segment of rigid
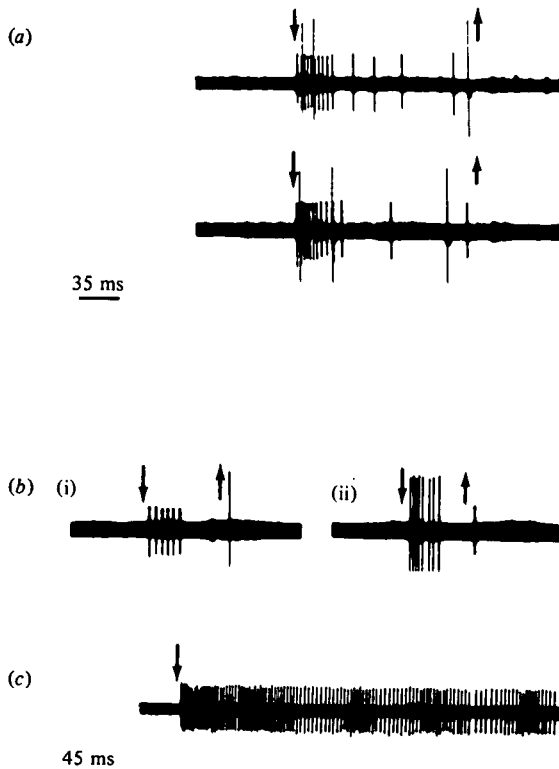
Fig. 7. Response of tibial campaniform sensilla to applied torques and unresisted movement. (*a*) Torques. A heavy wire was attached with wax to the distal end of the tibia perpendicular to the leg axis. Force (0·30 g) was applied at the end of the wire (2 cm). Both proximal and distal sensilla responded. (*b*) Tibial movement in a normal preparation. (i) The joint was rapidly extended through approximately 90 ° and released. A proximal sensillum fires with extension and a distal sensillum fires upon release. (ii) The opposite movement, rapid flexion, results in the discharge of the distal sensillum with movement and the proximal sensillum upon release. (*c*) Tibial movement in a heat damaged preparation. Extension of the joint results in a prolonged intense discharge. Arrow down = stimulus on; arrow up = stimulus off.

tungsten wire waxed onto the distal end of the tibia at 90 ° to the leg long axis (*n* = 9). In theory, some slight bending invariably accompanied torques generated in this manner but most often no discernible lateral displacement occurred. The tibial campaniform sensilla responded to applied torques with a weak discharge from both the proximal and distal sensilla (Fig. 7*a*). These responses were often irregular and at low frequency (less than 100 Hz). No systematic difference could be discerned between anterior and posterior rotations. In this entire series of experiments, torques were the only applied forces that simultaneously activated proximal and distal sensilla.

Response to imposed forces with movement unresisted

These forces, only generated in the single plane of joint movement, actually constitute bending forces. In normal preparations the response of the tibial campaniform sensilla was slight to these imposed movements. The proximal sensilla responded with a short burst to rapid extension through approximately 90 °, the distal sensilla to
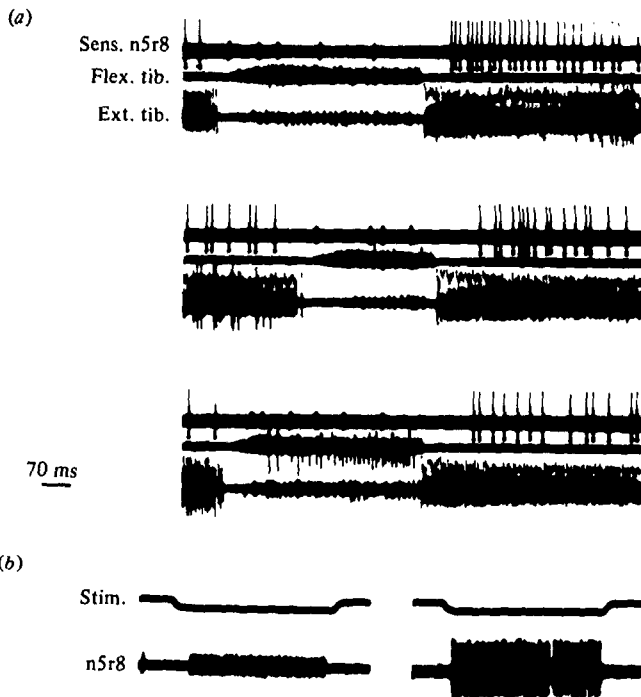
Fig. 8. Response of tibial campaniform sensilla to resisted muscle contractions. Flexions and extensions of the tibia were prevented by a small staple placed over its distal end. (*a*) Upper trace: sensory discharge in nerve 5r8. Middle trace: flexor tibiae myogram. Lower trace: extensor tibiae myogram. Rapid alternate bursting occurring in a preparation with cut anterior thoracic connectives. In rapid alternating attempted movements, the sensilla fire in association with muscle discharges. (*b*) Punctate stimulation reveals two sensillum axons in nerve 5r8, one proximal (at left) and one distal (at right) that match, in size, elements in (*a*). Stimulus duration in (*b*) = 400 msec.

rapid flexion through a similar angle (Fig. 7*b*). These discharges are qualitatively similar to those seen in previous experiments if it is assumed that transient resistance was supplied by tensions in the flexor and extensor muscles that were denervated in these experiments by cutting n3 and n5 close to the ganglion.

