

THE STRUCTURE, RESPONSE PROPERTIES AND DEVELOPMENT OF A HAIR PLATE ON THE MESOTHORACIC LEG OF THE LOCUST

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Summary

A hair plate is present on the proximal anterior face of the pro- and mesothoracic tibiae of the legs of the locust *Schistocerca gregaria*, but not on the metathoracic legs. The hair plate is in a depression of the cuticle and contains about 11 hairs, which are all polarised with their tips pointing towards the dorsal surface of the tibia. The hairs are all of the same trichoid sensilla type and vary in length from 90 to 140 μm . Associated with the hair plate is a pronounced distal extension of the anterior femoral coverplate, the inner face of which is concave, that makes contact with the hairs during flexion and extension movements of the tibia. During postembryonic development, no tibial hair plate hairs are present in the first four larval stages. In fifth-instar larvae just three hairs are present, while the full complement is attained only after the final moult to adulthood. The distal extension of the posterior coverplate is present through all instar stages, becoming more pronounced after each moult.

Sensory neurones innervating the hairs of an adult may be divided into two classes on the basis of their responses. The first type responds phasically to imposed deflections and is velocity-sensitive. The second type responds phasotonically and is also sensitive to the velocity of the stimulus but has an additional tonic component sensitive to maintained angular deflections. Both types of afferents are directionally sensitive and respond best to deflections against the natural bend of the hair, equivalent to extension movements of the tibia. The hairs are deflected by the coverplate only at femoro-tibial angles of less than 90°. During extension movements, they will be deflected in their most sensitive directions while during flexion movements they will be deflected in their least sensitive directions.

Key words: grasshopper, *Schistocerca gregaria*, mechanoreceptor, development, sensory neurone.

Introduction

Sensory information generated by an animal's own movements and by contact with external objects plays a crucial role in the precise coordination of limb movements. In insects, different classes of sensory receptors act in parallel to signal any change that occurs in the position of a leg joint. The proprioceptors can either be internal structures, such as the chordotonal organs that monitor changes in joint angle, or external structures, such as hair plates, which are groups of sensory hairs located close to joints that are stimulated when one leg segment moves relative to another (Pringle, 1938).

Hair plates play a major role in the coordination and control of walking. Ablation of a hair plate located on the trochanter of a metathoracic leg of a cockroach (Wong and Pearson, 1976) causes the leg to overstep and collide with the mesothoracic leg. This suggests a role for the hair plate in limiting the forward movement of the leg during the swing phase of the walking cycle. Similar results have also been demonstrated for homologous hair plates in stick insects (Dean and Wendler,

1983; Wendler, 1964) and locusts (Kuenzi and Burrows, 1995; Pflüger *et al.* 1981). In stick insects, waxing over a coxal hair plate, so that its hairs are continuously deflected, prevents the transition from stance to swing by maintaining the leg in contact with the substratum (Bässler, 1977). The hair afferents can encode different parameters of a stimulus, including both static and dynamic components and direction, implying that the hair plates are involved in the control of different aspects of leg movement. For example, hair plate afferents from trochanteral hair plates of the stick insect are of two distinct physiological types: type 1 afferents that respond phasically to imposed displacements of their hair and type 2 afferents that respond tonically to maintained deflections (Cruse *et al.* 1984; French and Wong, 1976).

Although we know much about the hair plates of adult insects, little is known of their presence and response properties in the preceding larval stages. We know that many exteroceptive hairs and their associated sensory neurones

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appear in the embryo as the first-instar cuticle is laid down (Hartenstein, 1988). However, many further hairs, such as those sensitive to air motion and to touch, are added to the surface of the body and limbs during each successive moult. Thus, on the prosternum of a first-instar locust there are about 30 hairs, whereas in the adult there are over 300 (Pflüger *et al.* 1994). On cricket cerci, not only are more hairs added during each moult but existing hairs increase in length. These developmental changes have important consequences for the processing and integration of their sensory input. For example, sensory neurones innervating long hairs on a cercus, which are the oldest hairs, make only weak connections with a medial giant interneurone in the terminal abdominal ganglion (Chiba *et al.* 1988), while those innervating shorter hairs, which are more recently added postembryonically, make stronger connections. Moreover, these postembryonic developmental changes are specific to particular interneurons so that some of the same hairs make progressively stronger divergent connections with non-giant interneurons during development. These changes are thought to result from a rearrangement of synaptic connections of a given sensory neurone from a medial giant interneurone to a non-giant interneurone.

