TARSAL RECEPTORS AND LEG REFLEXES
IN THE LOCUST AND GRASSHOPPER

By H. I. RUNION and P. N. R. USHERWOOD

Department of Zoology, University of Glasgow

INTRODUCTION

Proprioceptive leg reflexes have for some time been considered an integral part of the mechanisms involved in postural activity and terrestrial locomotion in insects (e.g. Wilson, 1965, 1966). Chordotonal organs and sensory appendages found in abundance in insect legs presumably supply information required for fine control of the leg musculature during various behavioural activities. For example, in the metathoracic leg of the locust and grasshopper a chordotonal organ in the femoral segment signals the position, velocity and direction of movement of the tibial segment with respect to the femur. The activity of the 'slow' excitatory neurone which innervates the metathoracic extensor tibiae muscle is partly determined by the input from this receptor (Usherwood, Runion & Campbell, 1968). Chordotonal organs found in other segments of the metathoracic legs of these insects are also presumably involved in controlling the contractions of the leg muscles.

In this paper the properties of some exteroceptors found in the tarsal segments of the metathoracic leg of the locust and grasshopper are described. Usherwood & Grundfest (1965) had previously found that the inhibitory axon which innervates the metathoracic extensor tibiae muscle in locusts and grasshoppers can be excited by gently touching the tarsi of the metathoracic legs with a fine brush. More vigorous stimulation activated the 'slow' excitatory neurone to the extensor tibiae muscle as well. It seemed possible therefore that tarsal receptors might play some role in controlling the activity of the extensor tibiae muscle. The results of the present studies on the tarsal sensilla trichodea (Wolbarsht & Dethier, 1958; Dethier, 1963) support this conclusion and emphasize the important contribution that these receptors make to the over-all sensory input from the leg receptors. Furthermore, by studying the reflex pathways involving these tarsal receptors it has been possible to gain considerable insight into the functional significance of the peripheral inhibitory axon which innervates the metathoracic extensor tibiae muscle.

METHODS

The properties of the metathoracic tarsal hair sensilla of the locusts *Schistocerca gregaria* (15 males, 10 females) and *Locusta migratoria* (10 males, 10 females) and the grasshopper *Romalea microptera* (5 males, 1 female) were examined. These insects were obtained from colonies fed on a diet of grass and Bemax and maintained at 32° C. The physiological studies were made at 22 °C.

Three types of preparation were used. Descriptions of the methods used to make

two of these, intact restrained preparations and free-walking preparations, have already been published (Runion & Usherwood, 1966; Galloway, Runion & Usherwood, 1966; Usherwood *et al.*, 1968*a*). The third type of preparation was made by severing the metathoracic tibial and tarsal segments at the tibia–femur articulation. These isolated segments were then fixed with Tackiwax to a Perspex block with the ventral surface of the tarsal pads uppermost (Text-fig. 1). Two small punctures were made in the dorsal ridge of the tibia. Extracellular recording electrodes prepared from 40 μ insulated
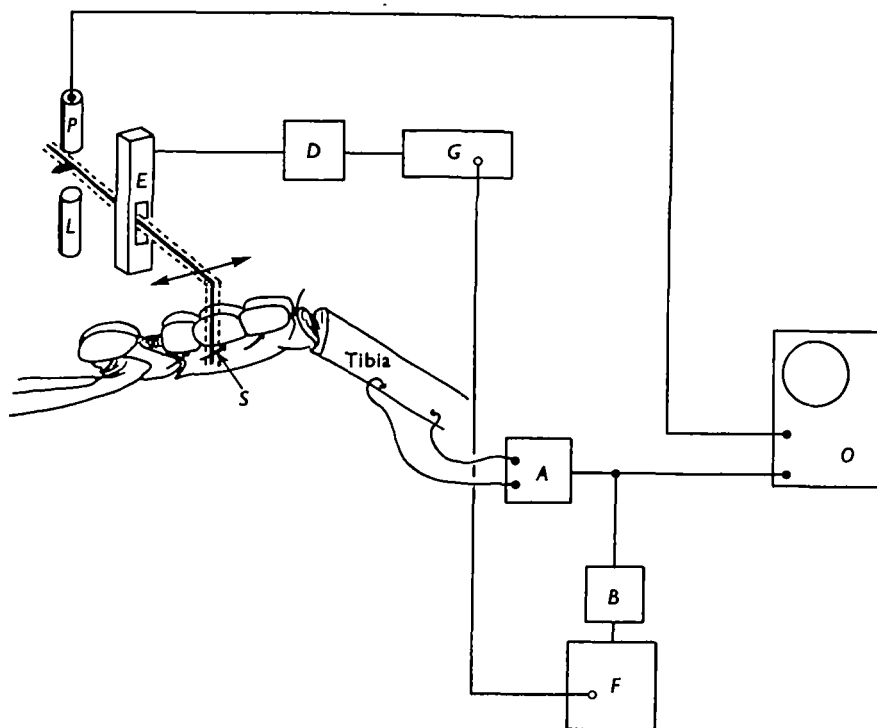

Text-fig. 1. Diagram of the apparatus used for mechanical stimulation of the tarsal sensilla trichodea of the locust and grasshopper. The instrumentation for recording the activity of the tibial nerve is also illustrated diagrammatically. *A*, differential amplifier; *B*, biopotential analyser (converts biological signals to suitable waveforms for frequency scaling); *D*, driver amplifier, *E*, electromechanical chopper, *F*, frequency counter; *G*, linear function generator; *L*, light source; *P*, photoconductive cell; *O*, oscilloscope; *S*, hair sensillum. See text for further explanation.

copper wire were inserted through the holes in the cuticle so that they lay in juxta-position to the tibial nerve (nerve 5*b*, Snodgrass, 1935). The electrical recordings from the nerve were amplified and displayed on a Tektronix 565 oscilloscope. Discharges recorded from the tibial nerve were counted on a Hewlett Packard 522*b* frequency rate counter. The counter was externally gated by a function generator to count only those discharges that occurred during a single cycle of an applied stimulus.

The hair sensilla were stimulated mechanically by a bent steel pin connected to a modified Collins Electric electromechanical chopper. The chopper was operated by a linear power amplifier which was in turn driven by a function generator with a