These discharges often became more pronounced when the leg had been immobilized for long periods or when the leg muscles had been damaged by heat (Fig. 7*c*). This observation can be explained by assuming that damage by heat or anoxia results in a decrease in the compliance of the muscles that are stretched by the imposed movement. This type of response is of interest since forced joint movements have been extensively used to study reflexes in many invertebrates (Delcomyn, 1969; Ayers & Davis, 1977; Burrows & Horridge, 1974). Undetected damage to muscles could account for the substantial variability of reflex responses seen in some preparations (Wilson, 1965; Delcomyn, 1969).

Response to muscle contractions with movement resisted

The responses of tibial campaniform sensilla to strains generated by spontaneous ontractions of the tibial extensor and flexor muscles were tested with all movement
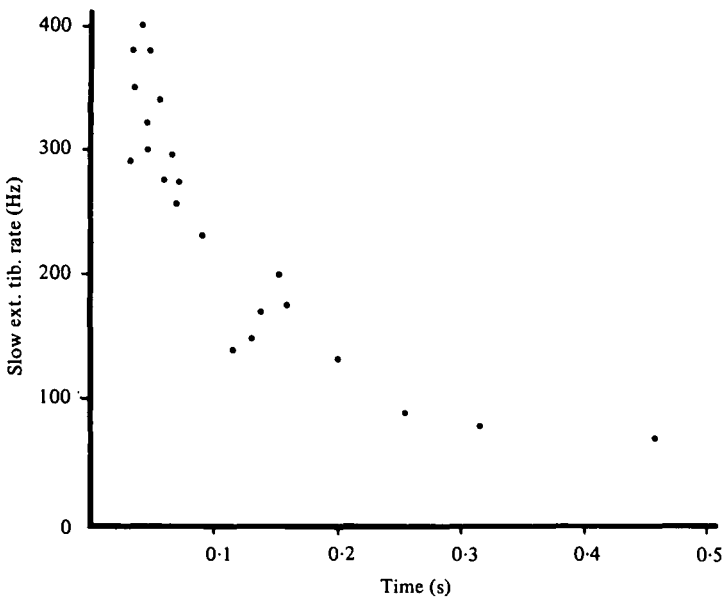
Fig. 9. Latency to excitation of distal campaniform sensilla depends upon the rate of extensor motoneurone discharge. Ordinate: rate of slow extensor junctional potentials. Abscissa: time between onset of discrete extensor tibiae bursts and the initiation of distal sensillum firing. See text for discussion.

resisted by a staple placed over the distal end of the tibia ($n = 18$). Group 6 activity was monitored in the dorsal nerve (n5r8) in the femur. This nerve was cut proximal to the electrodes to prevent potential reflex activity. Muscle activities were recorded myographically. The tibial extensor myogram typically showed one junctional potential of moderate amplitude that was correlated with firing of its slow excitatory motoneurone and another, much larger potential from its fast axon (Pringle, 1939; Atwood, Smyth & Johnston, 1969). The slow excitatory potentials could only produce tibial movement with iterative activity. Single unit activity could not regularly be discerned on the flexor tibiae myogram. The flexor tibiae muscle receives a complex, multiple excitatory innervation (Dresden & Nijenhuis, 1958).

With movement resisted, individual campaniform sensilla responded to contractions of either the flexor or extensor tibiae muscles according to sensillum cap orientation: the distal campaniform sensilla responded only to contractions of the extensor tibiae muscle, the proximal sensilla only to the flexor tibiae (Fig. 8a). The identity of the individual campaniform sensilla was again confirmed by punctate stimulation (Fig. 8b) and cap ablation.

