Peripheral representation of antennal orientation by the scapal hair plate of the cockroach *Periplaneta americana*

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Summary

Arthropods have hair plates that are clusters of mechanosensitive hairs, usually positioned close to joints, which function as proprioceptors for joint movement. We investigated how angular movements of the antenna of the cockroach (*Periplaneta americana*) are coded by antennal hair plates. A particular hair plate on the basal segment of the antenna, the scapal hair plate, can be divided into three subgroups: dorsal, lateral and medial. The dorsal group is adapted to encode the vertical component of antennal direction, while the lateral and medial groups are specialized for encoding the horizontal component. Of the three subgroups of hair sensilla, those of the lateral scapal hair plate may provide the most reliable information about the horizontal position of the antenna, irrespective of its vertical position. Extracellular recordings from representative sensilla of each scapal hair plate subgroup revealed the form of the single-unit impulses in response to hair deflection. The mechanoreceptors were characterized as typically phasic-tonic. The tonic discharge was sustained indefinitely (>20 min) as long as the hair was kept deflected. The spike frequency in the transient (dynamic) phase was both velocity- and displacement-dependent, while that in the sustained (steady) phase was displacement-dependent.

Key words: cockroach, *Periplaneta americana*, antenna, hair plate, mechanoreceptor, proprioception.

Introduction

The two antennae in insects function as multimodal sensors for monitoring the chemical and physical environment. Chemoreceptors on the antenna are important in searching for, recognizing and discriminating appropriate foods, mates and habitats. Mechanoreceptors on the antennae play critical roles in avoiding sudden attacks by predators (for a review, see Comer and Dowd, 1993) and in perceiving physical objects around an animal (for a review, see Bell, 1991). The tactile sense from the antennae may be especially important in nocturnal insects, which often have to recognize the physical environment in more-or-less complete darkness. A particular behaviour seen in insects is that they move their antennae in an exploratory fashion during environmental searching (for a review, see Bell, 1991). This active antennal movement (scanning) may provide tactile information about the physical environment that is more effective than the information that could be obtained by a walking insect with immobile antennae.

The insect antenna consists of three kinds of segment: the first proximal segment termed the scape, the second segment termed the pedicel and the larger group of similar distal segments collectively termed the flagellum (Fig. 1). The joints connecting each flagellar segment are flexible but can only move passively, whereas those between the scape and the pedicel and between the head and the scape are supplied with muscles allowing them to move actively. Thus,

mechanoreceptors on the flagellum make actual contact with objects, while those in the two basal segments (scape and pedicel) may play a proprioceptive role to monitor antennal orientation. Detection of object position may be computed centrally when the tactile outputs from the flagellum and the proprioceptive outputs from mechanoreceptors at the scape and pedicel are combined in the central nervous system.

In the cockroach *Periplaneta americana*, the head–scape joint forms a ball-joint-like structure that can be moved in any direction, while the scape–pedicel joint is a hinge that can be moved only in the vertical plane. Most mechanoreceptors in the scape and the pedicel are known to be proprioceptors for antennal position (Schafer and Sanchez, 1973; Toh, 1981) (for a review, see Seelinger and Tobin, 1981). We recently reported that hair plates on the scape of *P. americana* are important for tactile detection of objects in the horizontal plane (Okada and Toh, 2000). The scapal hair plate (S-HP) is a cluster of approximately 200 mechanosensitive hairs. The sensilla of the S-HP are probably activated by the movement of the scape at its joint with the head capsule as they become deflected under the joint membrane. Thus, the direction in which the antenna points might be signalled proprioceptively by the specific sub-area on the S-HP that is deflected.

The response of hair-plate sensilla was first described by Pringle (Pringle, 1938) for the cockroach leg. There have been

many reports on hair-plate responses, on the neck of locusts (Haskell, 1959), honeybees (Thurm, 1963) and mantids (Liske, 1982), on the legs of cockroaches (Wong and Pearson, 1976) and locusts (Kuenzi and Burrows, 1995; Newland et al., 1995) and on the antennae of cockroaches (Schafer, 1971) and crustaceans (Vedel, 1986). Of these, a report on the cockroach antenna (Schafer, 1971) briefly described the response properties of the sensilla, but many details remain unresolved. In particular, it is not known which sub-area of the S-HP is deflected and activated by the adjacent joint membrane when the antenna is held in various orientations.