frequency range of o·1 to 200 Hz., for sinusoidal, ramp and square-wave functions. The amplitude of the signal from the function generator could be varied. Movements of the steel pin were monitored by a position indicator employing a cadmium sulphide photoconductive cell (Text-fig. 1), the response of the cell being displayed on the oscilloscope with the tibial neurogram. The steel pin was positioned at right angles to the sensillum. It was necessary to glue the pin to the sensory appendage with Eastman 910 adhesive to achieve adequate coupling between the pin and receptor, especially during mechanical stimulation at frequencies in excess of 10 Hz.
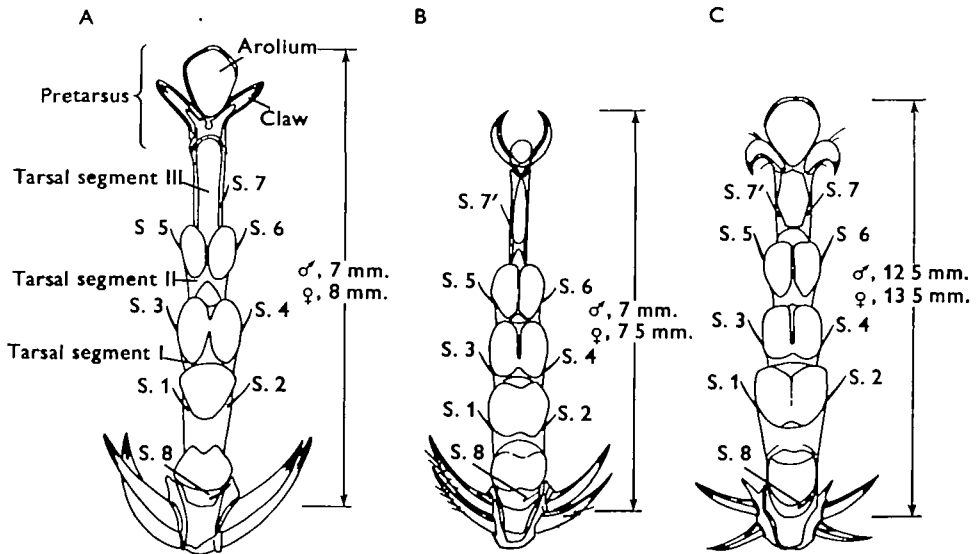

Text-fig. 2. Diagram to show position of sensilla trichodea (*S*) on the metathoracic tarsa segments of (A) *Schistocerca gregaria*, (B) *Locusta migratoria* and (C) *Romalea microptera*. Other hairs found on the tarsal segments of these insects probably have a sensory function, although they do not respond to mechanical stimulation when stimulated individually. The size of the sensilla has been greatly exaggerated for clarity.

RESULTS

Anatomy and histology of the tarsal receptors

The tarsal hair receptors can be clearly seen when the tarsal segments are viewed under a low-power microscope. There are eight or nine receptors of this type on the tarsal segments and they occupy almost identical positions in the three species of insects studied. Diagrammatic representations of the tibia-tarsal segments of the metathoracic legs are illustrated in Text-fig. 2. Albrecht (1953) has described the gross anatomy of the tarsal segments of the locust. There are four segments, three tarsi and a pretarsus. Tarsal segment I has three prominent membranous pads on its ventral surface and carries five hair sensilla. Tarsal segment II bears a single pair of pads and two sensilla, while segment III is characterized by a single long narrow membranous pad, with either a single sensory hair (sensillum 7) as in the two locusts or, in *Romalea*, with a pair of sensory hairs (sensilla 7 and 7′).

The hair sensilla in all three insects are more or less identical histologically. They consist of a sensory cell body surrounded by three accessory cells; a trichogen cell, a cuticular sheath cell and a tormogen cell (Text-fig. 3). This arrangement is characteristic of insect sensilla trichodea. Campaniform sensilla and other receptors, as yet unidentified, are also found on the tarsal segments of the locust leg and grasshopper leg.
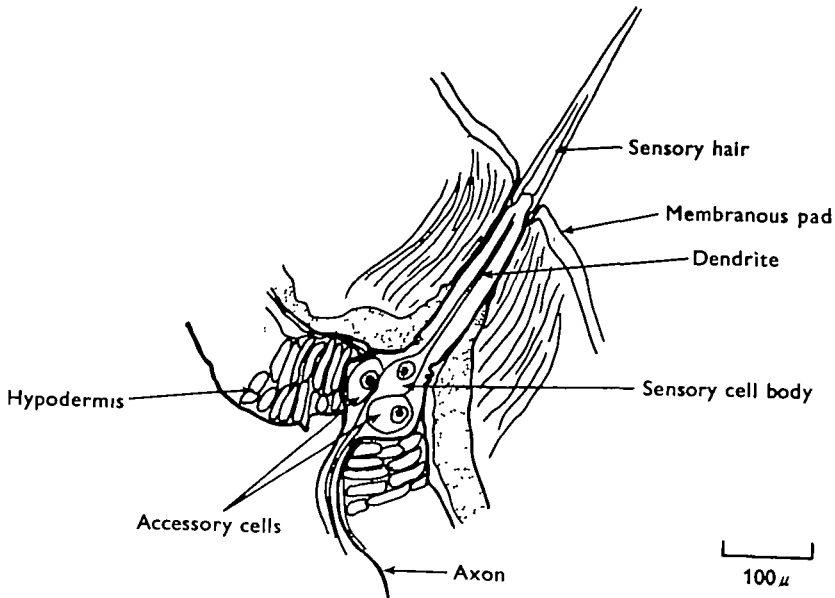

Text-fig. 3. Diagrammatic representation of the histological structure of a tarsal sensillum trichodeum of the locust *Schistocerca gregaria*. The diagram is principally derived from the phase-contrast micrograph shown in Pl 1.

Physiology of the tarsal sensilla trichodea

Oscillograph recordings from the metathoracic tibial nerves of *Locusta* and *Schistocerca* during mechanical stimulation (sinusoidal and ramp modes) of individual tarsal sensilla are illustrated in Text-figs. 4 and 5. The receptors are phasically responsive and remain electrically silent when the tarsal sensilla are at rest. A constant-amplitude sinusoidal input is accompanied by a phasically related output provided the input frequency does not exceed 100 Hz. (Text-fig. 4). When these receptors are stimulated at frequencies greater than 100 Hz. they respond asynchronously, i.e. they do not discharge at any particular time during the input cycle (Text-fig. 4). With sinusoidal stimuli of frequencies less than 100 Hz. the number of impulses generated by the receptors is inversely proportional to the input frequency, whereas the discharge frequency increases as the input frequency is raised (Text-fig. 6). The various sensilla respond differently to low-frequency sinusoidal stimulation. For example, in one *Locusta* preparation, sensillum no. 6 discharged approximately 70 times during one cycle of stimulation at 0·1 Hz., whereas sensillum no. 4 discharged only 20 times on average during one cycle at this frequency. With sinusoidal inputs of 3 Hz. or greater the response characteristics of the different sensilla in the three insects were more or less identical to those shown in Text-fig. 6 from sensillum nos. 1–6 of *Locusta*. The

sensilla were most sensitive to movements in a plane parallel to the longitudinal axis of the tarsi. Maximal responses were recorded when the sensilla were moved in a proximal direction, i.e. towards the tibia–tarsal articulation.