Several observations strongly suggested that contractions of the tibial extensor also inhibited activity of the proximal sensilla and flexor contractions inhibited the distal sensilla. First, some background activity of the proximal sensilla regularly occurred in these preparations. This activity probably resulted from a small dorsal bending force exerted by the weight of the leg which was supported only by the femoro-tibial joint. This background discharge invariably ceased during extensor muscle contraction█
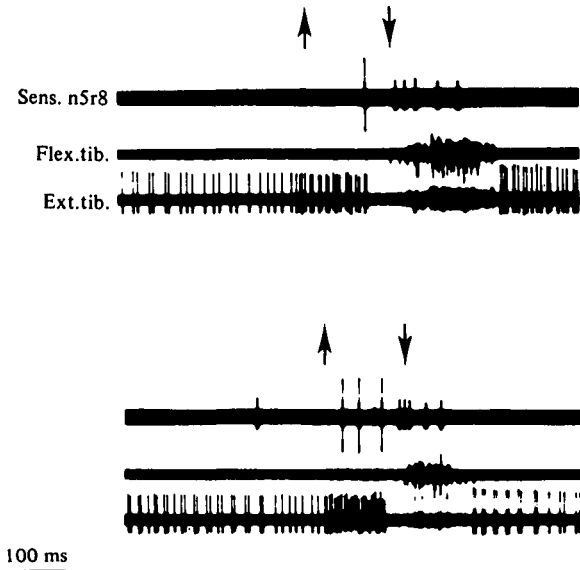
Fig. 10. Response of the tibial campaniform sensilla to muscle forces with movement not resisted. Upper trace – sensory nerve, middle trace – flexor tibiae myogram, lower trace – extensor tibiae myogram. In both recordings rapid spontaneous extension was followed by flexion. A distal sensillum fires in association with extension, a proximal sensillum with flexion. In the lower recording, the proximal sensillum fires before detectable flexor tibiae discharge. Arrow up – approximate time of extension. Arrow down – approximate time of flexion.

Second, during rapid alternating contractions of the antagonist muscles, distal sensillum firing ceased when the flexor contracted and proximal sensillum activity stopped when the extensor contracted (Fig. 8*a*). Thus, it appears that contractions of individual muscles can override or balance the strains produced by external forces or antagonist muscle contractions and directly regulate the activity of the tibial campaniform sensilla.

There was an appreciable latency between the appearance of muscle junctional potentials from slow motoneurones and the onset of sensillum activity. This was best seen in activity of the distal campaniform sensilla. The firing of the proximal sensilla was not invariably indicative of this for two reasons: first, these sensilla exhibited some background activity and would fire without the flexor contracting. Second, the smallest flexor junctional potentials were not always detectable in the myogram and the exact time of onset of flexor bursting could not be reliably determined.

The clarity of the extensor myogram permitted study of the dependence of this latency upon the rate of slow extensor motoneurone firing. In insect muscles, the rate of tension development is considerably affected by accelerations or decelerations of slow motoneurone activity (Pringle, 1939; Hoyle, 1955). To compare the latency of firing of sensilla that monitor the effects of these tensions, discrete, spontaneous extensor bursts, in which firing frequency did not vary more than 10%, were selected from tape recordings. In Fig. 9, the latency of onset of distal sensillum firing at different frequencies of slow extensor activity is plotted for 22 such discrete bursts from 5 preparations. These latencies are considerable for low rates of muscle junc-

tional potential activity and decrease dramatically for rates over 250 Hz. At high rate
of firing, however, the slow motoneurone that produced these junctional potentials
could not develop threshold tensions with sufficient rapidity to reduce the latency
below 30 ms.

This finding implies that there is an inherent peripheral delay in feedback from
campaniform sensilla to slow motoneurones generating graded tensions.

Response to muscle contractions with movement unresisted

Unresisted contractions of tibial muscles could produce rapid movements that were
often accompanied by short bursts from campaniform sensilla. These bursts occurred
in individual sensilla with the same directional sensitivity shown to resisted muscle
contractions: the distal sensilla fired briefly to extension, the proximal sensilla to
flexion (Fig. 10). Strains that excited sensilla probably resulted from transient bending
forces due to the drag exerted by the distal end of the tibia. This conclusion is sup-
ported by the observation that burst activity was increased when the distal end of the
tibia was weighted with wax. In some instances, a rapid full extension movement (that
elicited a burst from the distal sensilla) was followed by a small burst of the proximal
sensilla before discernible flexor firing occurred. This rebound discharge is probably
caused by tibial momentum that produced transient dorsal bending after the joint
locked in extension.

DISCUSSION

The responses of tibial campaniform sensilla to externally imposed and internally
generated forces can be summarized as follows:

Imposed bending forces in the plane of joint movement excite individual campani-
form sensilla according to cap orientation: the proximal sensilla, oriented perpendicu-
lar to the tibial axis, respond to dorsal bending forces; the distal sensilla, oriented
parallel to the tibia, respond to ventral bending.

Imposed bending forces in other planes also elicit responses according to cap
orientation. These discharges are less intense than those in the single plane of move-
ment defined by the dicondylic femoro-tibial joint.