In view of the importance of postembryonic development in refining the patterns of sensory structures on the body, the patterns of connections of neurones and the receptive fields of interneurons, it is perhaps surprising that few sensory structures have been examined during this period of development. Two recent studies note the presence of a hair plate on the proximal tibia of the moth *Manduca sexta* (Kent and Griffin, 1990) and of the locust *Schistocerca gregaria* (Mücke, 1991), which might signal changes in the angle of the femoro-tibial joint. Since we know nothing of the coding properties of the afferents of this hair plate and nothing of its role in the control of leg movements of locusts, the aim of this study was to describe its structure and development and some of the physiological properties of the individual sensory afferents.

Materials and methods

Adult and juvenile male and female desert locusts *Schistocerca gregaria* (Forskål) were used from our crowded colony. Locusts were immobilised dorsal-side-uppermost in Plasticine with either the left or right mesothoracic legs fixed with the tibia extended to provide access to the hair plate. Recordings were made from individual hairs by placing a blunt glass microelectrode filled with locust saline over the cut end of a hair shaft (Hodgson *et al.* 1955). Signals recorded with this electrode were amplified using a standard high-impedance amplifier and then a.c.-coupled. The methods used for stimulation and the controls taken have been described in detail elsewhere (Newland, 1991). Briefly, the electrode holder was fixed to a vibrator (Ling-Altec type M-1) driven by ramp-and-hold and sinusoidal waveforms delivered from a microcomputer. Thus, the hair could be moved by the electrode and the evoked action potentials recorded simultaneously. Signals were stored on a Racal FM tape recorder for subsequent

display and analysis. Movements of a hair were measured directly from video images using an HVS Image (VP112) video analyser and computer. Maps of the position of the individual hairs within a hair plate were made by capturing digitised video images using an Electric Studio digitising card and correlated with their physiological properties. Hair plates were examined by scanning electron microscopy (Cambridge S4 Stereo-scan) of legs that had been removed from locusts just after the appropriate moult, dehydrated and then coated with gold.

Results

Structure of the tibial hair plate

A hair plate is present in a slight depression on the very proximal anterior surfaces of both the mesothoracic and prothoracic tibiae (Fig. 1A), but not on the metathoracic legs of adults. In the adult, the hair plate consists of about 11 hairs (11.8 ± 3.7 , mean \pm S.E.M., range 6–22, $N=39$ locusts), all orientated with their tips pointing towards the dorsal surface of the tibia at an angle of $60.3 \pm 3.76^\circ$ ($N=21$) to the longitudinal axis of the tibia (Fig. 1B). This means that they are polarised in a different direction to all the tactile hairs on the leg, which are polarised towards the tarsus (Newland, 1991). The hairs vary in length from 90 to 140 μm ($105.6 \pm 23.5 \mu\text{m}$, $N=31$ from three locusts), have diameters near their bases of $9.2 \pm 0.5 \mu\text{m}$ ($N=11$) and are spaced at intervals of 70–100 μm (Fig. 1C). All hairs are of the same trichoid sensilla type and are not clearly divisible into groups of different lengths.