The relationship between the frequency of a sinusoidal input of constant amplitude and the phase angle of the first discharge of a cycle for a single sensillum is illustrated in Text-fig. 7. There was a noticeable shift in the phase angle of the first impulse of a
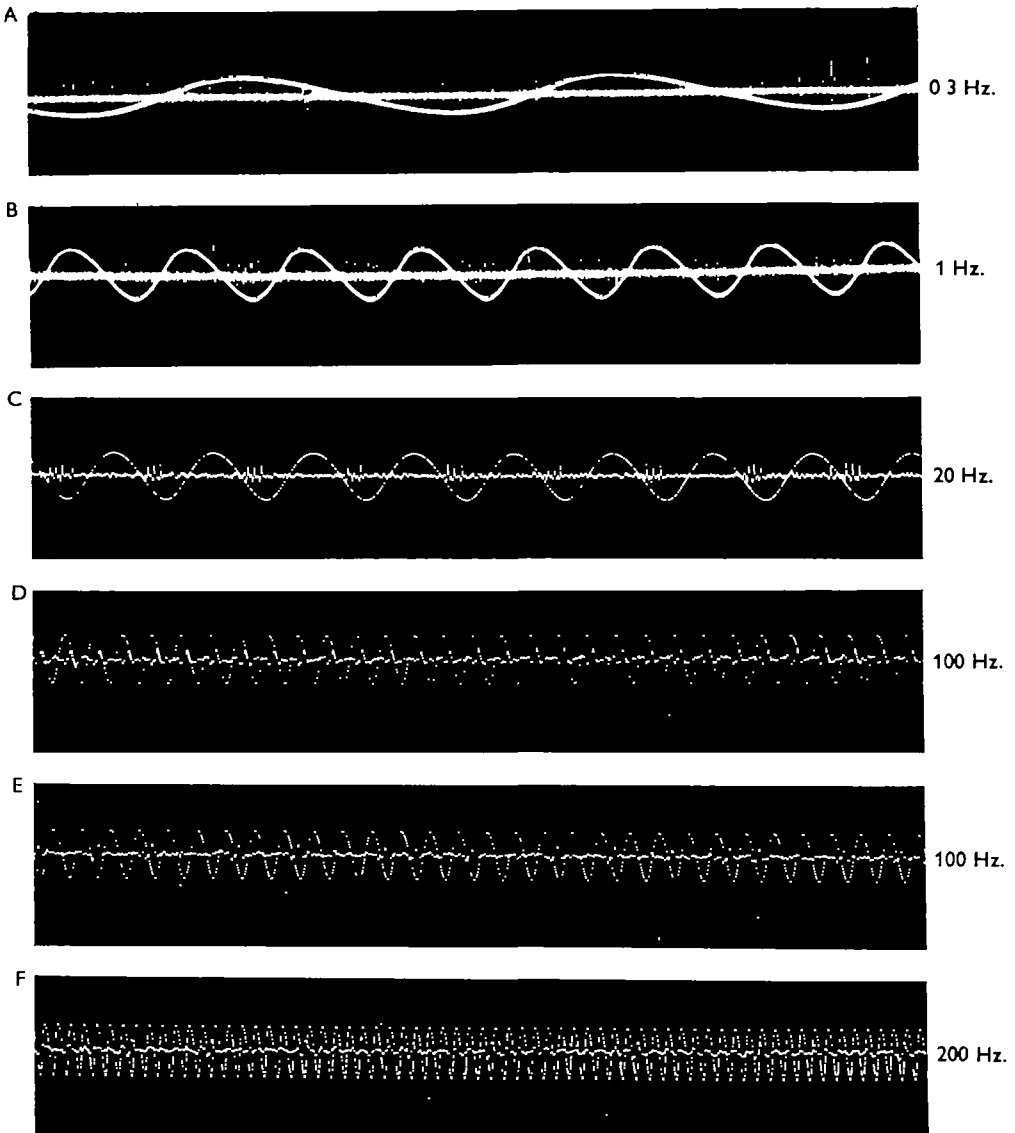
Text-fig. 4. Phasic responses of a tarsal sensillum trichodeum of the locust *Schistocerca gregaria* to sinusoidal movements (2° peak to peak) of the sensory hair at different frequencies. A photoconductive cell monitored the movements of the sensory hair and the output of this cell is displayed on the records from the tibial nerve. The records are complicated by discharges from other tarsal receptors although the output from these receptors was not phasically related to the sinusoidal input to the sensillum trichodeum. The relationship between stimulus frequency and the response of the hair sensillum is illustrated in Text-fig. 6.

cycle during long periods of sinusoidal stimulation at constant frequency, when the input frequency was greater than 5 Hz. In other words, the time of occurrence of the first impulse during a cycle of sinusoidal stimulation became progressively delayed with successive cycles.

With sinusoidal inputs of less than 3 Hz. the number of discharges per cycle of stimulation and the discharge frequency increased as the stimulus amplitude was increased. The excitation threshold of the sensillum, i.e. minimum sinusoidal input amplitude necessary for evoking a response from a sensillum, varied with the input frequency. At 5 Hz. an angular displacement of about 30' was sufficient to excite the
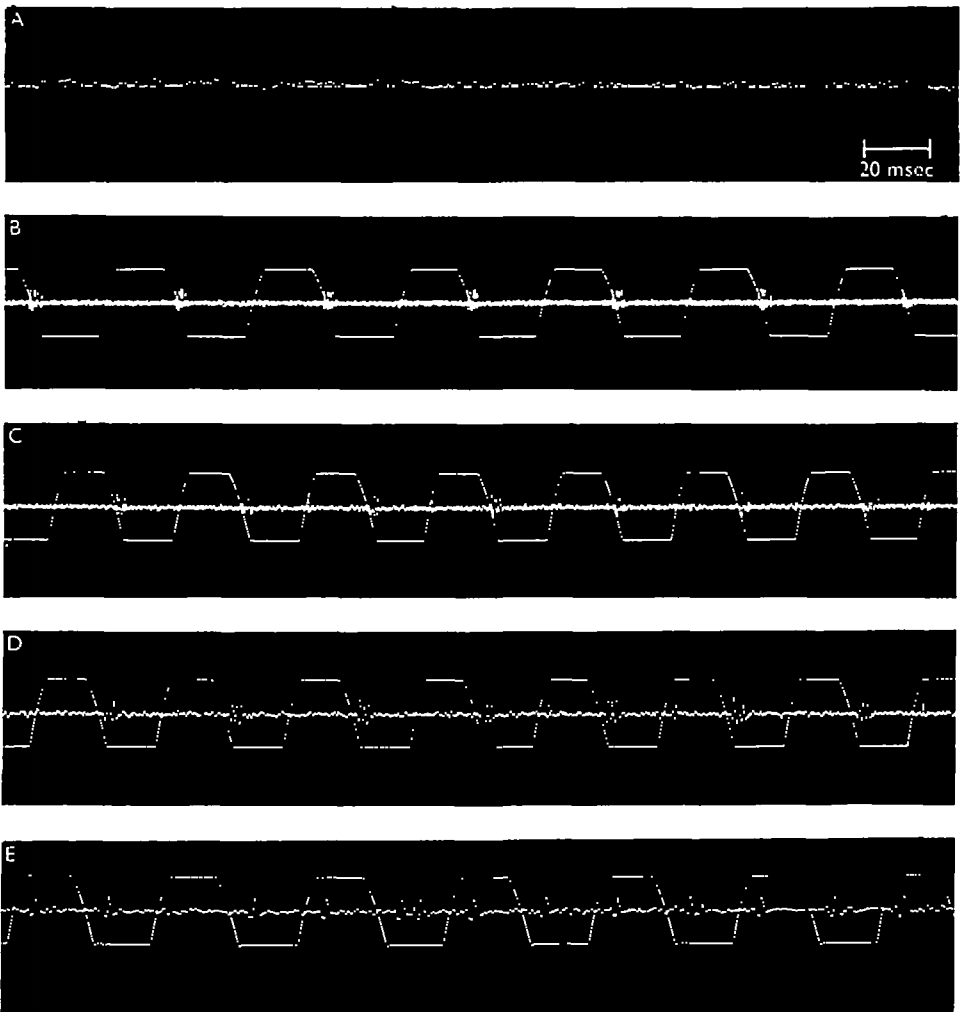
Text-fig 5. Response of a locust (*Schistocerca gregaria*) sensillum trichodeum to ramp move-ment of the sensory hair. The hair was alternately deflected through an angle of 2° and moved back to its initial position. Each complete cycle of movement was repeated: (B), twice per sec.; (C), 5 times per sec.; (D), 10 times per sec.; and (E) 20 times per sec. As the ramp velocity was increased the discharge frequency of the tarsal receptor increased. In (A), a recording from the tibial nerve, immediately following a prolonged ramp stimulation at 100/sec., is illustrated to demonstrate the low resting activity of the tarsal sense organs.