Forces developed by muscle contractions produce strict orientation-dependent
responses. Proximal sensilla respond only to flexor muscle contractions: distal sensilla
respond only to extensor contractions.

Afferent discharges to both external and internal forces are greater when movement
is resisted.

Imposed axial forces produce only slight sensory discharges: the proximal sensilla
respond nominally to compression, the distal sensilla to tension.

Imposed torques excite, at low firing frequency, both proximal and distal sensilla.
Torque is the only stress that elicits co-activation of subgroups.

These responses of the Group 6 campaniform sensilla are determined by the way
strains that result from each of these forces are distributed through the tibia. Despite
many irregularities, the tibia may be considered a simple cylinder. The mechanics of
strain distribution in cylindrical structures is well known (Timoshenko, 1930;
Higdon, et al. 1967) and provides a useful model for interpreting these responses.

Bending

(a) (i)   (a) (ii)

Ext.   Ventral

Dorsal

Flex.

Axial

(b) (i)   (b) (ii)

➤ – Applied force
→ ← – Compression
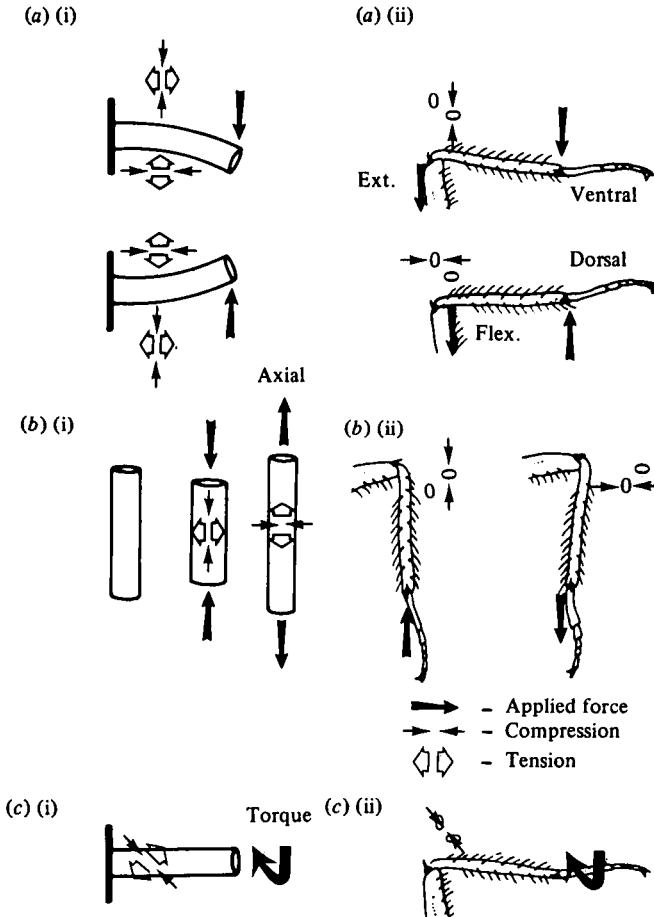◁ ▷ – Tension

(c) (i)   Torque (c) (ii)

Fig. 11. Forces on a cylinder compared with the forces upon the leg. (a) Bending force:
(i) Bending force applied at the free end of a cylinder results in longitudinal compression of the
contralateral side and transverse compression of the ipsilateral side. (ii) In the leg, ventral
bending force or extensor muscle contraction produce transverse compressions and excite the
distal sensilla. Dorsal bending or flexor muscle contractions produce longitudinal com-
pressions and excite the proximal sensilla. (b) Axial force: (i) Axial compressive forces produce
uniform compressions and transverse tensions. Axial tensions are accompanied by transverse
compressions. (ii) In the leg, proximal sensilla are excited by the axial compressions. Distal
sensilla respond to transverse compressions that accompany axial tension. (c) Torques:
(i) Applied torques produce helical compressions and tensions. (ii) In the leg both groups of
sensilla could respond to a component of this compression.

(1) *Strains in cylinders.* A hollow cylinder reacts to imposed stress (force/unit area)
by generating strains (changes in length/unit length) that can be considered simple
compressions or tensions on its surface.

    (a) Bending forces, which act perpendicular to the long axis of a cylinder, pro-
duce strains that are not uniformly distributed. This fact is best visualized if the
cylinder is mounted like a diving board – that is, fixed only at one end (Fig. 11*a*i).

