

PHYSIOLOGICAL PROPERTIES OF AFFERENTS FROM TACTILE HAIRS ON THE HINDLEGS OF THE LOCUST

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Summary

1. The spatial distribution and physiological properties of the tactile hairs and their sensory afferents of the hindlegs of the locust *Schistocerca gregaria* are described. Hairs occur in a consistent position from animal to animal. Hairs on the dorsal tibia are of a greater mean length, $403.1 \pm 17.9 \mu\text{m}$, than hairs on the ventral tibia, $265.2 \pm 10.44 \mu\text{m}$. Hairs on the dorsal and ventral femur are approximately $310 \mu\text{m}$ long and hairs on the tarsus are shorter, approximately $200 \mu\text{m}$.

2. Based on their threshold responses to sinusoidal mechanical stimulation, the tactile hairs are of two basic physiological types. High-threshold hairs occur only on the proximal dorsal tibia and at the proximal base of each tibial spine, whereas low-threshold hairs are found on the femur, tibia and tarsus.

3. High-threshold hair afferents respond phasically to imposed deflections of the hair shaft and have mean velocity thresholds of $21.1 \pm 4.2 \text{ s}^{-1}$. They adapt rapidly to repetitive stimulation, after as few as 11 cycles at 5 Hz. Low-threshold hairs respond in a more phaso-tonic manner to imposed deflections and have velocity thresholds of less than 3 s^{-1} . They adapt to repetitive stimulation at a similar rate to the high-threshold hairs, but continue to respond to stimulation after 200 cycles at 5 Hz.

4. All the hairs are directionally sensitive, with the preferred direction being oriented proximally and medially (i.e. proximally and towards the body); they are least sensitive to deflections in the opposite direction.

Introduction

Mechanical stimulation of tactile hairs on a leg of a locust elicit well-defined reflex movements of that leg such that it is moved away from the stimulus (Pflüger, 1980; Siegler and Burrows, 1986). A great deal is known about how the sensory signals from these hairs are processed by the local circuits of interneurons and motor neurons controlling leg movements (reviewed by Burrows, 1989). The sensory afferents initially converge onto local spiking interneurons that act as the primary integrators and from which information diverges to other local spiking and non-spiking interneurons. There is, however, much parallel and distributed

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processing (Laurent and Burrows, 1989). The non-spiking interneurons exert a fine control over the motor neurons, controlling leg position and movements in a graded manner. Spatial information is preserved in these local circuits, but it is not known what other features of tactile sensory information, such as the directionality or velocity of the stimulus itself, may also be preserved.

Most studies on the response properties of sensory hairs have concentrated on hairs that are sensitive to wind currents or air vibration, such as those on the head, thorax and abdomen of the locust (Pflüger and Tautz, 1982; Tyrer *et al.* 1979), on the cerci of crickets (Palka *et al.* 1977) and cockroaches (Westin, 1979) and on the surface of caterpillars (Tautz, 1978*a,b*). The directional and velocity sensitivities, threshold levels and adaptation rates of some of these wind-sensitive hairs have been described in detail (Gnatzy and Tautz, 1980; Shimozawa and Kanou, 1984*a,b*; Tautz 1978*b*). By contrast, little is known of the physiological properties of tactile hairs, although it is assumed that they are sensitive to contact with objects during normal behaviour.

It is important to know the physiological properties of the hair afferents because they may contribute substantially to the properties of the interneurons. For example, in crickets, only cercal afferents with specific directionalities or threshold responses connect with particular interneurons (Bacon and Murphey, 1984; Kanou and Shimozawa, 1984; Shimozawa and Kanou, 1984*a*). The postsynaptic interneurons have specific threshold, direction, velocity and acceleration responses related to the afferents from which they receive inputs. In turn, these interneurons influence motor neurons differentially (Kanou and Shimozawa, 1985). Thus, the information encoded in the afferents may be preserved through specific connections to the motor neurons.

To understand in more detail how the local circuit interneurons of the locust might process sensory signals from hairs to preserve the features encoded by the afferents, it is clear that we must also attempt to understand the basic properties of the tactile hairs themselves. In this paper I describe some of the physiological properties of the tactile afferents of locust hindleg hairs and draw three main conclusions. First, that the tactile afferents are of two physiological types based upon their threshold responses; second, that the two classes have different velocity sensitivities; and third, that all hairs examined have distinct directional responses.

Materials and methods

Experiments were performed on male and female desert locusts, *Schistocerca gregaria* (Forsk.) taken from our crowded colony. They were mounted dorsal side uppermost in Plasticine with the femur of a hindleg held rigidly at 90° to the long axis of the body. It could be released and rotated about the thoraco-coxal joint to gain access to the tactile hairs on other surfaces of the leg.

Recording and stimulation of the hair afferents were made using a modification of the 'tip recording' technique (Hodgson *et al.* 1955). Hairs were cut to approximately half their length and a glass microelectrode filled with locust saline

was placed over the cut end of the hair. The tip size of the electrode was tailored to fit over the hair to be recorded. Signals from the electrode were amplified initially with a standard high-impedance d.c. preamplifier and subsequently with an a.c.-coupled low-impedance amplifier.

The microelectrode holder itself was fixed to a Perspex probe mounted on a precision vibrator. The vibrator was driven by a BBC microcomputer, programmed to produce sine and ramp waveforms of variable frequency and amplitude. Thus, the same electrode could be used to record the spikes of the single afferent innervating each hair and to move the hair shaft. Upon stimulation no bending of the hair shaft was evident.

All hair displacements were measured directly using a video camera (JVC TK-10) mounted on the trinocular head of a dissecting microscope. Video signals were mixed with a time mark generator (FORA VTG33) before being stored on a video recorder (Panasonic AG-6200). A subsequent frame-by-frame analysis, using a video analyser (HVS Image VP112) connected to a microcomputer programmed to calculate distances and angles, was used to determine the threshold angles at which afferents produced a single spike per stimulus cycle. Hair lengths were measured using the same video analysis system.

All recordings were stored on an FM tape recorder (Racal) for subsequent analysis or display on a digital oscilloscope (Gould 1604) and *x-y* plotter. Data were obtained from 32 animals.