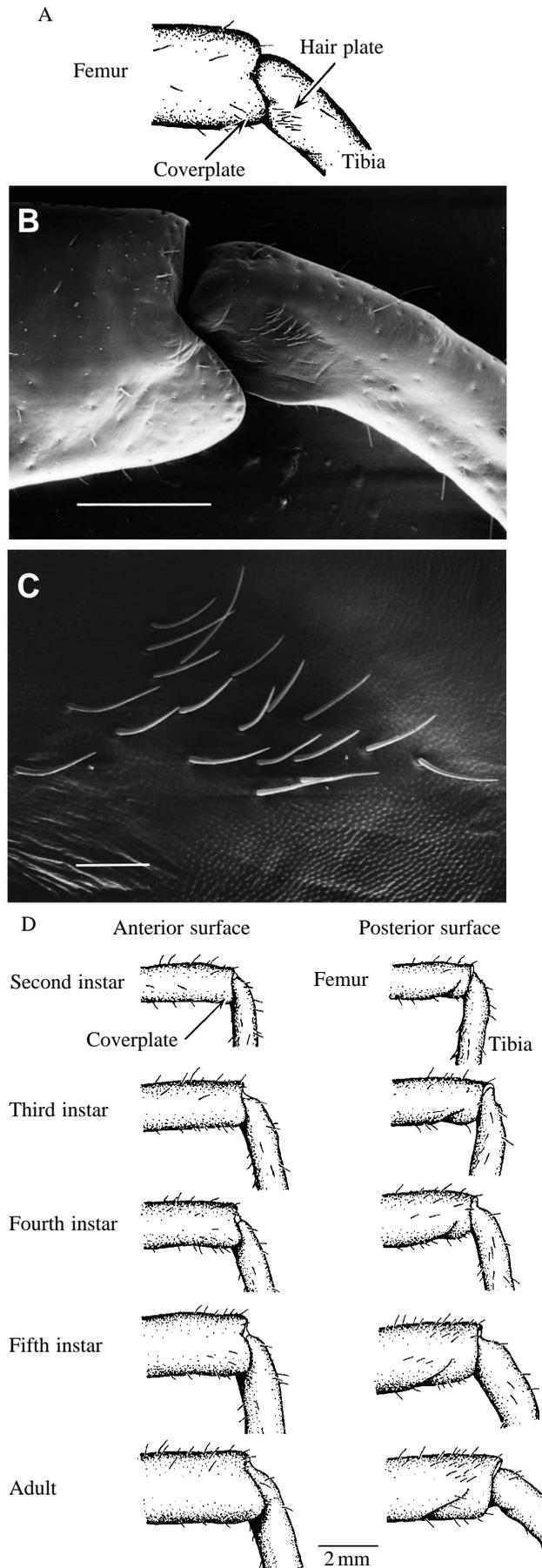
Associated with the hair plate is an asymmetry in the shape of the femoral coverplates. The coverplate on the anterior surface of the distal femur has a pronounced extension (Fig. 1D), the inner face of which is concave, and which makes contact with the hairs of the hair plate when the leg is moved at femoro-tibial angles of less than 90° . This extension of the coverplate is not present on the posterior surface of the pro- and mesothoracic legs (Fig. 1D), nor is it present on either surface of the distal femur of the hind leg.

Development of the tibial hair plate

From the first instar onwards, a depression of the cuticle on the anterior surface of the tibia is the only indication of where the hair plate will be located in the adult. No hairs are present in the instars 1–4. About three hairs (3.23 ± 1.65 , mean \pm S.E.M., $N=34$ locusts) first appear on the mesothoracic hair plate in the fifth instar, while the full complement of hairs is attained only after the final moult to the adult stage. Similar numbers of hairs appear at similar times on the prothoracic leg. The asymmetries of the femoral coverplates on both the pro- and mesothoracic legs are, however, present from the first instar onwards and progressively increase through each moult to be most pronounced in the adult (Fig. 1D).

Physiological properties of the hairs

Recordings from individual hairs reveal action potentials of a single amplitude, indicating that each is singly innervated, as are the tactile hairs on the surface of the leg (Newland, 1991). In



adult locusts, the sensory afferents innervating the hairs can be divided into two physiological types on the basis of their responses to imposed deflections of the hair shaft. Type 1 afferents respond phasically and are only active during the dynamic movement phase of ramp-and-hold stimuli (Fig. 2A), while type 2 afferents respond phaso-tonically to both the dynamic and static components of the stimulus (Fig. 2B). In adults, up to three hairs are of the phasic type and, where present, they are positioned towards the distal end of the hair plate. There appears to be no relationship, however, between the length of a hair and the physiological properties of its afferent.

Velocity sensitivity

Both types of afferent are velocity-sensitive. An increase in the stimulus velocity, in the range $2\text{--}400^\circ\text{ s}^{-1}$, evokes a higher frequency of spikes in both types of afferents (Fig. 2C), although the spike frequency is not linearly related to stimulus velocity. The response to increasing velocity is, however, similar for both types of afferent. The velocity thresholds of both afferent types were lower than the minimum velocity of 2° s^{-1} that we could generate.

Position sensitivity

The greater the deflection of the hair by ramp stimuli, the greater is the firing frequency of type 2 afferents measured during the hold phase of the ramp (Fig. 3A). The spike frequency of these afferents is linearly related to the maintained angle of deflection of the hair (Fig. 3B).

Adaptation

The spike responses of both types of afferent adapt during repetitive stimulation (Fig. 4A). During the first cycle of a 5 Hz sinusoidal stimulus, the type 2 afferents produce more spikes (11 ± 1 spikes) than the type 1 afferents (6.2 ± 0.8 spikes, means \pm S.E.M., $N=6$). Both types of afferent produce approximately half as many spikes by the second cycle, but thereafter the type 1 afferents adapt at a greater rate than the type 2 afferents for up to 50 cycles of stimulation (Fig. 4B). The responses of both types of afferent to subsequent stimulation are maintained for at least 100 cycles. The response of type 2 afferents to maintained deflections of the hair shaft also declines with time. For example, the spike frequency at the end of a 10 s hold is less than 20% of the initial frequency, for a peak displacement of 20° at 20° s^{-1} (Fig. 4C).