Bending force imposed on one side of the cylinder at its free end increases the length of that side and shortens the opposite side. These length changes result in strains. Increases in length produce tensions; decrease in length produce compressions. These strains are graded along the length of the cylinder; they approach zero close to the point of force application and reach their maximum near the point of attachment (where a diving board inevitably breaks when over-stressed). Between stretched and compressed areas lies a midline plane along which no length changes occur, the 'neutral plane'. The magnitude of strains at any point in a transverse plane, perpendicular to the long axis of the cylinder, is linearly related to the distance of that point from the neutral plane. Strains are therefore maximal along the lower and upper edges (where an overstressed diving board begins to break). Strains along the axis of the cylinder are accompanied by opposing strains in transverse planes: for example, longitudinal tensions are associated with transverse compressions (a rubber band becomes thinner when it is stretched).

(b) Axial forces directed parallel to the long axis of the cylinder produce strains that are uniformly distributed (Fig. 11 b i). Under compressions a cylinder acts like a simple structural support column and reacts with uniform compression parallel to its axis and perpendicular tension. Because of their uniform distribution, the strains that result at any one point are small relative to the considerable strains that occur near the point of attachment when bending forces are imposed.

(c) Torques imposed at the end of a cylinder generate helical compressions that are maximal along a line oriented 45 ° to the long axis (Fig. 11 c i). These compressions are also uniformly distributed along the length of the cylinder and are accompanied by tension perpendicular to them.

(2) *The tibial campaniform sensilla act as strain gauges on a cylinder.* This analysis of strains in cylinders is consistent with a single directional sensitivity of the tibial campaniform sensilla to each of these forces.

(a) Bending forces are generated in two ways – by applying force to the end of the tibia and by resisting muscle contractions (Fig. 11 a ii). Thus, both flexor muscle contractions and imposed dorsal bends generate longitudinal compressions along the dorsal surface of the tibia; extensor muscle contractions and ventral bends generate lateral compressions along this surface.

The individual Group 6 campaniform sensilla that respond to these strains have their cap long axes oriented perpendicular to the compression. The proximal sensilla respond to both flexor muscle contractions and ventral bending, the distal sensilla to extensor muscle contractions and dorsal bending.

(b) Axial forces were much less effective in exciting the tibial campaniform sensilla as would be expected from their uniform distribution (Fig. 11 b ii). However the responses obtained were consistent: the proximal sensilla respond to axial compressions, the distal sensilla respond to the transverse compressions that accompany axial tensions.

(c) Torques excited both groups of sensilla. This response is again in accord with the directional sensitivity of these receptors since the helical orientation of these strains could produce compressive components perpendicular to the axis of both groups of sensilla (Fig. 11 c ii).

Analysis of strain in cylinders also provides insight into how the position of the
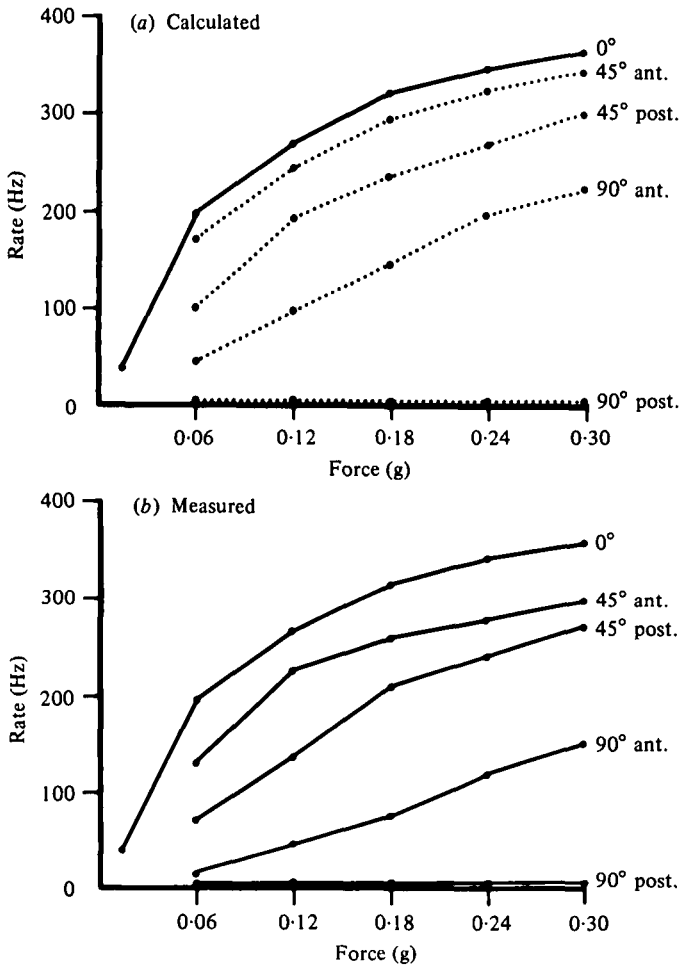
Fig. 12. The tibia as a cylinder. (*a*) Rates of discharge to bending in different planes were calculated from the discharge of a proximal sensillum in the plane of joint movement (o °). Each rate was calculated by considering the distance of the tibial campaniform sensilla from the neutral plane (see text). The slight posterior position of group 6 makes the response to anterior bending larger than that of posterior bends at the same angle. (*b*) Measured rates of discharge for a proximal sensillum. The hierarchy of responses in different planes is the same as calculated. The magnitude of the responses differs slightly but falls within the estimated error (± 5 °).