sensillum, at 10 Hz. a displacement of 10′ was sufficient, while at 100 Hz. a displacement of only 3′ excited the sensillum. Similar changes in excitability of insect mechanoreceptors have been reported by Pumphrey (1940) and Pringle & Wilson (1951). The phase relationship between sinusoidal input and discharge of the tarsal sensilla also changes when the input amplitude is altered. This is, of course, to be expected, since the tarsal sensilla are velocity receptors and will therefore respond earlier during the cycle of a constant-frequency sinusoidal input as the input amplitude is increased, simply because the threshold velocity for excitation of the receptor will occur earlier during the cycle.
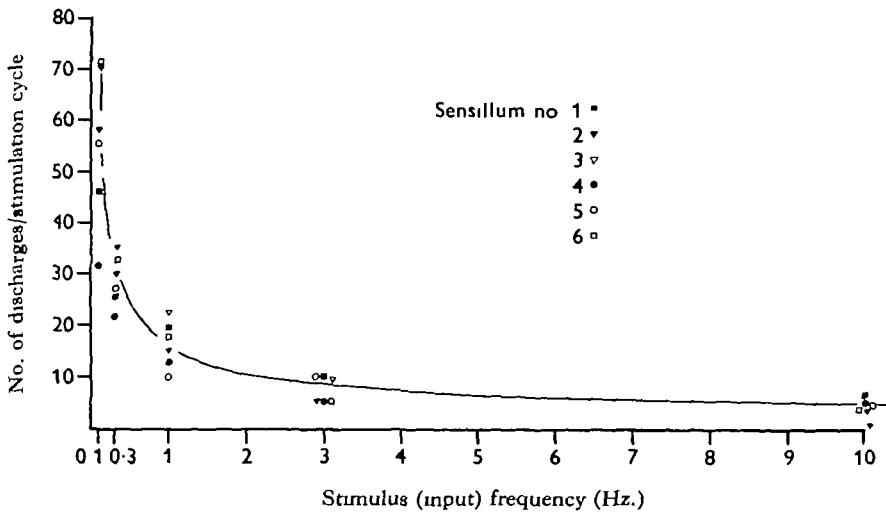
Text-fig. 6. Relationship between number of discharges of the tarsal sensilla (1–6) of *Locusta migratoria* per cycle of stimulation and the frequency of the sinusoidal input.

The effect of change in the velocity of the stimulus on the output of the tarsal sensilla was examined using cyclic ramp inputs, i.e. the sensillum was moved through different angles at different but constant velocities (Text-fig. 5). The number of discharges from these tarsal receptors decreased as the input velocity increased, probably due to the concomitant reduction in the duration of the ramp, but the discharge frequency increased with increasing input velocity.

The present examination of the sensory systems in the tarsal segments of locusts and grasshoppers was completed by briefly studying the activity of the tibial nerve during mechanical stimulation of complete tarsal segments rather than individual tarsal receptors. When the segments were moved individually in either sinusoidal (Text-fig. 8) or ramp modes a large burst of activity was recorded from the tibial nerve. Presumably this large discharge represents the activity of a host of different mechanoreceptors in the tarsal segments including a chordotonal organ which stretches from tarsal segment I to segment III.

Studies of the tarsal mechanoreceptors in situ

The inhibitory and excitatory neurones which innervate the metathoracic extensor tibiae muscle of the locust and grasshopper can be excited by stimulating metathoracic

tarsal receptors (Usherwood & Grundfest, 1964, 1965). Galloway *et al.* (1966) and Usherwood *et al.* (1968) suggested that these reflexes could be of significance in controlling the activities of the leg muscles during walking and postural behaviour. In the present experiments the relationship between activity of tarsal receptors and contractions of the metathoracic extensor tibiae muscle have been studied using intact restrained and free-walking locust preparations. In the intact restrained preparations,
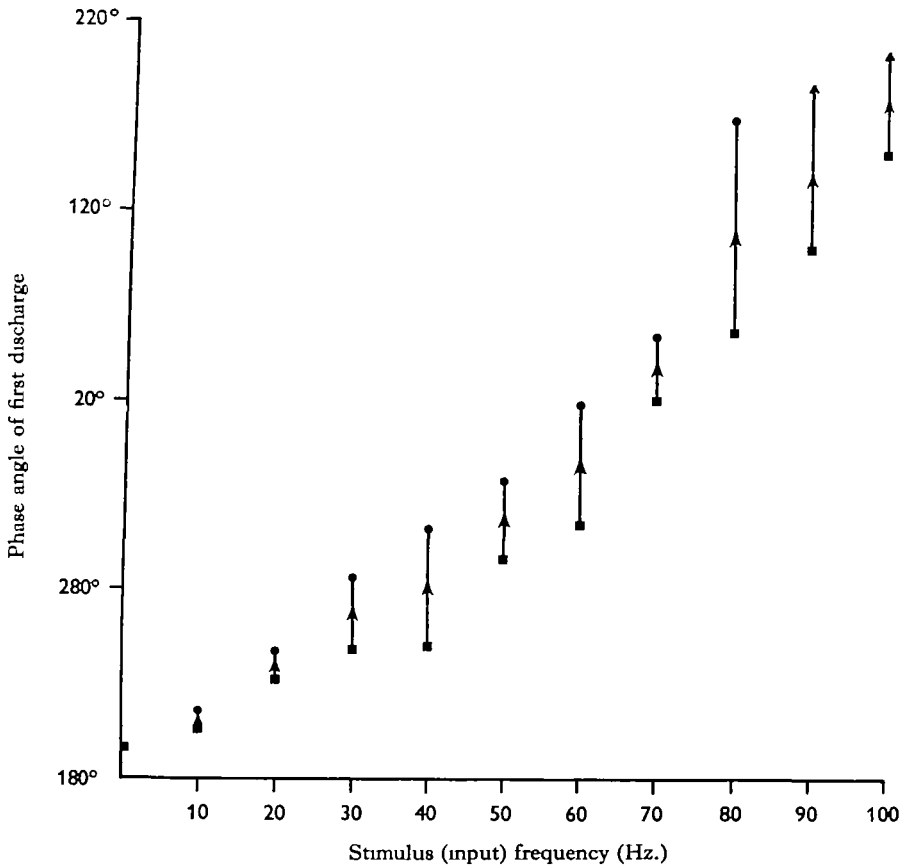
Text-fig. 7. Relationship between phase angle of first discharge of a locust (*Schistocerca gregaria*) sensillum trichodeum and the sinusoidal stimulus frequency. The phase angles during the first cycle of stimulation at different frequencies are indicated by the filled squares, while the phase angles during the 100th stimulus cycle are identified by the filled circles. The phase angle of the first discharge during a cycle shifts during prolonged stimulation at any one frequency (change indicated by arrows). With stimulation frequencies greater than 80 Hz. the receptors responded asynchronously after the first few cycles of stimulation. Phase angle was 0° when sensillum was in its natural resting position. Stimulus amplitude was constant throughout.
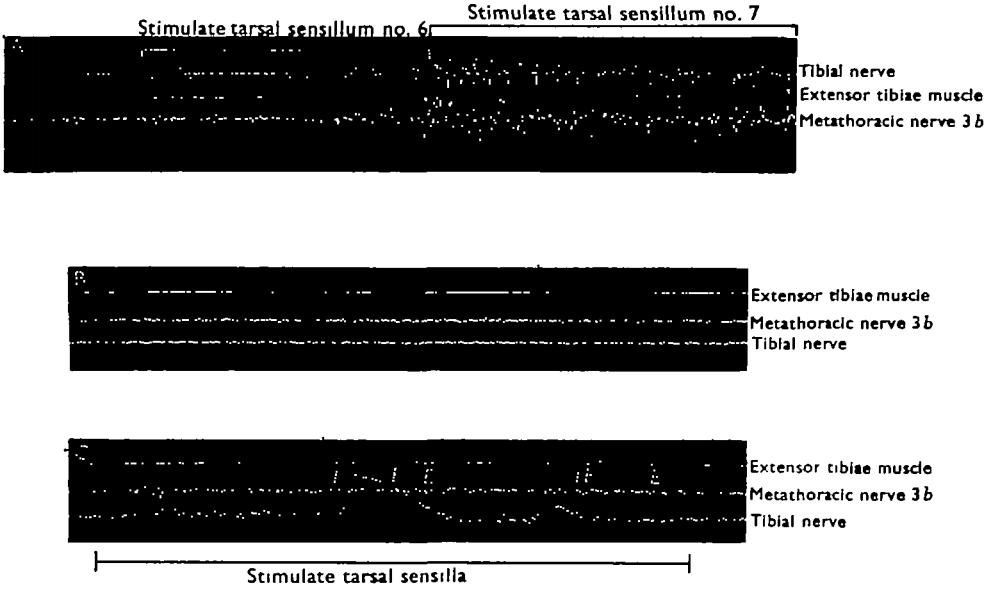
mechanical stimulation of individual tarsal sensilla failed to excite either the excitatory or inhibitory neurones to the extensor tibiae muscle, with the notable exception in some preparations of tarsal sensillum no. 7. In these preparations when this receptor was stimulated mechanically on its own, a series of four to six discharges of the 'fast' excitatory axon to the ipsilateral metathoracic extensor tibiae muscle was recorded