Results

Tactile hair distribution

The surface of the locust is covered with mechanosensory hairs. These tactile hairs, on a metathoracic leg, appear to occur in a consistent pattern from animal to animal and are always found directed distally towards the tarsus. Particular landmarks on the surface of a leg, such as the tibial spines, the femoral coverplates and groups of campaniform sensilla, aid in the identification of particular hairs, allowing comparisons to be made, both anatomically and physiologically, in one animal or between animals.

The hairs on a hindleg range in length from 60 to 780 μm and are not uniformly distributed. On the tibia, the hairs on the dorsal surface are of a greater mean length than those on the ventral surface ($403.1 \pm 17.98 \mu\text{m}$ and $265.2 \pm 10.44 \mu\text{m}$, means \pm s.e., respectively) (Fig. 1A). This difference is due to a group of long hairs, the longest on the leg, ranging in length from 450 to 780 μm that are located individually at the proximal base of each of the 19 tibial spines. Hairs of this length are not present on the ventral surface. Hairs on the dorsal ridge and the anterior ventral ridge of the femur have similar mean lengths of approximately 310 μm , and hairs on the dorsal and ventral surfaces of the tarsus are shorter with a mean length of approximately 200 μm (Fig. 1B,C). Hairs are most abundant on the proximal femur and distal tibia, while few hairs are present at the femoro-tibial joint or on the proximal tibia.

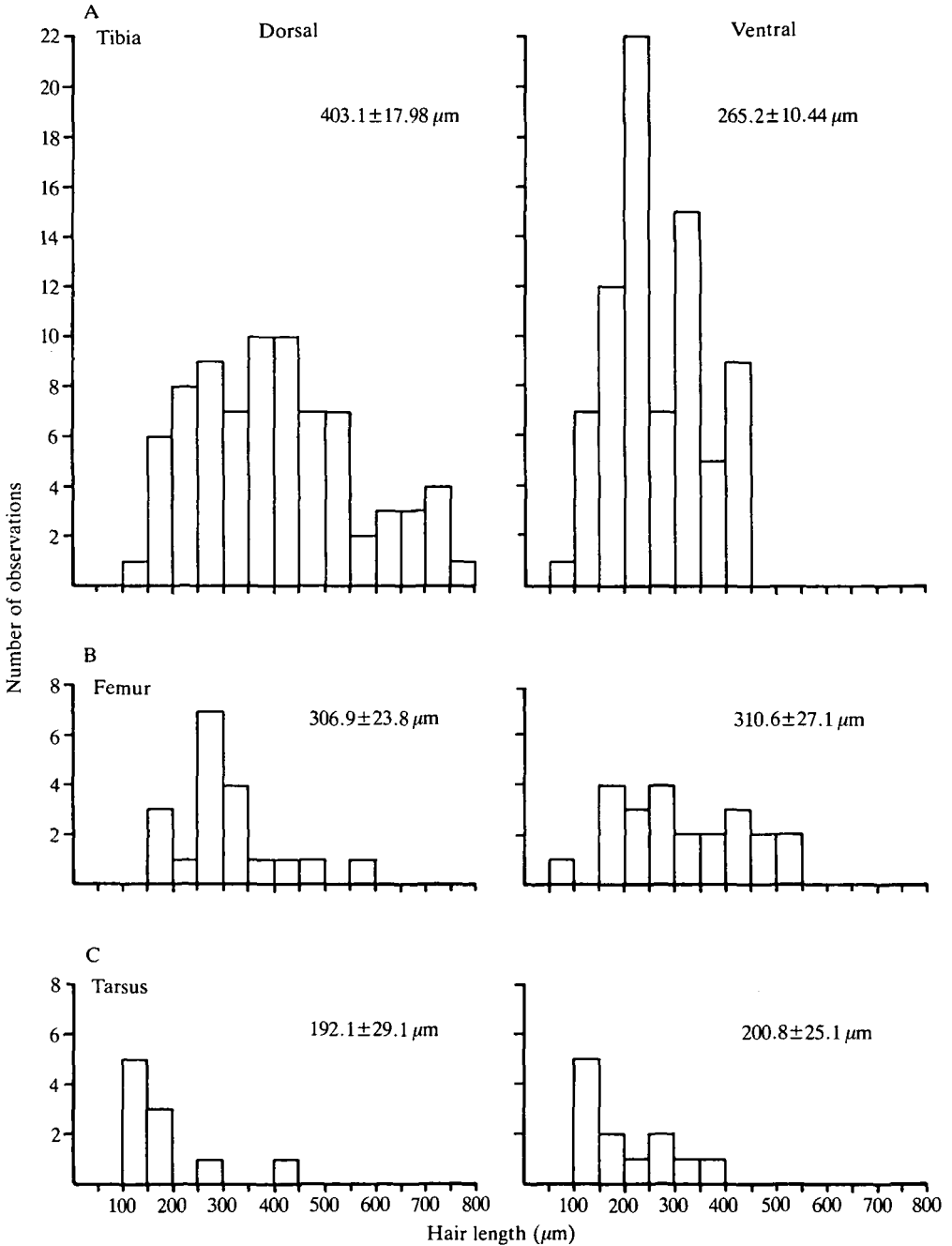


Fig. 1. Length distributions of some of the tactile hairs on (A) the dorsal and ventral surfaces of the tibia, (B) the dorsal and ventral ridges of the femur, and (C) the dorsal and ventral surfaces of the tarsus. Note the presence of long hairs on the dorsal tibia that are absent elsewhere. Values are mean \pm s.e.

Physiological properties of the tactile hair afferents

Individual hairs were displaced in their most sensitive directions (see below, Directional sensitivities). The single afferent that innervates an individual hair is not spontaneously active and responds phasically or phaso-tonically to an imposed deflection of the hair shaft.