Here, we explore the peripheral representation of antennal orientation in the S-HP by means of microscopic inspection and electrophysiology. Areas of activation on the S-HP were determined morphologically for antennae pointing in various directions. To characterize the physiological properties of the sensilla, the responses of single hairs were recorded extracellularly while they were deflected with a micropositioner.

Materials and methods
Animals
Adult male cockroaches (*Periplaneta americana*) raised in a laboratory culture kept at 28 °C were used.

Morphology
The areas of the S-HP that were activated at various antennal orientations were determined by microscopic inspection, as shown in Fig. 2. An animal was cooled on ice to immobilize it, and its neck was tied tightly with a thin thread before decapitation. The isolated head was then mounted on a small ball-joint stage (5 mm in diameter) movable in any direction. The joint between the scape and the pedicel was immobilized with glue to keep these two antennal segments straight. To hold the antenna in a given orientation, it was attached to one end of a flexible thin steel wire protruding from the stage. The orientation of the scape–pedicel was set according to two parameters, the horizontal angle and the elevation angle. The horizontal angle was measured when viewed from above as the lateral deviation of the scape–pedicel from a zero position pointing straight ahead of the animal; lateral displacements were defined as positive (see inset at bottom in Fig. 3). The angle of elevation was measured similarly, viewing from the side, with dorsalwards deviations from the same forward axis defined as positive (see inset at left in Fig. 3). The hair plate and its adjacent joint membrane were photographed from at least three different views (dorsal, medial and lateral) for each antennal orientation using a dissecting microscope.

When these sets of photographs had been taken with an antenna at 18 angles, the scape was isolated and soaked in concentrated HCl overnight to soften the cuticle. The exoskeleton of the scape was divided into three pieces so that each included one of the three subgroups of hairs, and the pattern of sensilla was then photographed under a light microscope. The area activated was mapped by comparing the whole sensillar pattern with the relationship between the S-HP and the joint membrane.

The relative number of hairs deflected (R_N) was calculated for each antennal position as:

$$R_N = N/N_{max},$$

where N is the number of hairs deflected at a given antennal position, in each subgroup, and N_{max} is the maximum number of hairs deflected for all antennal directions in the same subgroup.

Electrophysiology
An animal immobilized by cooling on ice was mounted on an experimental stage. The head capsule and the base of the antenna were tightly attached to the stage with dental wax using a soldering iron. A tungsten electrode with an electrolytically sharpened tip was inserted through the cuticle at a point just proximal to the base of a selected hair. A reference electrode (Ag/AgCl wire) was inserted into the cut end of the flagellum. Signals from the electrodes were fed to a conventional a.c. amplifier.

Sensilla were deflected by pulling a fine tungsten hook attached to the hair. The hook was fixed to the end of a precision linear drive modified by a hydraulic micromanipulator. A stepping motor (1.8 ° per step) was attached to the drive shaft of the micromanipulator through a reduction gear (ratio 1:5). This system could produce two-way linear movements of the hook with a sensitivity of 0.25 μm per step. The driver software for the stepping motor was programmed using Quick Basic (Microsoft), and the driver interface was made from a stepping motor driver chip (TA8415P, Toshiba) and a high-power transistor (TD6308, Toshiba). TTL step pulses and directional (CW/CCW) signals were generated from the serial port of the host PC. The parameters of hair movements (displacement, velocity and holding period) were controlled by altering the number of steps and the inter-step interval. Over the range studied, the relationship between the linear displacement of the hook and the deflection angle of the hair was approximately linear (correlation coefficients of the linear fits were all close to unity; $0.9884 < r < 0.9996$) for all 27 hairs studied in detail. The individual steps may each cause a synchronized spike discharge at each step, even for a very small displacement, when the inter-step interval (ISI) is long. The threshold ISI for step detection was determined in 14 hairs to be 47–117 ms. We therefore set the ISI at <20 ms in all experiments to avoid this problem.