campaniform sensilla influences their responses. The Group 6 campaniform sensilla are located on the dorsal surface of the tibia, slightly (10–15 °) away from the plane of movement of the femoro-tibial joint. The function of this offsetting is unclear. In an ideal cylinder, strains in any transverse plane are linearly related to their distance from the neutral plane. The tibial campaniform sensilla are thus close to the point where maximum strains are elicited by forces acting in the plane of joint movement.

How does their offset from the joint plane affect their responsiveness ? In a cylindrical cross section the distance of points on the surface from the neutral plane is the product of the radius and the sine of the angle between that point and the plane (Higdon *et al.* 1967). Strains are maximal at 90 ° (sine = 1) and zero at o ° (sine = o).

The responses of the Group 6 campaniform sensilla, being slightly off axis, a▉
reduced, in theory, by a factor of $(1 - \text{sine } 75°)$. Because of the gradual decrement
of the sine function from $90°$ this factor produces only a 4% decrease in sensitivity.
In actual experiments it has not been possible to detect any difference in receptor
discharge between forces imposed in the plane of the joint or in the plane directly
opposite the sensilla.

The responses of the Group 6 campaniform sensilla to forces in other planes can
be similarly predicted. In each case forces applied in other planes can be viewed as
shifting the neutral plane closer to or further from the sensilla. It is possible to
calculate theoretical values for these strains from curves of the response to force
applied in the plane of the joint (Fig. 12a). The slight offset of the sensilla from the
joint axis implies that responses to forces applied $45°$ anterior to the joint plane
should be greater than those applied $45°$ posterior. Small compressions could occur
at $90°$ anterior but slight tensions might result at $90°$ posterior. These calculated
curves match, within a range of experimental error of $\pm 5°$, those seen in actual
tests of the responses to bending (Fig. 12b). The responses of the tibial sensilla
approximately monitor the vectorial component of these forces that acts in the plane
of joint movement. It can also be noted that, despite its irregularities, the tibia
transmits strains remarkably like a uniform cylinder.

In their position close to the femoro-tibial joint the Group 6 campaniform sensilla
are biased considerably toward the detection of bending forces applied at the distal
end of the tibia since, in bending, resultant strains are linearly related to the distance
from the point of force application. In the normal use of the leg, however, forces
applied at the distal end of the tibia are balanced by much greater forces developed by
the tibial muscles that operate at a much shorter lever arm. The position of the tibial
campaniform sensilla would tend to equalize the detection of these two forces of
dissimilar magnitude.

(3) *Directional sensitivity of campaniform sensilla.* These experiments conclusively
answer the question of the directional sensitivity of these receptors. Campaniform
sensilla respond to compressions *perpendicular* to the long axis of their cuticular caps.
This conclusion is in complete agreement with the findings of Spinola & Chapman
(1975) in their preliminary investigations of the campaniform sensilla of the cock-
roach, *Blaberus discoidalis* and confirms incidental observations of Schnorbus (1971)
in studies of the American cockroach. This view is, however, counter to that of Pringle
(1938a, b) who assumed that compressions parallel to the cap axis represented the
adequate stimulus. Pringle's original hypothesis was formulated without the benefit
of extensive recordings from single identified campaniform sensilla but was instead
based upon assumptions about the morphology of the cuticular caps and the behaviour
of rubber models. In these models, doming of the cuticular cap was considered the
mechanical link between exoskeletal strain and dendritic deformation. Spinola &
Chapman (1975) have since elegantly demonstrated that cap indentation, not doming,
produces sensillum excitation. In Pringle's own model (1938b) cap indentation would
result from compression perpendicular to the cap axis. In all, Pringle's early recog-
nition that asymmetry in the cuticular cap produces directional sensitivity has
remained a decisive insight.