Fig. 1. (A) Drawing of the anterior face of the mesothoracic leg showing the location of the hair plate receptor and coverplate on the proximal tibia. (B,C) Low- and high-power electromicrographs, respectively, showing in more detail the location and organisation of the hairs. Note that the hairs are all polarised with their tips pointing dorsally. Scale bars: B, 1 mm; C, 0.1 mm. (D) Asymmetry in the anterior and posterior femoral coverplates. The anterior coverplate has a distal extension (arrowed) from the second instar through to the adult, which is completely lacking on the posterior face. This extension becomes more pronounced during subsequent moults to the adult stage.

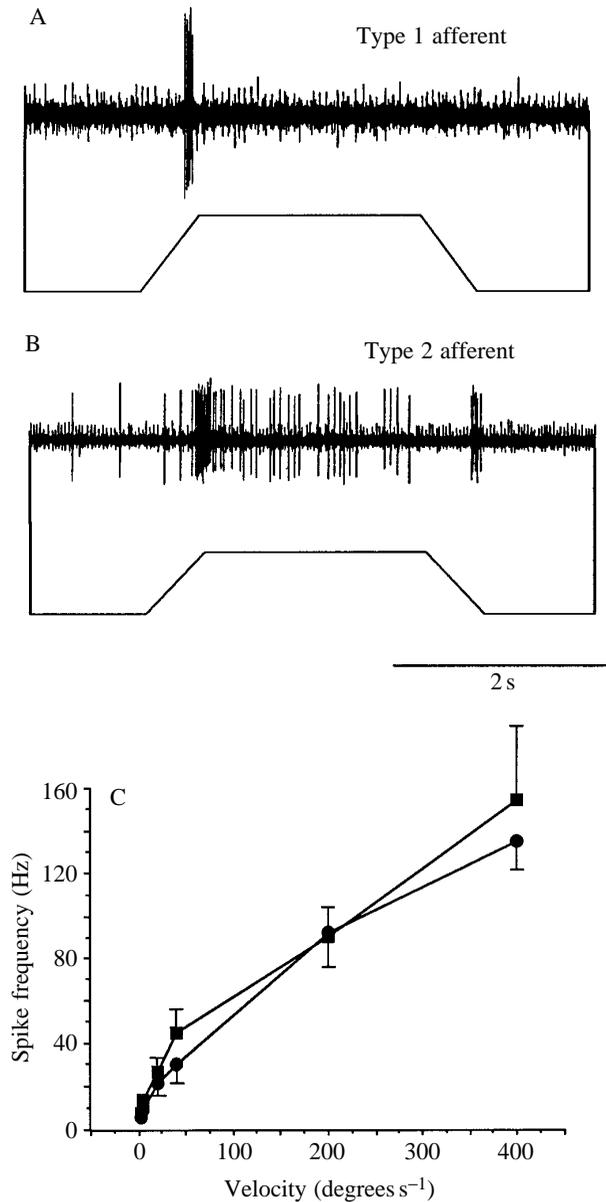


Fig. 2. Hair plate afferents are of two physiological types. (A) Type 1 afferents respond only to the dynamic component of imposed ramp-form stimuli. (B) Type 2 afferents respond to the dynamic component of the stimulus and to the static component with a continued burst of spikes. Ramp stimuli are shown with peak displacements of 20° and velocities of 40° s^{-1} . (C) Responses of afferents to imposed constant-amplitude (peak displacements of 20°) ramp movements of increasing velocities. The mean instantaneous firing frequency (\pm S.E.M.) is plotted against stimulus velocity for both the type 1 afferents (squares) and type 2 afferents (circles) ($N=8$ hair afferents of each type).