Frequency–threshold responses

The angle through which a hair must be moved to elicit a single spike in the hair afferent, defined as its threshold response, was determined for 26 hairs on different leg segments and on different surfaces. The threshold response curves of the hair afferents are of essentially two types; one showing a high threshold to a particular stimulus frequency and a second with a twofold lower threshold at the same frequency (Fig. 2A). For example, at 0.1 Hz high-threshold hairs must be deflected by 37–47° to produce a single spike in the afferent, whereas low-

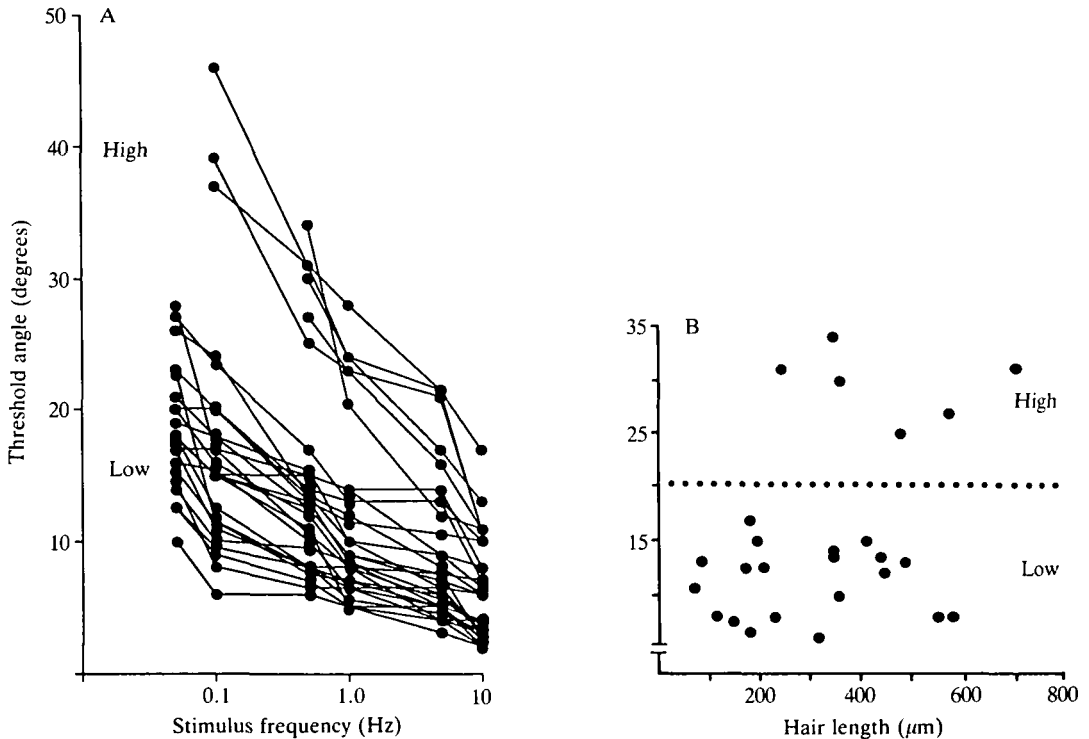


Fig. 2. (A) Frequency–threshold curves of the afferents from tactile hairs ($N=26$) on the femur, tibia and tarsus of a hindleg of one locust. The hairs are divided into two groups of low threshold (low) and high threshold (high) based on their response properties. Regression lines (with equations $y=9.69-4.82\log x$ and $y=25.94-13.59\log x$ for low- and high-threshold type hairs, respectively) fitted to the data for each type of hair are significantly different ($P<0.05$) (B) No correlation is evident between threshold and hair length when the receptor is deflected with a 0.5 Hz sine wave.

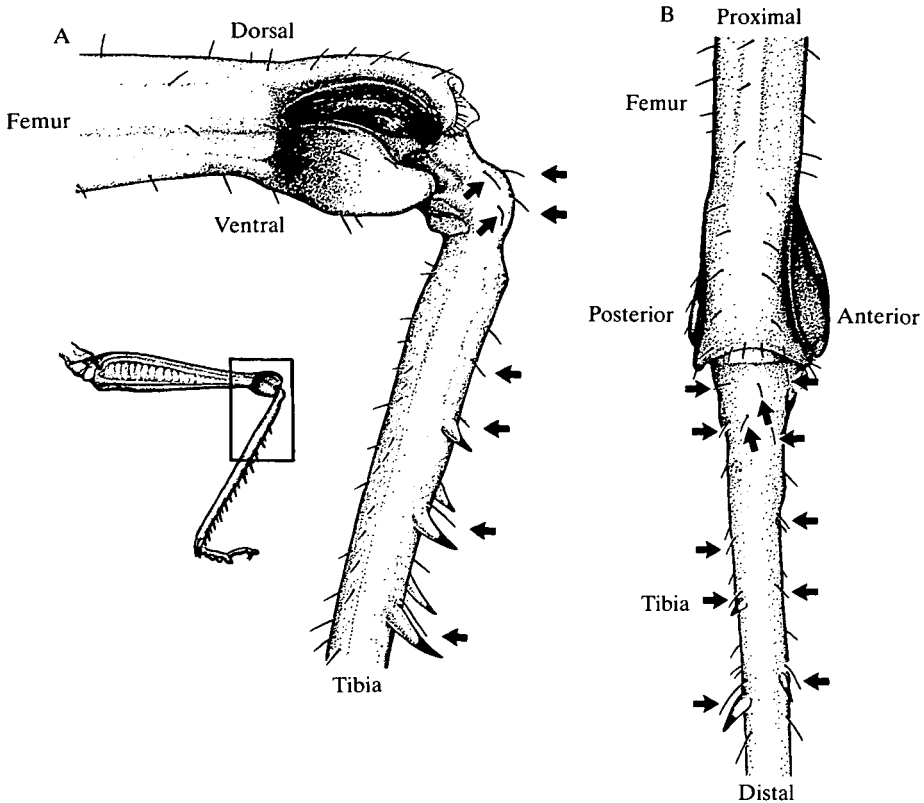


Fig. 3. The spatial distribution of low- and high-threshold hairs on the metathoracic leg. (A) Posterior and (B) dorsal views of the leg. A single high-threshold hair is located at the base of each of the tibial spines (arrowed). High-threshold hairs are also found on the most proximal region of the dorsal tibia. Low-threshold hairs are found on all other areas of the leg. Inset shows the orientation of the expanded views.

threshold hairs needed to be moved by only $10\text{--}28^\circ$. The threshold angles vary inversely as a function of stimulus frequency. There is a considerable overlap of response curves at higher frequencies of stimulation. For example, high-threshold type hairs must be moved through $7\text{--}17^\circ$ at 10 Hz, whereas low-threshold type hairs must be moved through $2\text{--}11^\circ$. However, the threshold curves of these two types of afferent response are significantly different ($P < 0.001$). The threshold response is correlated with the position of the hair on the leg. It does not, however, correlate with hair length at any of the frequencies tested (Fig. 2B). Hairs of approximately $430\ \mu\text{m}$ in length may have a threshold value of $10\text{--}14^\circ$ or $30\text{--}34^\circ$ depending upon where they are located on the leg. High-threshold hairs occur only on the proximal region of the dorsal tibia and at the proximal base of each tibial spine (Fig. 3). All other hairs are of the low-threshold type. This pattern is consistent between animals.