(4) The adequate stimuli of the tibial campaniform sensilla. The tibial campanifor▉

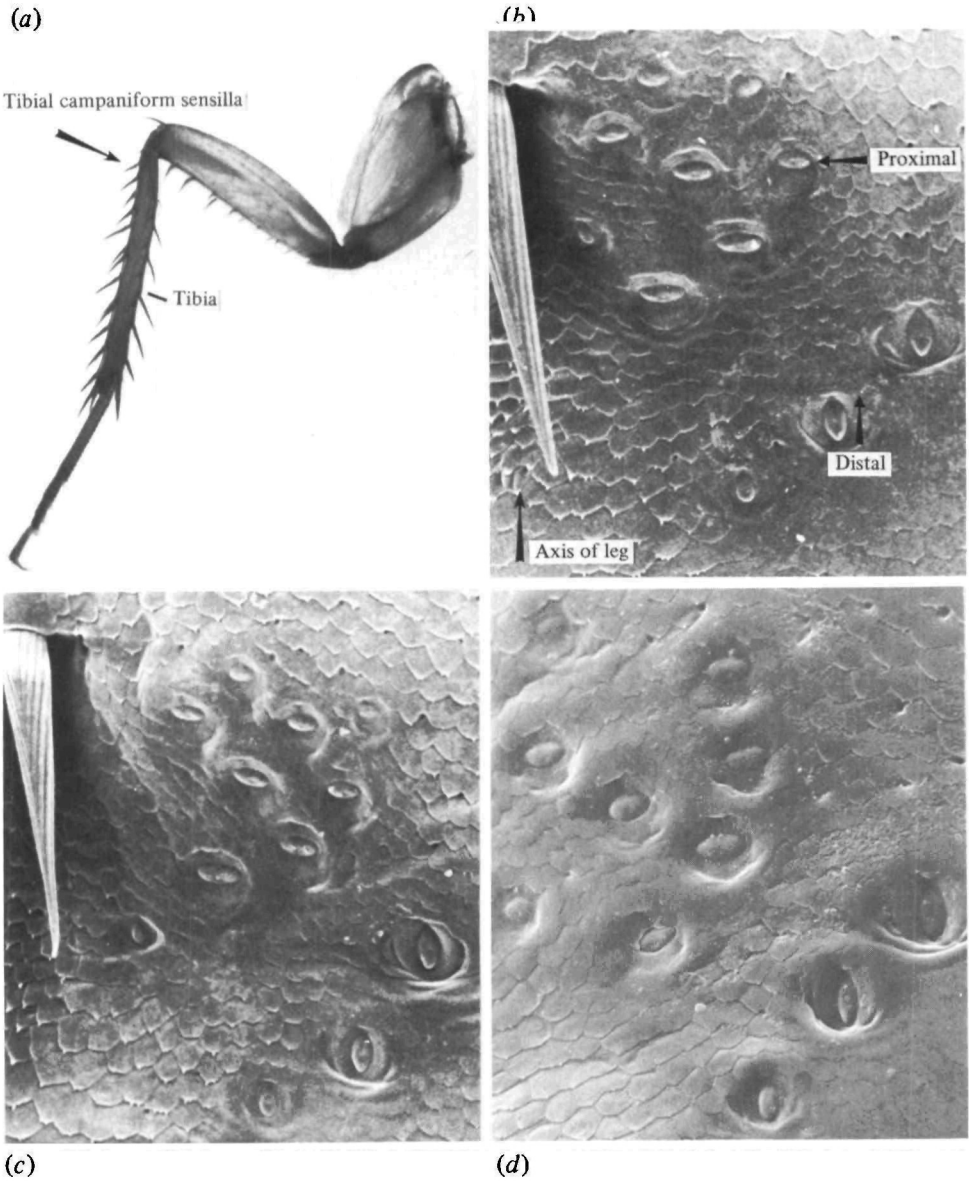(a)   (b)

Fig. 13. Location and orientation of the tibial campaniform sensilla. *a*: The tibial campaniform sensilla are located on the proximal end of the tibia slightly posterior to the plane of movement of the femoro-tibial joint. *b, c, d*: Scanning electron micrographs of the cuticular caps of the tibial sensilla from three different animals. These caps exhibit a consistent orientation. The long axes of the distal sensilla are parallel to the leg axis. The caps of the proximal sensilla are nearly perpendicular to the leg axis. These two subgroups are spatially separated. Magnification = 500 ×.

nsilla respond most vigorously to bending forces imposed in the plane of joint movement or generated by contractions of the tibial muscles. In normal leg use, external bending forces are developed by the animal's weight and balanced by the action of the leg muscles. The tibial campaniform sensilla are positioned to best monitor these load compensatory interactions.

The Group 6 sensilla were far less responsive to axially imposed forces. In standing or walking, forces are transmitted to the tibia by the tarsus and femur. These leg segments are positioned, for most of their operating range, at a severe angle to the tibia (Hughes, 1952; Reingold, 1975). Most of the force developed by the tibial muscles would be needed to resist the bending moment of these forces, which would be much greater than their axial components.