Directional sensitivity

The hairs of the hair plate will normally be deflected by extension or flexion movements of the tibia about the femur, corresponding to ventral and dorsal deflections of the hairs, respectively. Both types of hair afferent respond best to deflections towards the ventral surface of the tibia, against the

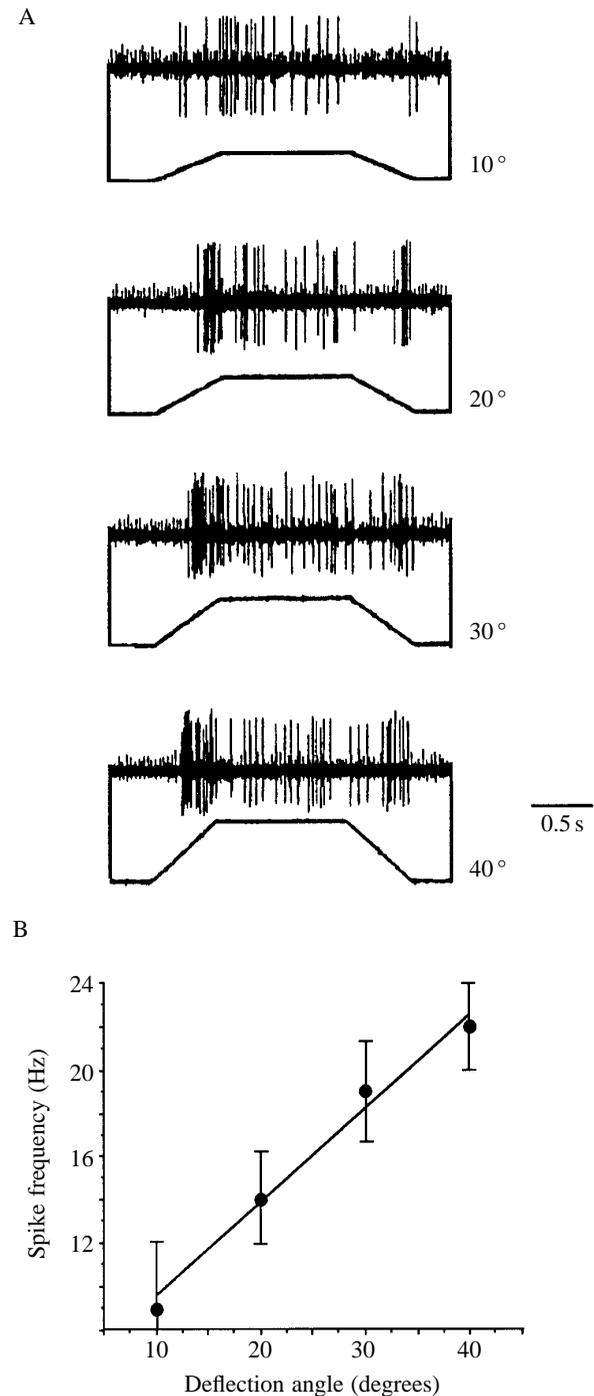


Fig. 3. Responses of the type 2 afferents to maintained deflections of a hair shaft. (A) Responses to four different amplitudes of peak displacement, 10° , 20° , 30° and 40° , are shown. (B) Plot of the mean frequency response of the afferents to increasing peak displacement. Note the linear relationship between the stimulus and response ($y=0.44x+5$, $r=0.993$, $P<0.001$). Each point is the mean (\pm S.E.M.) from four different type 2 afferents.

direction to which the hairs are orientated (Fig. 5A,B). During flexion movements of the tibia at angles of approximately 90° and less, the hairs of the hair plate will be deflected dorsally

by the anterior coverplate. This is in the same direction in which the hairs are pointing, which is the least sensitive direction for the afferents. During extension movements of the tibia, however, the hairs are trapped within the coverplate and are therefore deflected ventrally against the direction in which they are pointing, i.e. in their most sensitive direction. Thus, the hairs respond best to extension movements of the tibia at femoro-tibial angles of less than 90°. At femoro-tibial angles of greater than 90°, the hair plate hairs will be exposed and

could therefore be deflected by such tactile stimuli as may stimulate the surrounding tactile hairs (Fig. 5C).

Hair afferents of fifth-instar locusts show similar properties to those of type 1 afferents of adults. Deflection of the shafts of hairs of fifth-instar locusts show that all respond phasically to an imposed movement with no response to a sustained deflection. In addition, the afferents respond best to ventral deflections of the hair shafts and adapt rapidly during repetitive stimulation.