Velocity sensitivity

The two types of hair afferents showed a clear difference in response to the

velocity of the stimulus. High-threshold hairs respond phasically to imposed deflections and are sensitive to sinusoidal hair deflections at frequencies down to 0.1 Hz (Fig. 2A). They have velocity thresholds to rampform displacements with constant velocity, and of peak displacement of 30° , of $21.1 \pm 4.2^\circ \text{s}^{-1}$ ($N=20$) (Fig. 4A). By contrast, low-threshold hairs are sensitive to even lower frequencies of sinusoidal stimulation (<0.05 Hz) and to constant-amplitude ramp movements of less than 3°s^{-1} (Fig. 4B) (lower velocities of stimulation could not be generated at this peak displacement). Both types of hair were sensitive to stimulus velocities of over 600°s^{-1} . The low-threshold hairs produced significantly ($P < 0.05$) more spikes in response to a given angle of deflection (a mean of 11.3 ± 0.8 spikes compared to 6.1 ± 0.7 spikes for high-threshold hairs at 600°s^{-1}) and responded phaso-tonically to the imposed ramp-and-hold stimuli.

Adaptation rates

The two types of hair afferents have similar adaptation rates. High-threshold hairs adapt to approximately 50% of their initial firing levels after as few as 2 cycles at 1 Hz (Fig. 5). At all frequencies tested they adapt completely to continuous sinusoidal stimulation. Low-threshold hairs also adapt to approximately 50% of their initial firing level after 2 cycles at 1 Hz (Fig. 6). They then, however, continue to respond to subsequent repetitive stimulation for over 50 cycles at 1 Hz. This difference in the response properties of the two types of hair afferent is due simply to the different sensitivities of the two types (Fig. 7). At 5 Hz stimulation the high-threshold type hairs produce an initial response of approximately 5 spikes cycle⁻¹. This rapidly declines to a single spike after as few as 8 cycles before failing after 11 cycles. The low-threshold hairs, however, produce approximately 10 spikes in response to the initial stimulus cycle, and adapt at a similar rate to the high-threshold hairs for the first 4 cycles. The response to subsequent stimulation is maintained at about 4 spikes cycle⁻¹ for at least 200 cycles (Fig. 6).

Directional sensitivities

Threshold responses depend upon the direction in which the hair is deflected. For example, a high-threshold hair at the base of the first tibial spine reaches threshold with a 22.5° deflection when bent proximally towards the coxa (Fig. 8A). A bend distally towards the tarsus requires a 27° deflection in order to reach threshold (Fig. 8B). Increasing amplitudes of stimulation in both directions evoke more spikes. This difference in threshold is consistent between animals (means of $22.8 \pm 2.9^\circ$ and $34.4 \pm 4.5^\circ$ ($N=5$) for proximal and distal deflections, respectively). These observations suggest that the hairs may be directionally sensitive. To examine the directional responses in more detail, hairs were deflected by 30° from their rest positions at 30° intervals around their bases. The resulting response curves show clear, although broad, directional responses. Fig. 9A shows the mean response curve and typical responses of a high-threshold afferent from a hair on the proximal tibia near the femoro-tibial joint. This hair