The effect of torques upon the tibial campaniform sensilla appears paradoxical. These forces could be taken as the most effective stimuli of the tibial sensilla since they excite receptors of both orientations. However, several factors argue against the importance of torques in the spectrum of forces to which these sense organs respond. First, large torques produce only a small transient afferent response. Second, the joint between the tarsus and tibia is a loose ball and socket while the proximal joint between the tibia and femur is a rigid hinge (Guthrie & Tindall, 1968). In the normal use of the leg, torques applied to the tarsus would readily produce rotation at the tibio-tarsal joint with little force transmission directly to the femoro-tibial joint. Third, as described in the next paper in the series, reflex effects of the tibial campaniform sensilla depend upon sensillum cap orientation. Excitation of the entire group of sensilla produces little overall effect due to mutual inhibition in their reflex pathways.

In summary, the tibial campaniform sensilla respond most effectively to those components of imposed forces that the animal can control by the action of its muscles.

(5) Comparison with other groups of campaniform sensilla. The legs of many insects possess groups of campaniform sensilla in positions comparable to the tibial Group 6 of the American cockroach (McIndoo, 1914; Pringle, 1938b; Knyazeva, 1974; Knyazeva et al. 1975; Heitler, 1977). These groups, generally located on the femur and tibia, are at the proximal ends of long cylindrical structures and are associated with muscle insertions. These sensilla also show consistent cap orientations. In the house cricket, for example, a mutually perpendicular cap orientation occurs in at least one group (Knyazeva et al. 1975). While the responses of these sensilla have not been directly recorded, consideration of their cap orientation and location relative to muscle insertions could permit simple structural analysis of possible strains and sensillum response.

This type of analysis is probably of limited application to groups of campaniform sensilla, such as those of the trochanter, that are associated with extensive modifications of the surrounding cuticle (Pringle, 1938b; Pearson, 1972). Changes in cuticle thickness and shape could substantially alter the distribution of strains on these segments (Barth & Pickelmann, 1975). Direct recordings of the sensillum response of some of these groups would lead to better understanding of the effect of cuticle shape upon the responses of mechanoreceptors.

Other groups of campaniform sensilla, such as those of the tarsus or maxillary palp Pringle 1938a; McIver & Siemicki, 1975), are located upon the distal ends of

cuticular segments. These sensilla are often located adjacent to loosely coupled join
and are close to the points of force application by more distal leg segments. The
cuticle in these areas could readily be subjected to 'unsymmetrical' bending (Popov,
1952) for which the mechanical analysis is quite complicated. Pringle (1938*a*)
described a recording from one of these groups on the maxillary palp that exhibited
a maximal response to bending forces imposed perpendicular to the joint plane.
This type of response should severely limit the use of these campaniform sensilla
in reflex load compensation.

The apparent diversity of the possible responses of campaniform sensilla warns
against a single general description of their function. Campaniform sensilla also
occur in association with other sensory receptors, such as the large cuticular spines
(Chapman, 1965) or filiform hairs (Dumpert & Gnatzy, 1977). In these receptors,
the campaniform sensilla are likely to serve a predominantly exteroceptive function.
The maximal responses of these ·campaniform sensilla should, however, still be
determined by their position and cap orientation.

(6) Comparison with other mechanoreceptors. There are two major conclusions
of this study. First, tibial campaniform sensilla are directionally sensitive and respond
to compressive forces perpendicular to their cap axis. Second, Group 6 – and
potentially many other groups of campaniform sensilla – respond both to imposed
forces and muscle contraction and could readily function in load compensation.

In their directional sensitivity, campaniform sensilla closely resemble cuticular
mechanoreceptors of other arthropods (Wright, 1976; Walthall & Hartman, 1978;
Dumpert & Gnatzy, 1977). Close parallels may be drawn with arachnid slit sensilla
described by Barth & Stagl (1976). These sense organs, morphologically similar to
campaniform sensilla, have dendrites that insert into elongated cuticular slits rather
than ovoid caps. Model studies (Barth & Pickelmann, 1975) and direct recordings
(Barth, 1972), show that slit sensilla respond to cuticular compressions perpendicular
to the long axis of the slit; this response is identical to that of Group 6 campaniform
sensilla.

Mechanoreceptors that closely resemble campaniform sensilla have been morpho-
logically identified in several species of crustaceans (Shelton & Laverack, 1968) but
the responses of these receptors are, at present, unknown.

In both vertebrates and invertebrates, many mechanoreceptors that monitor
muscle contractions are directionally sensitive (Granit, 1970). In crustacean muscle
receptor organs (Kuffler, 1954), vertebrate muscle spindles (Matthews, 1964), and
Golgi tendon organs (Houk & Henneman, 1967), directionality in coupling limits
responsiveness to provide essential proprioceptive information. The findings of the
present study suggest that insects may utilize the directional sensitivity of campani-
form sensilla to similar advantage.

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