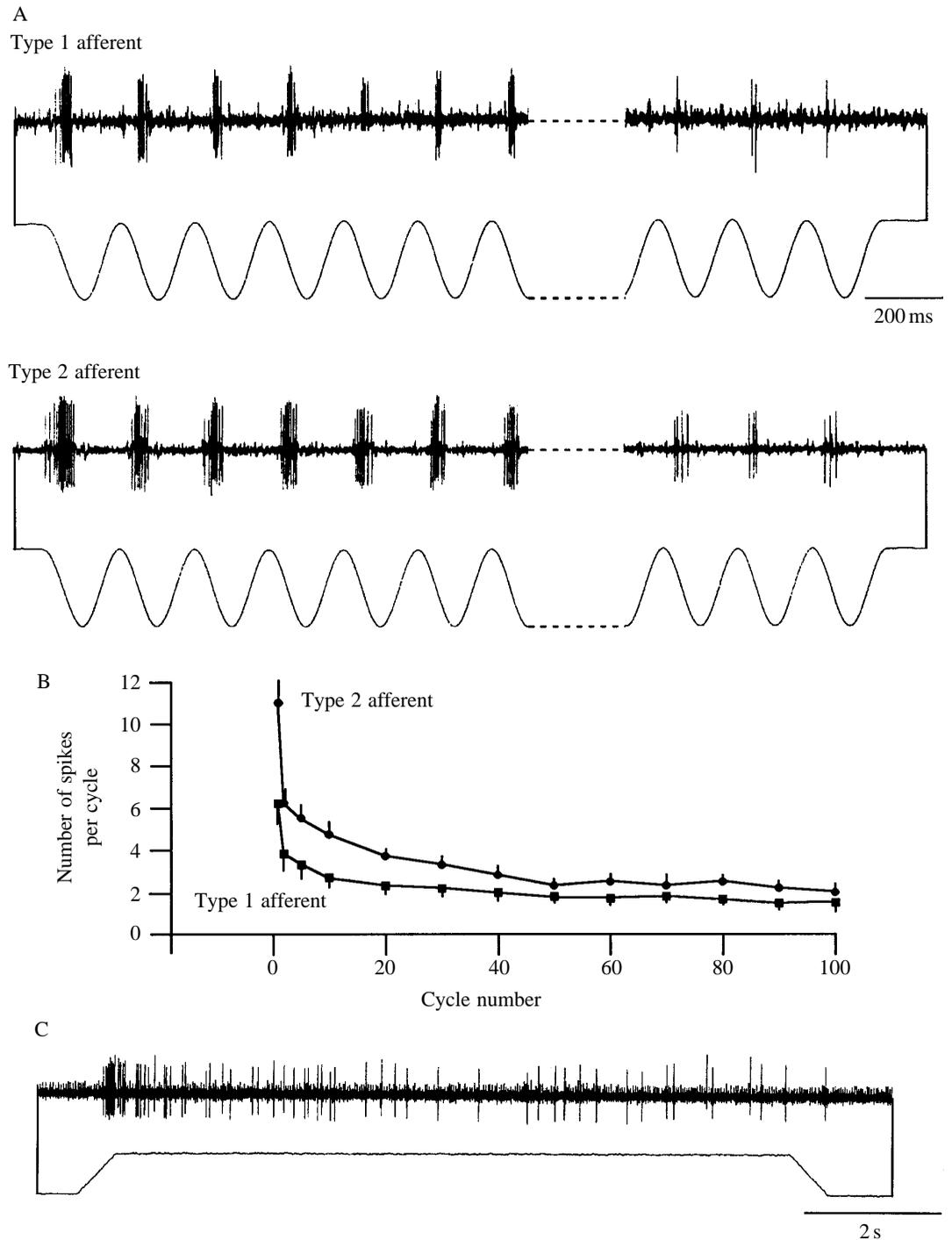


Fig. 4. Adaptation rates of hair plate afferents. (A) Responses of type 1 and type 2 afferents to sinusoidal stimuli of 100 cycles at 5 Hz (20° peak displacement). The first six and last three stimulus cycles are shown for each afferent type. (B) The mean number of spikes per cycles (\pm S.E.M., $N=6$) for each afferent type. The rate of adaptation was less for type 2 afferents. (C) Adaptation of the tonic component of a type 2 afferent to a maintained deflection. The spike frequency was reduced to 20% of the initial level at the end of a 10 s maintained deflection.