,(Text-fig. 9 A). This reflex was rapidly extinguished with repeated stimulation of the sensillum and in most of these preparations only the first stimulus of a series evoked a response from the 'fast' excitatory neurone; a long period of rest was then required before the reflex could be initiated once again. In view of the rather limited use of the 'fast' excitatory axon which innervates the metathoracic extensor tibiae muscle, the occurrence of this vigorous reflex is somewhat surprising. In order to excite 'slow' excitatory and inhibitory neurones it was necessary to stimulate at least four sensilla either simultaneously or in close succession.

Tarsal segment 1

Tarsal segment 2
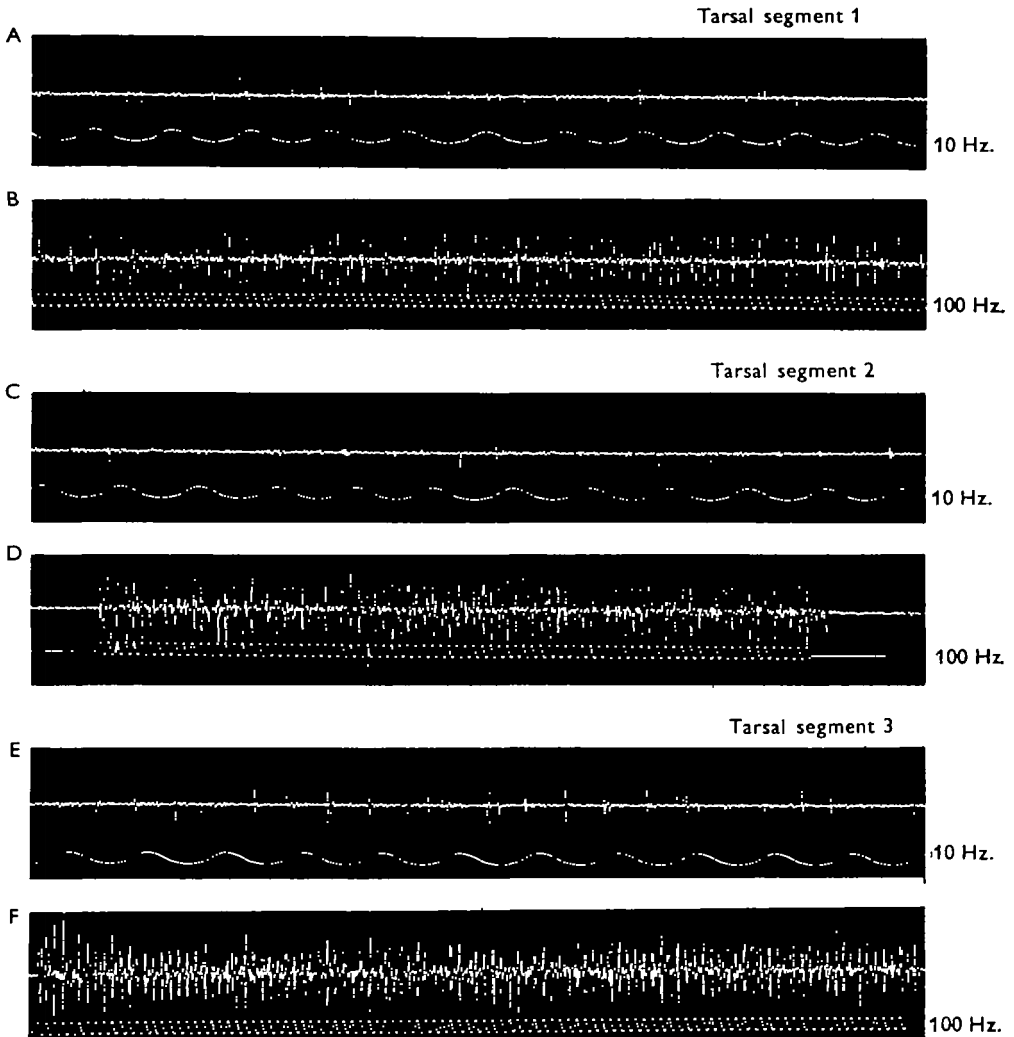
Tarsal segment 3

Text-fig. 8. Extracellular recordings from the metathoracic tibial nerve of *Schistocerca gregaria* during sinusoidal stimulation (peak to peak displacement of 4°) of tarsal segments I (A and B), II (C and D) and III (E and F). The segments were stimulated at 10 Hz. (A ,C and E) and at 100 Hz. (B, D and F).