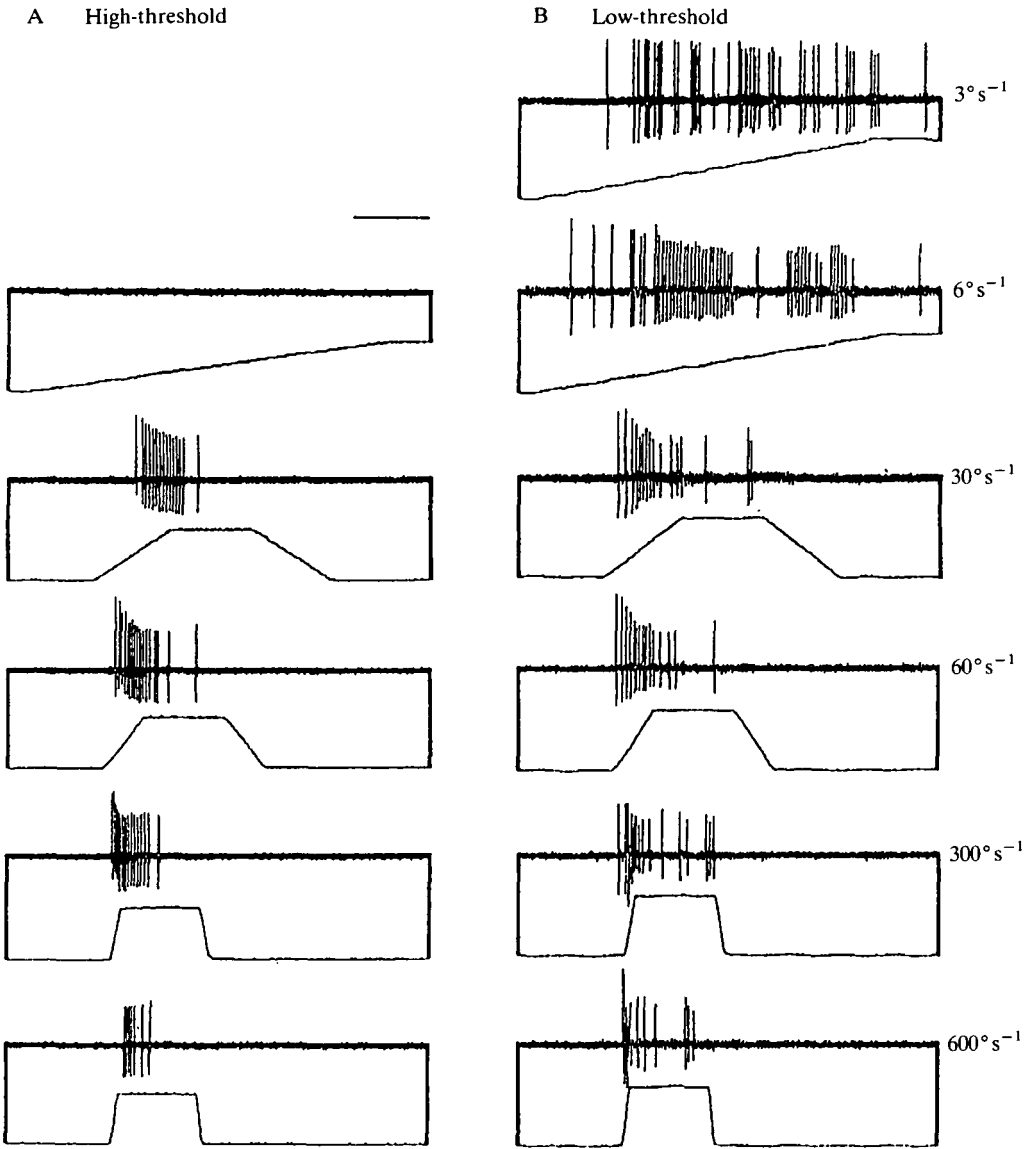


Fig. 4. (A) Responses of a high-threshold hair to imposed constant-amplitude ramp movements of increasing velocities. The hair afferent only responds to velocities greater than 30°s^{-1} . The upper trace shows the afferent response and the lower trace the displacement. The hair was deflected through 30° in each test. (B) Responses of a low-threshold hair to constant-amplitude imposed ramp movements of increasing velocities. It responds to stimuli at all velocities tested. The hair was again deflected through 30° in each test. Scale bar, 2 s for low-threshold hairs at 3°s^{-1} and 1 s for all others.

afferent is most sensitive to deflections proximally towards the coxa and medially towards the abdomen/thorax. Deflections distally and laterally, at 180° to the most sensitive directions, result in few spikes. The responses of a further five hairs,

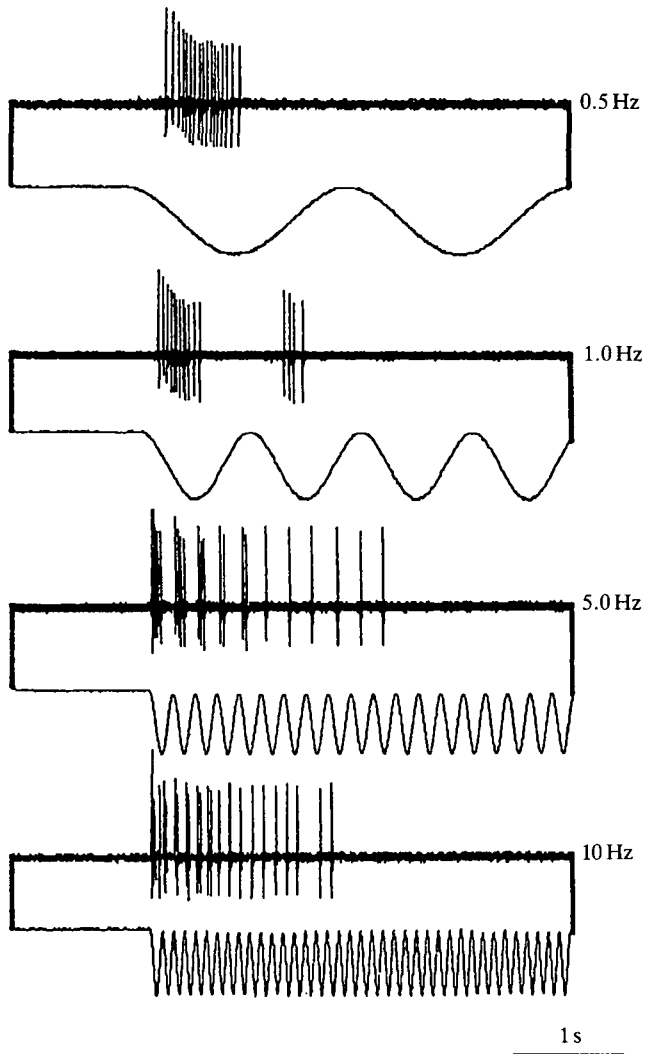


Fig. 5. Adaptation of a high-threshold hair afferent in response to repetitive sinusoidal stimulation of a peak deflection of 30° at 0.5, 1, 5 and 10 Hz. The afferent adapts rapidly to repetitive stimulation.

of both high- and low-threshold types, are similar in being most sensitive to proximal/medial bending and least sensitive to distal/lateral deflections (Fig. 9B). There are no significant differences in the response curves of the low- and high-threshold hairs. The low-threshold hairs, however, produce more spikes in response to a given deflection than do the high-threshold hairs.