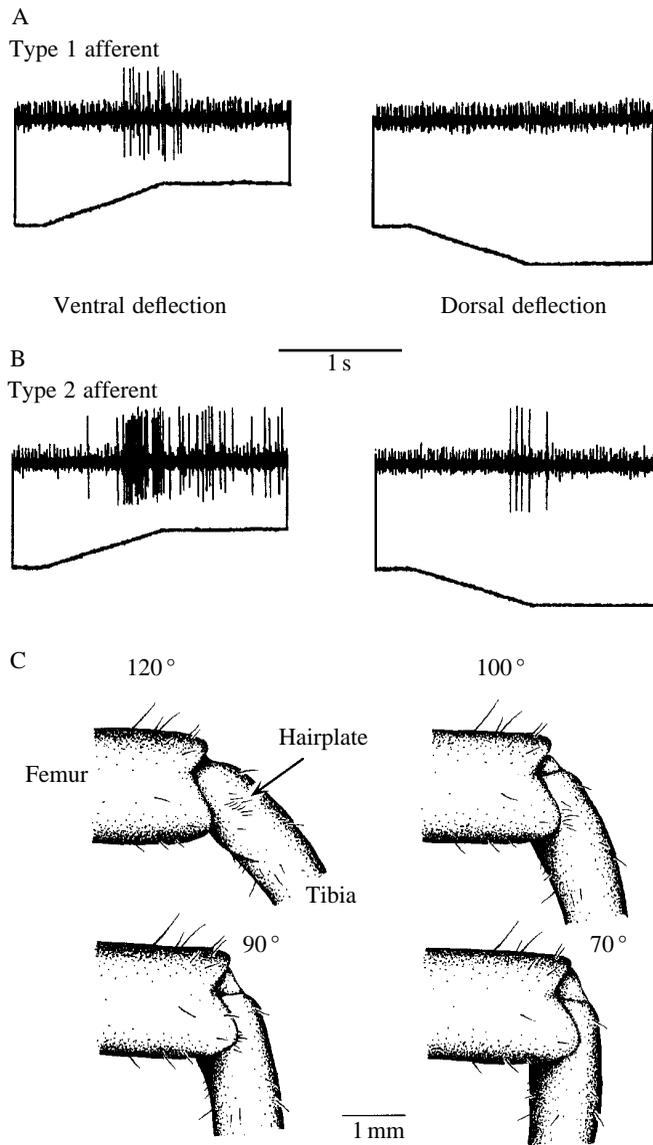


Fig. 5. Directional responses of the hair plate afferents. (A) Type 1 afferent and (B) type 2 afferent. Ramp-form stimuli with a peak displacement of 20° and velocity of 20° s^{-1} were applied. Deflections of a hair ventrally (such as would be produced by an extension of the tibia) against the direction in which it points elicited maximal responses (left-hand panels), whereas deflections of a hair dorsally in the direction in which the hair points (equivalent to a flexion movement of the tibia) elicited smaller responses. (C) Hairs are deflected by the coverplate at angles of less than 90° .

Discussion

Anatomy of the tibial hair plate

The tibial hair plates of the locust pro- and mesothoracic tibiae are located on the proximal anterior surface near the femoro-tibial joint and might therefore contribute to the control of the movements of the tibiae. They are, however, unlike any other hair plate on the leg for three reasons. First, a tibial hair plate consists of approximately 11 hairs of similar lengths.

Three other hair plates on the locust leg, two on the coxa and one on the trochanter, are each composed of about 30 hairs of two different lengths (Pflüger *et al.* 1981). For example, in the trochanteral hair plate on the mesothoracic leg of two species of locusts, *Schistocerca gregaria* and *Locusta migratoria*, one subgroup of hairs is greater than $50 \mu\text{m}$ in length, the other less than $20 \mu\text{m}$ (Pflüger *et al.* 1981). The tips of the long hairs are in continuous contact with, and are deflected by, the overlying joint membrane and are thought to monitor joint position continuously. The short hairs, however, are only deflected by the joint membrane when the leg is levated. Distinct populations of hairs of different length are also present in locust coxal hair plates (Pflüger *et al.* 1981) and in the hair plates of cockroaches (Pringle, 1938; French and Sanders, 1979; Wong and Pearson, 1976), stick insect legs (Bässler, 1965), the wings of crickets (Elliot, 1973) and also in the hair plates on the legs of spiders (Seyfarth *et al.* 1985). Second, the hairs of a locust tibial hair plate are typically loosely spaced at $70\text{--}100 \mu\text{m}$ intervals compared with the much denser packing of hairs in other hair plates $10\text{--}20 \mu\text{m}$ (Pflüger *et al.* 1981; French and Sanders, 1979). Third, while a previous study described the presence of a hair plate on the tibia of a mesothoracic leg, it did not describe the homologous hair plate on the prothoracic leg, or its absence on the hind leg. This distribution is unlike that of locust coxal and trochanteral hair plates, which occur on all legs (Pflüger *et al.* 1981), and contrasts with the tibial hair plate of the moth *Manduca sexta*, which occurs on all legs (Kent and Griffin, 1990).