The relationship between afferent information from the tarsal receptors and activity of the extensor tibiae muscle is illustrated in Text-figs. 9B and C. Information from the tarsal hair sensilla was almost zero when the animal was fixed on its back and the

Stimulate tarsal sensillum no. 6

Stimulate tarsal sensillum no. 7

Tibial nerve
Extensor tibiae muscle
Metathoracic nerve 3 b

Extensor tibiae muscle
Metathoracic nerve 3 b
Tibial nerve

Extensor tibiae muscle
Metathoracic nerve 3 b
Tibial nerve

Stimulate tarsal sensilla

Text-fig. 9. Recordings from an intact restrained locust (*Schistocerca gregaria*) preparation during mechanical stimulation of metathoracic tarsal sensilla trichodea. Recording electrodes were placed in metathoracic extensor tibiae muscle and on metathoracic nerve 3 b (contains 'slow' excitatory and inhibitory axons to the extensor tibiae muscle). Mechanical stimulation of individual tarsal sensilla failed to activate either the 'slow' excitatory or inhibitory neurones in nerve 3 b. However, in some preparations, stimulation of sensillum no. 7 evoked a brief series of 'fast' contractions of the extensor tibiae muscle (A). When the tarsal segments are off the ground, the level of activity of the tarsal receptors is very low and the 'slow' excitatory and inhibitory axons in nerve 3 b are completely silent (B). However, when the tarsal segments are gently touched with a fine hair, activity is recorded from the tibial nerve. At the same time, impulses are recorded from the 'slow' excitatory (E) and inhibitory (I) axons in nerve 3 b (C).


Seconds
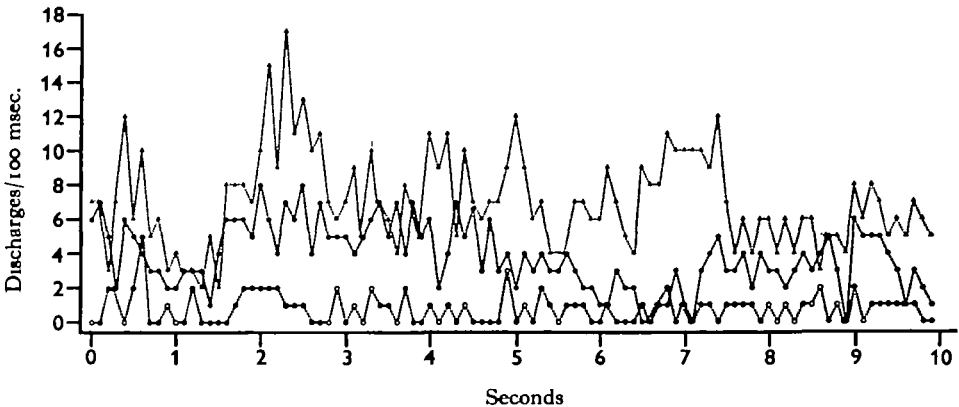
Text-fig. 10. Relationships between input from the metathoracic tarsal receptors of a free-walking locust (*Schistocerca gregaria*) preparation and activities of the 'slow' excitatory and inhibitory neurones to the metathoracic extensor tibiae muscle, when the insect is standing still. The points on the graph represent the number of discharges (sensory ▲, 'slow' excitatory ●, and inhibitory ○) recorded during consecutive sampling periods of 100 msec. It is significant that, during postural activity, both the activities of the 'slow' excitatory and inhibitory neurones are to some extent correlated with the input from the tarsal receptors.
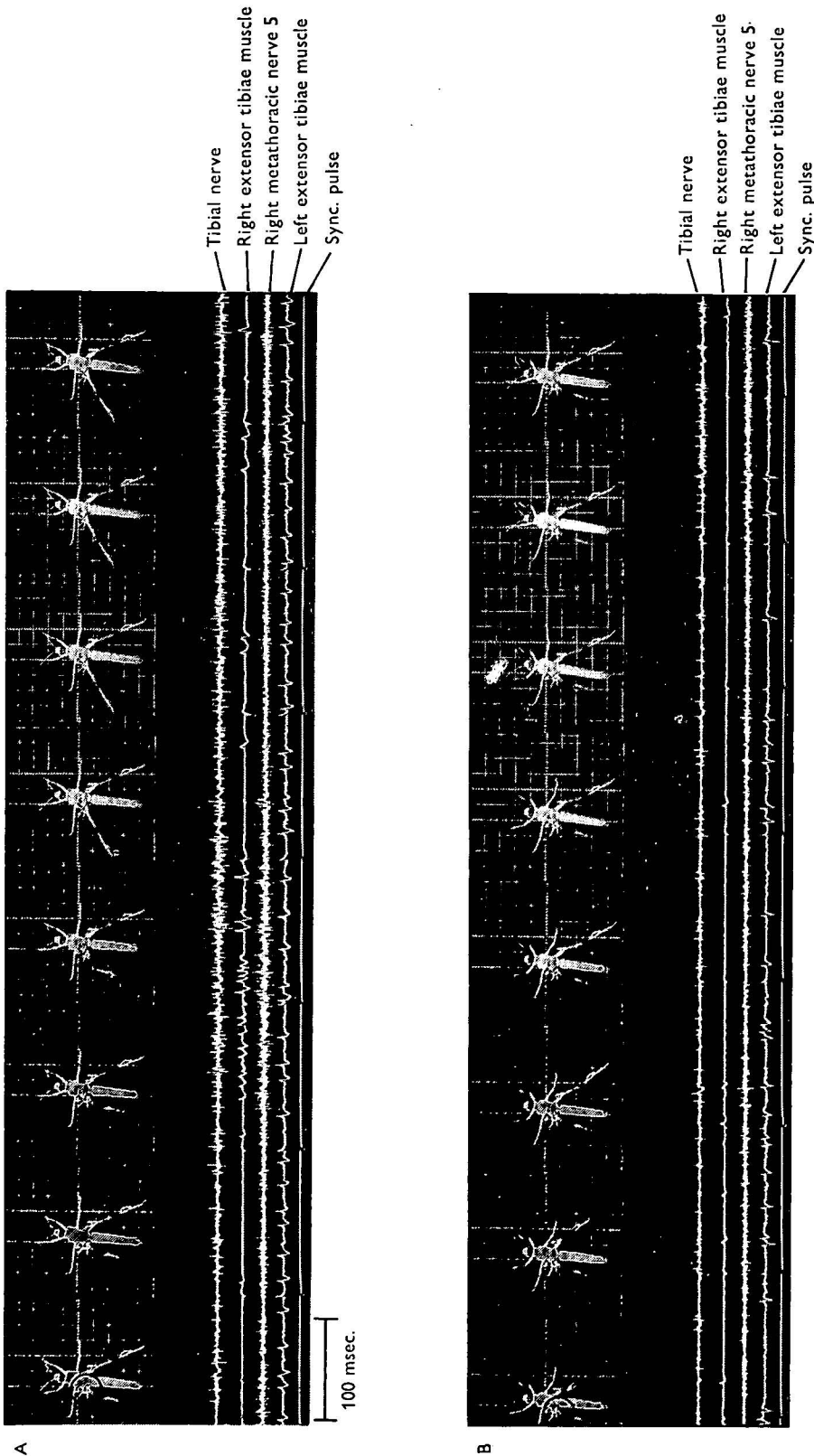
Text-fig. 11. Simultaneous photographic records and electrical recordings from a free-walking locust (*Schistocerca gregaria*) preparation. Recording electrodes were located on the right metathoracic nerve 5 and on the tibial nerve of the right metathoracic leg. Other recording electrodes were placed in the right and left metathoracic extensor tibiae muscles. Movement of the right metathoracic leg (A) is signalled by an increase in sensory input from the receptors in this leg (see tibial neurogram and recordings from nerve 5). There is some 'slow' excitatory activity in the right metathoracic extensor tibiae muscle, but it is in the contralateral metathoracic extensor tibiae muscle that most activity is seen; i.e. as the weight of the insect is transferred to that leg. In (B) there is no perceptible movement of the right metathoracic leg, although shifts in the centre of gravity of the locust are reflected by transient changes in the tibial nerve activity of right metathoracic nerve 5. These changes are associated with 'slow' contractions of right and left metathoracic extensor tibiae muscles.