Discussion

The hairs on the surface of the leg of locusts can generate complex avoidance

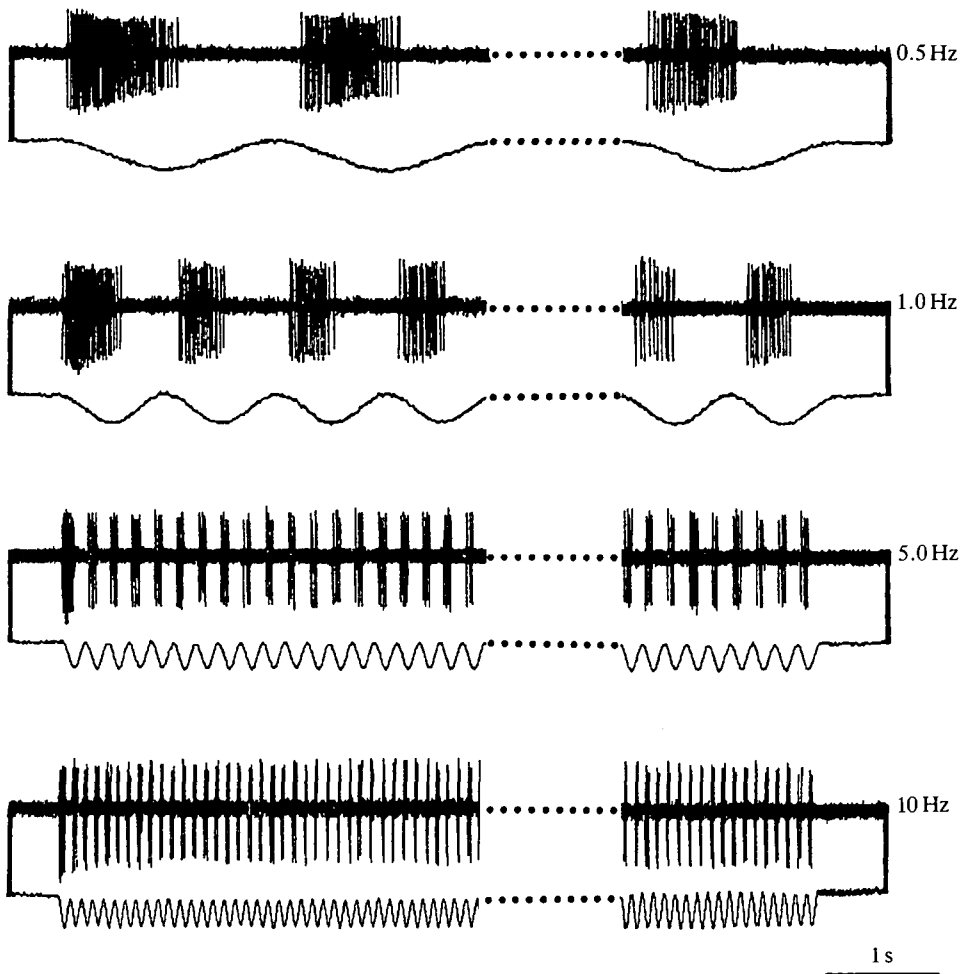


Fig. 6. Adaptation of a low-threshold hair in response to sinusoidal stimulation of 30° at 0.5 (20 cycles), 1 (50 cycles), 5 (200 cycles) and 10 Hz (200 cycles). The first and last cycles are shown for each stimulus frequency.

movements of the leg when only a single hair is deflected (Pflüger, 1980). This study has shown that the hairs on the metathoracic leg are of two distinct types; one responds phasically and with low-threshold responses to imposed movements and is sensitive to low-velocity stimulation; the second responds more phasically with much higher thresholds and is sensitive to higher-velocity stimulation. Both types of hair respond either phasically or phasically to an imposed stimulus and are velocity and direction sensitive.

The tactile hairs on the cerci of cockroaches *Periplaneta americana*, have also been examined in some detail. These tactile hairs are of a single physiological type but have displacement and velocity thresholds of the same order of magnitude as the tactile hairs of the locust (Buño *et al.* 1981). The cockroach tactile hair

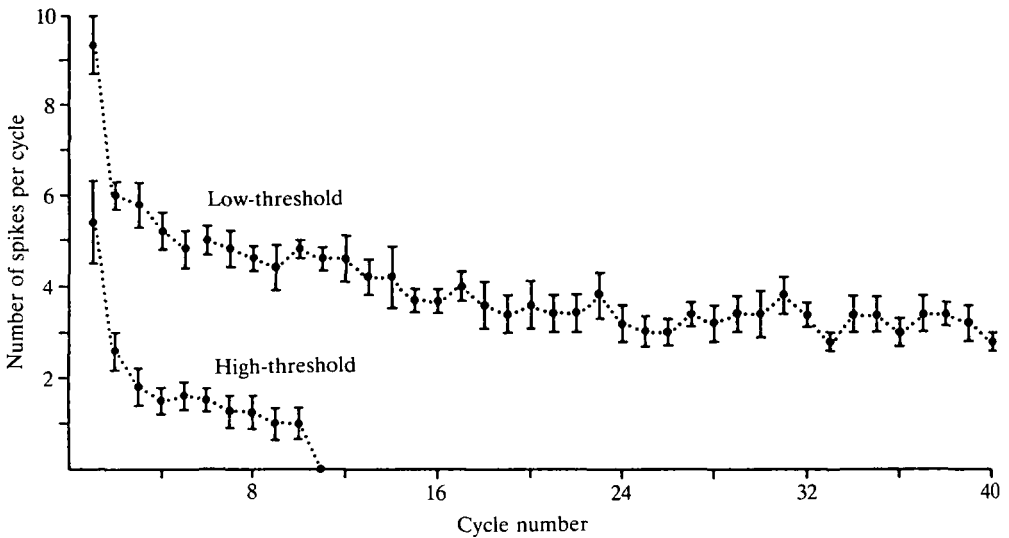


Fig. 7. Comparison of adaptation rates of the low- and high-threshold hair afferents to sinusoidal stimulation of 30° at 5 Hz. The mean numbers of spikes per cycle (\pm s.e., $N=5$) are shown for one of each hair type. The adaptation rates are similar and the difference in response is due simply to the different sensitivities of the hair afferent types.

afferents have displacement thresholds of about 5° at 1 Hz, which compares to mean threshold displacements of 8.5° and 20° for low- and high-threshold hair afferents of the locust leg, respectively, at a similar frequency. Similarly, the velocity threshold of the cockroach afferents is between 8 and 16°s^{-1} , which again compares well to less than 3°s^{-1} for low-threshold locust hairs and 21°s^{-1} for high-threshold hairs.