Physiological properties of hair plate afferents

Despite the anatomical differences between a tibial hair plate and other leg hair plates, the physiological properties of the afferents and the manner in which they are activated show many similarities. The responses of the tibial hair plate afferents of the locust were of two distinct types: type 1 afferents responded only to dynamic displacements whereas type 2 afferents responded to both dynamic and static displacements. These response properties are similar to those of afferents from the trochanteral hair plate in the cockroach (French and Wong, 1976; Wong and Pearson, 1976), where this difference in physiological type is related to hair length. Unlike the cockroach afferents, however, the response properties of the locust hair plate afferents are not related to the length of the hair they innervate.

The stimulus regime we used did not allow us to determine the velocity thresholds of either type of hair plate afferent since both responded strongly to our lowest testable velocity of 2° s^{-1} . These hairs are, therefore, much more sensitive than many of the long high-threshold tactile hairs on the locust tibia, which have velocity thresholds of $20\text{--}30^\circ \text{ s}^{-1}$, but are similar to the low-threshold tactile hairs that cover most of the leg and which respond to velocities as low as $2\text{--}3^\circ \text{ s}^{-1}$ (Newland, 1991).

Although the responses of both types of hair plate afferents to increasing velocities were non-linear over the range of velocities tested, the static responses of type 2 afferents to

ramp-and-hold stimuli were linear for displacements in the range 10–40°. This coding property of the type 2 afferents is the only one not shared by tactile hair afferents (Newland, 1991). Moreover, the adaptation rates of both types of hair plate afferent to repetitive stimulation at frequencies at which locusts normally walk (Burns, 1973), while initially being rapid, still permit the afferents to encode tibial movements for over 100 cycles of continuous movement. Again these properties are similar to those of the low-threshold tactile hairs.

The tibial hair plate afferents can encode direction like other tactile afferents from hairs on the leg (Newland, 1991). Since their tips point towards the dorsal surface, deflection by the femoral coverplate during an extension movement of the tibia will bend the hairs in their most sensitive direction and this will evoke maximal responses in the afferents. During flexion movements, however, the hairs will be deflected in their least sensitive direction. These results contrast with the suggestions of Kent and Griffin (1990) and Mücke (1991) that tibial hair plates monitor flexion movements. This difference highlights the problems involved in ascribing a function to a receptor based on knowledge of its location alone.

The tibial hair plate afferents are thus able to monitor continuously both static and dynamic components of tibial movement. All of the coding properties of the hair plate afferents are shared, however, with the femoro-tibial chordotonal organ, whose afferents are sensitive to position, velocity, acceleration and direction (Field and Pflüger, 1989), and also with other joint receptors acting in parallel such as multipolar joint receptors (Coillot and Boistel, 1969) and a tension receptor (Theophilidis and Burns, 1979; Matheson and Field, 1995). This therefore points to parallel coding of tibial position and movement, as occurs in the hind leg, and may explain why changes in leg movements produced by ablating hair plates appear relatively small (Bässler, 1977; Cruse *et al.* 1984).

Postembryonic development of the hair plate

Throughout development there is a progressive increase in the number of hairs on the body, although many are present in the first instar. For example, there are only two filiform hairs on the cercus of first-instar cockroaches (Blagburn, 1989). The number rises to 39 in second instars (Thompson *et al.* 1992) and reaches approximately 208 in the adult (Nicklaus, 1965). Pflüger *et al.* (1994) showed that the majority of hairs on the prosternum of a locust are added between the fourth instar and adult stage and at the same time many new tactile hairs appear on the legs (P. Newland, unpublished observation). The hairs of the tibial hair plate also first appear in the fifth instar. The asymmetry in the anterior femoral coverplate, however, is clearly present as early as the second instar. In contrast, the hairs of the coxal and trochanteral hair plates of all legs are present from the first instar (P. Newland, unpublished observations), as are the hair plates on the cervical sclerites of locusts (Goodman, 1959; Mittelstaedt, 1950). Although we do not yet know the function of the tibial hair plate, it is possible that its development and appearance in the adult may be linked

to some change in behaviour that occurs after the final moult. Three obvious behavioural changes occur in the adult in addition to increases in size and weight. The first is a change in the mode of locomotion from hopping in instars to walking in the adult, the second is the development of flight and the third is the development of reproductive behaviour. Given that there are other sensory receptors coding movements of the tibia, such as the femoral chordotonal organ which is present throughout the different instars, then it is not clear what the specific role of this tibial hair plate is. What is needed now is a study of the central connections of the hair plate afferents. When this has been achieved, we may then be able elucidate the role of this hair plate in the control of limb movement.

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