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tarsal segments were not in contact with the substratum. In Text-fig. 9C the tarsal segments were gently touched with a fine brush and the resultant discharges of the tarsal receptors was accompanied by activity of the 'slow' excitatory and inhibitory neurones to the ipsilateral extensor tibiae muscle. Evidence for cross-reflexes involving the tarsal receptors and the contralateral extensor tibiae muscle was obtained, although these cross-reflexes are much weaker than those reflexes involving a single side only (P.N.R. Usherwood & H.I.Runion, to be published).
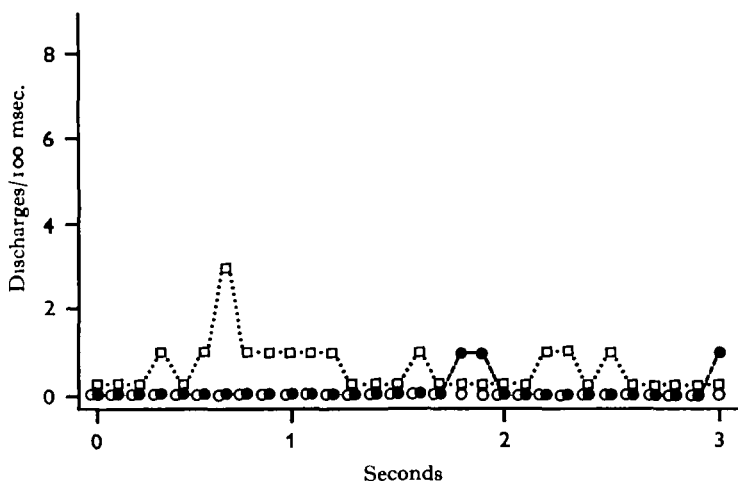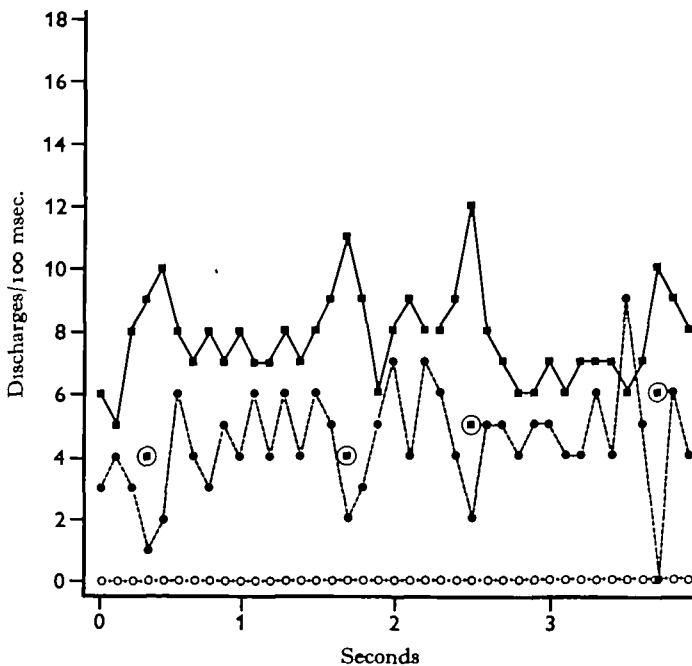

Text-fig. 12. As for Text-fig. 10, except that the locust was holding the metathoracic tarsal segments off the ground. Note decreased input from tarsal receptors and decreased activity of the 'slow' excitatory and inhibitory neurones to the metathoracic extensor tibiae muscles compared with Text-fig. 10. □, sensory discharge; ●, 'slow' excitatory discharge; O, inhibitory discharge.

The results of studies on free-walking locust preparations were very informative. When the animal is standing still with the metathoracic tarsal segments in contact with the substratum, a constant stream of information passes down the tibial nerve from the tarsal receptors to the central nervous system (Text-fig. 10). Changes in the frequency of this afferent discharge are frequently accompanied by alterations in activity of the 'slow' excitatory and inhibitory neurones which innervate the metathoracic extensor tibiae muscle. Both these neurones are very active during postural activity and are presumably involved in controlling the tonic state of the extensor tibiae muscle (Usherwood, 1967; P. N. R. Usherwood & H. I. Runion, to be published). Changes in the activity of the tarsal receptors following slight adjustments in the balance of the insect, with resultant changes in the activities of the extensor tibiae muscle and the other leg muscles, could provide the basis for a very useful feedback system for stabilizing the insect (Text-fig. 11). When the tarsal segments are lifted off the ground the discharges of the tarsal receptors fall almost to zero and when this occurs the inhibitory and excitatory outputs to the extensor tibiae muscle cease (Text-fig. 12).

When the metathoracic tarsal segments are removed the angle between the tibia and femur changes in a similar fashion to that seen on removal of the metathoracic femoral chordotonal organ (Usherwood *et al.* 1968). Normally, when the animal is standing
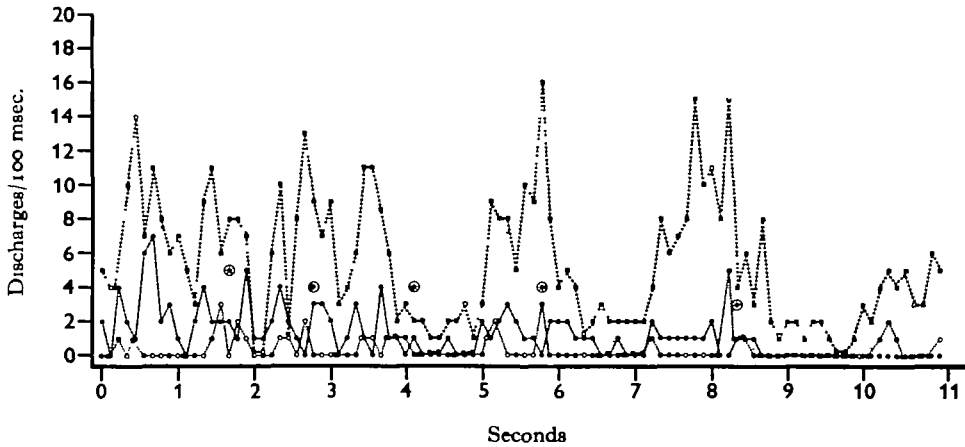
Text-fig. 13. As for Text-fig. 10, except that the locust (*Schistocerca gregaria*) was walking slowly but regularly. Note that in this preparation, just prior to flexion (⊕), the inhibitory neurone to the metathoracic extensor tibiae muscle discharges 2–4 times. The activity of this neurone is preceded by a marked increase in the level of input from the tarsal receptors. ■, sensory discharge; ●, 'slow' excitatory discharge; ○, inhibitory discharge.