These results on the locust tactile hairs differ from those described by Pflüger (1980), who showed that the hairs responded phasically to imposed deflections, but did not show any differences in other physiological properties or specific directional responses. These differing results may reflect the method of stimulating the afferents used by Pflüger (1980) in which the hairs were bent manually. Such a stimulus is neither constant between hairs of one animal nor between similar hairs on the legs of different animals. Bässler (1977) found that the tactile hair afferents of the stick insect *Carausius morosus* again responded only phasically to imposed deflections, but he too suggests that they were not directionally sensitive. These experiments were also carried out by deflecting the tactile hairs by hand with the aid of a micromanipulator. It is not yet known if these hairs on the stick insect are of a single physiological type or whether this method of stimulation failed to reveal differences.

The spatial distribution of the high- and low-threshold hairs is consistent from locust to locust. For example, the hair at the base of each tibial spine is always of the high-threshold type, regardless of its length. In contrast, the threshold

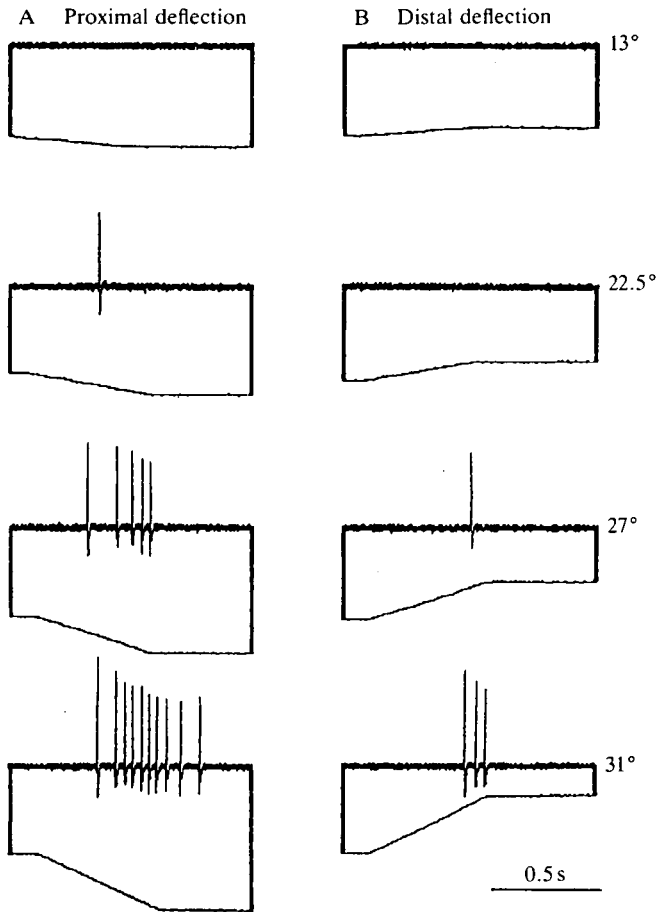
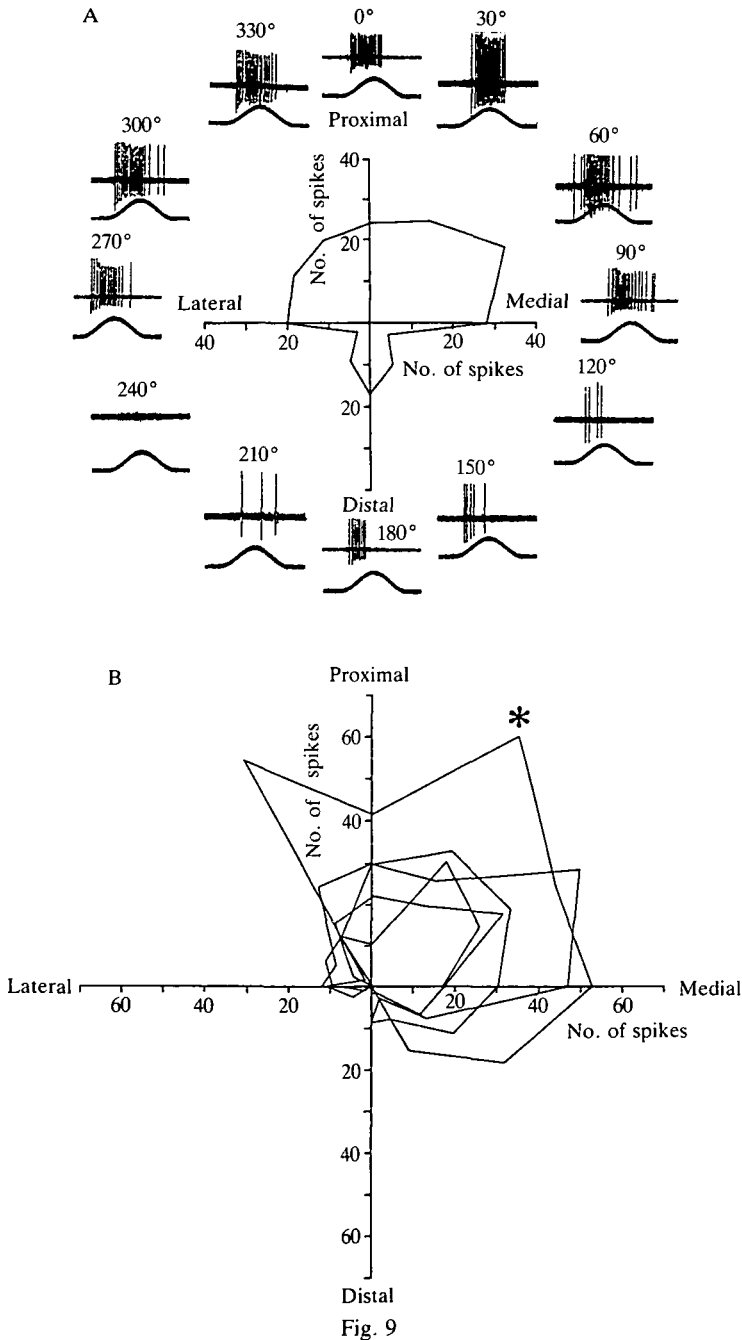


Fig. 8. Threshold responses vary with the direction of hair deflection. (A) Proximal deflection and (B) distal deflection. A 22.5° deflection of a high-threshold type hair on the tibia is required for threshold to be reached when the hair is deflected proximally towards the coxa. A 27° deflection is required for threshold to be reached when the hair is deflected distally towards the tarsus. The firing rate increases with an increase in velocity in both directions; however, the relative difference in response remains constant.

Fig. 9. Directional sensitivity of the hair afferents. (A) The mean response curve ($N=5$) of a high-threshold type hair on the proximal dorsal tibia. Typical responses are shown for each tested angle of 30° around a full circle. The hair was deflected by 30° at 1 Hz during each test. Maximal responses are obtained by deflecting the hair proximally and medially. (B) The mean directional response curves ($N=5$) for a further four high-threshold and one low-threshold (asterisk) hairs. Again the maximal responses are obtained when the hair is deflected proximally and medially, and minimal responses are obtained at 180° to their most sensitive directions. The relatively small standard error for each point, in the range 0.1–3.5 spikes, has been omitted for clarity.

response of the mechanosensory hairs on the cerci of crickets *Gryllus bimaculatus*, is dependent on hair length, with short hairs having higher thresholds and long hairs having lower thresholds. These threshold responses are based on the mechanical properties of the wind-sensitive hairs themselves (Shimozawa and Kanou, 1984b). The hair afferents of the locust, however, are not tuned or



matched to the length of the external hair shaft so that no correlation between threshold and hair length is evident (Fig. 2B).

Directional properties

This study has shown, for the first time, that the tactile hairs of the locust leg have clear directional responses. Hairs of both physiological types show similar responses orientated in similar directions. Stimuli deflecting hairs proximally and medially (i.e. towards the body) elicit maximal responses in the receptor afferents, while stimuli at 180° to this elicit minimal responses. Thus, the hair afferents respond maximally to stimuli involving direct contact with objects or other animals moving from behind and towards the locust. Similarly, the tactile hair afferents on the cerci of the cockroach have specific directional sensitivities such that stimuli moving proximally towards the base of the cercus elicit maximal responses (Buño *et al.* 1981). The properties of the tactile hairs are, therefore, similar to those of the wind-sensitive hairs of the cockroach (Westin, 1979) and cricket (Palka *et al.* 1977) and the vibration-sensitive thoracic hairs of the caterpillar of *Barathra brassicae* (Tautz, 1978a). The basis for the directional properties of the tactile afferents may be due to the attachment point of the afferent dendrite to the hair shaft (French and Sanders, 1979; Tautz, 1978a).

Sensory processing of mechanosensory information

Particular features of sensory input gathered by the mechanosensory receptors on the body surface can be preserved through the different layers of processing within the nervous system. For example, spatial information is preserved within the local circuits controlling leg movements of the locust. Mechanical stimulation of the tactile hair afferents on the dorsal tibia results in an avoidance reflex of the leg in which the trochanter/femur is levated, the tibia flexed and the tarsus depressed. Conversely, when the ventral tibia is stimulated the trochanter/femur is again levated, but this is accompanied by an extension of the tibia (Siegler and Burrows, 1986). Different avoidance reflexes are produced when other leg surfaces are stimulated.

The leg hair afferents of the metathoracic leg of the locust are somatotopically arranged in the segmental ganglion so that all three leg axes are represented centrally (P. L. Newland, in preparation; Pflüger *et al.* 1981). Local spiking interneurons and intersegmental interneurons have overlapping receptive fields from hairs on the leg that also map the entire surface of the leg (Nagayama, 1989; Newland, 1990; Siegler and Burrows, 1984). Thus, within these first two levels of neurons, spatial information is preserved and, by virtue of specific connections between the local spiking interneurons and premotor and motor neurons (Burrows, 1980; Burrows and Pflüger, 1986; Laurent and Burrows, 1988), spatially organised avoidance reflexes can be produced.

In the cricket, particular interneurons preserve certain physiological characteristics of the afferents which excite them. For example, wind-sensitive hairs on the

cerci are divisible into two types based on their threshold responses to air currents. Short hairs, less than 500 μm in length, are acceleration sensitive, while long hairs, over 500 μm in length, are velocity sensitive (Shimozawa and Kanou, 1984a). Interneurones 8-1 (the medial giant interneurone) and 9-1 (the lateral giant interneurone) receive input from the short hairs and are acceleration sensitive, whereas interneurones 10-2 and 10-3 receive input from the afferents of the long hairs and are velocity sensitive. This was demonstrated initially by Shimozawa and Kanou (1984a) by depriving interneurones of certain hair inputs while measuring the threshold responses of the interneurones. Subsequently, Shepherd *et al.* (1988) demonstrated direct connections between the different types of afferents and interneurones. The different types of interneurones, in turn, appear to exert different effects on the levator and depressor motor neurones of the trochanter of the mesothoracic leg. Acceleration-sensitive interneurones 8-1 and 9-1, driven by the short hairs, produce an excitation of the motor neurones, while 10-2 and 10-3, driven by the long hairs, produce an early inhibitory response (Kanou and Shimozawa, 1985).

In the cockroach *Periplaneta americana*, wind-sensitive hairs on the cerci are directionally sensitive to air currents (Dagan and Camhi, 1979), and the giant interneurones with which they synapse preserve these differing directional sensitivities (Daley, 1982; Westin *et al.* 1977). The giant interneurones again exert different effects on the depressor and levator motor neurones and the common inhibitor of the metathoracic hindleg. The ventral giant interneurones make weak connections with the slow depressor motor neurone but strongly excite the common inhibitor (Ritzmann and Camhi, 1978). However, the dorsal giants excite the slow depressor motor neurone and, with a delay, may also weakly excite the slow levator motor neurone (Ritzmann and Camhi, 1978).

In the locust, it remains to be shown how sensory inputs from the two types of tactile hair afferent are processed by the local circuits controlling leg movements. Until now, however, these tactile hairs have been regarded as a rather uniform group of phasically responding receptors lacking directional properties. The results presented here show that, on the contrary, the hairs represent a more elaborate tactile detector system. Further experiments are now required to examine, in more detail, the behavioural significance of the two different types of hair and how the input from the two types of afferents is processed within the local circuits. Do the afferents connect with different local interneurones? Similarly, are the directional properties of the afferents reflected in the interneurones with which they make connections?

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