Text-fig. 14. As for Text-fig. 10, except that the locust (*Schistocerca gregaria*) was walking slowly and irregularly. This graph also includes data on activity of the metathoracic flexor tibiae muscle. The level of input from the tarsal receptors is greatest just prior to and during flexion (◉) and is correlated partly with a large transient reduction in the activity of the 'slow' excitatory neurone to the extensor tibiae muscle. The 'fast' neurone which innervates the extensor tibiae muscle is not active during walking. In this particular preparation, the inhibitory neurone to the extensor tibiae muscle was completely inactive throughout the period that the locust was walking. ■, sensory discharge; ○, inhibitory discharge; ●, excitatory discharge.

still the tibia–femur angle is between 60° and 70° but, following removal of the tarsi, the angle increases to about 80°. At the same time there is a significant fall in the activities of the 'slow' and inhibitory neurones to the metathoracic extensor tibiae muscle. The insect makes repeated 'searching' movements with the tibial stump, but these eventually disappear as the insect accommodates to the new situation. This usually takes about 2–3 days. However, the activities of the excitatory and inhibitory neurones never return to normal, but remain at an abnormally low level. When both sets of metathoracic tarsal segments are removed, the prothoracic and mesothoracic legs assume full responsibility for postural maintenance while the metathoracic legs are either dragged or held off the substratum.

During slow walking the locust takes small jerky steps and alternation of the contractions of the metathoracic flexor tibiae and extensor tibiae muscles is not particularly clear-cut. The input from the tarsal receptors increases to some extent just prior to and during flexion of the tibial segment and 'slow' contractions of the metathoracic extensor tibiae muscle alternate with 'fast' contractions of the flexor tibiae muscle of this leg (Text-fig. 13). The inhibitory neurone to the extensor tibiae muscle of the metathoracic leg is sometimes inactive during slow walking (Text-fig. 14) although this is not usually the case. During fast walking, however, where regular alternation of flexor and extensor contractions occurs and the insect steps very precisely with its metathoracic legs, the inhibitory neurone to the extensor tibiae muscle always fires 2–4 times just prior to flexion when there is a large increase in the input from the tarsal receptors (Text-fig. 13). When the tarsal segments are removed there is a large reduction in the inhibitory activity. More information on this peripheral inhibitory system in the locust will appear in a later publication.

DISCUSSION

The phasically responsive tarsal sensilla provide the insect with information on the time of contact of the tarsal segments with the substratum and of changes in the load on the metathoracic leg. During walking activity the receptors could provide cues for timing the activities of the metathoracic leg muscles and possibly the muscles of the prothoracic and mesothoracic legs as well. Activity of the 'slow' excitatory and inhibitory neurones to the extensor tibiae muscle of the metathoracic leg is most pronounced during postural activity. Changes in the load on the metathoracic leg through postural adjustments of the insect produce large increases in the activity of the tarsal receptors of that segment and the increased input from these receptors is accompanied by changes in the inhibitory and/or excitatory output to the metathoracic extensor tibiae muscle. For example, when the insect is standing and shifts its centre of gravity by re-positioning one of its prothoracic or mesothoracic legs or its contralateral metathoracic leg the change in load on the ipsilateral metathoracic leg is signalled by an increase in activity of the ipsilateral metathoracic tarsal receptors (Text-fig. 11). Adjustments in the tonic state of the ipsilateral metathoracic extensor tibiae muscle and also presumably of other leg muscles then takes place to compensate for the changed conditions. It is probable that the output to the leg muscles is partly determined not only by the level of input from the tarsal receptors, but also by the quality of this input; i.e. the number of receptors excited; the sequence in which these receptors are excited; and the com-

bination of receptors excited. Information from other tarsal receptors, especially the campaniform sensilla (Pringle, 1938) and from receptors in other parts of the body also undoubtedly contributes to the information on which the commands to the postural muscles are based. Indeed it has already been shown (Usherwood *et al.* 1968) that information from the chordotonal organ in the femur of the metathoracic leg is of some importance in determining the level of activity of the 'slow' excitatory neurone which innervates the metathoracic extensor tibiae muscle. Cross-reflexes and intersegmental reflexes involving the tarsal sensilla have also been demonstrated.

The reflex relationship between the tarsal receptors and the peripheral inhibitory axon which innervates the metathoracic extensor tibiae muscle seems well founded. During postural activity, changes in the firing frequency of the inhibitory neurone frequently coincide with changes in the input from the tarsal receptors of the ipsilateral leg. Under these conditions it appears that the inhibitory neurone is used to vary the force developed by the tonic fibres (Usherwood, 1967) in the extensor tibiae muscle. The inhibitory neurone is also often active during postural activity when tension in the extensor tibiae muscle is falling, thereby accelerating the relaxation of the tonic fibres of the extensor tibiae muscle. Accelerated relaxation of these tonic fibres by this inhibitory neurone could also occur during fast walking activity, when the neurone fires just prior to flexion of the tibia. By increasing the relaxation rate of the tonically responsive extensor tibiae muscle fibres, an increase in the frequency of stepping can presumably be achieved. In this respect, it is significant that, during slow walking activity when the rate of relaxation of the extensor tibiae muscle might not be critical, the inhibitory neurone to the extensor tibiae muscle is often completely inactive. The activity of the inhibitory neurone during walking is presumably determined to some extent by the input from the metathoracic tarsal receptors and this input differs quantitatively and qualitatively during fast and slow walking activity (P. N. R. Usherwood & H. I. Runion, to be published).

SUMMARY

1. The physiological properties of hair sensilla found on the metathoracic tarsal segments of the locust and grasshopper are described.

2. The sensilla trichodea are phasically responsive mechanoreceptors. The discharge frequency of these receptors is proportional to the velocity of displacement of the sensory appendage. Phase-related responses are obtained with sinusoidal inputs less than 100 Hz. With higher input frequencies the receptors respond asynchronously.

3. The tarsal sensilla signal contact of the tarsal segments with the substratum and changes in the load on the metathoracic leg.

4. Reflexes involving these tarsal receptors and the 'fast' and 'slow' excitatory and inhibitory neurones which innervate the metathoracic extensor tibiae muscle have been demonstrated and appear to play a significant role during postural and walking activity.

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EXPLANATION OF PLATE

Phase-contrast micrograph of a tarsal sensillum trichodeum of the locust *Schistocerca gregaria*. See text and Text-fig. 3 for further explanatory details.

100 μ