Hairs were inclined towards the tip of the antenna from the natural erected position by the fine hook. The movement was always monitored by a CCD video camera positioned just lateral to the hair (the images were enlarged through a dissecting microscope). The video images, TTL step pulses from the PC and response signals from the a.c. amplifier were simultaneously recorded onto single video- and dual audio-channels of a video recorder. The linear displacement of the hook was monitored optically by a set of infrared light-emitting diodes (IR-LED) and a phototransistor. An aluminium interrupter vane attached to the probe of the linear drive was

Fig. 1. Scapal hair plates (S-HPs) and their adjacent joint membrane. Views from three different (inner, top and outer) angles. An example of the right antenna. Note the structural partitioning of the joint membrane. HC, head capsule; JM, joint membrane; S, scape; P, pedicel; F, flagellum; Di, distal; Po, posterior; L, lateral; M, medial; Do, dorsal; V, ventral.
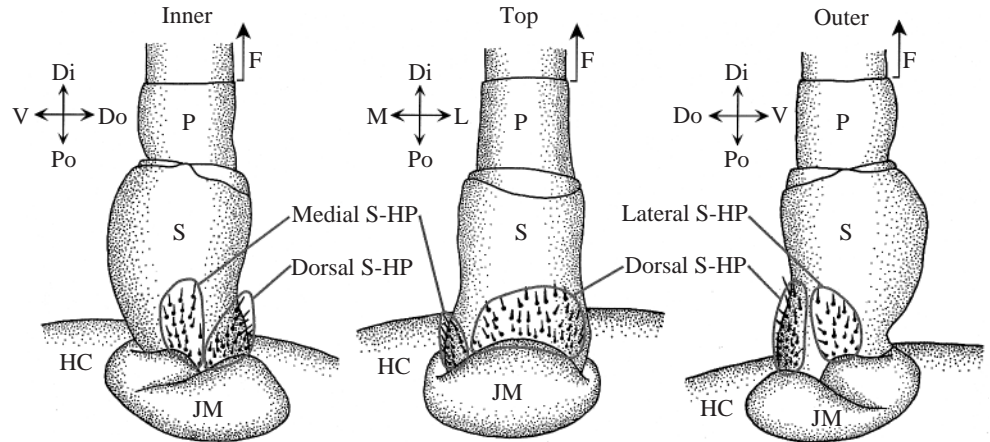
set at an appropriate position between the IR-LED and the phototransistor. Displacements as small as $0.1\,\mu m$ could produce detectable voltage changes (approximately $10\,mV$) in the output from the phototransistor. The delay between the onset of hair movement and that of the stepping signal was approximately $5\,ms$. Stored data were replayed, and re-acquisition and further analyses were performed by Spike2 (Cambridge Electronic Design).

Data analysis

The spike frequencies of sensilla were analyzed by making peri-stimulus time histograms (PSTHs) with a 0.1 s bin width. The highest frequency of spike discharge near the onset of the deflection was estimated as the maximum frequency in the PSTH and was referred to as the transient-phase frequency (TPF). The mean spike frequency 9–10 s after the onset of deflection was termed the sustained-phase frequency (SPF). Since the hairs are located just above antennal muscles, spontaneous electromyographic noise often interfered with the sensory signals. Trials were therefore repeated 5–6 times for each experimental condition at 20 s intervals and averaged to determine the SPF and TPF.

Results

Morphology of the S-HP and its adjacent joint membrane

The S-HP can be subdivided into three parts, the dorsal, lateral and medial subgroups (Figs 1–3) (Okada and Toh, 2000). The boundary between the dorsal and lateral S-HPs is obvious, but that between the dorsal and medial S-HPs is less clear. However, these two subgroups were distinguishable by carefully tracing the sparsely covered region. The dorsal, lateral and medial S-HPs consist of approximately 120, 60 and 30 sensilla, respectively (Okada and Toh, 2000). The type of sensillum making up the S-HP, referred to as the chaetic sensillum A, has smooth-surfaced walls (Schafer and Sanchez, 1973; Toh, 1981) and inclines slightly towards the tip of the antenna. The sensory hairs are shorter in the proximal S-HP and longer in its distal zone. The shaft has been measured as 6–75 µm long (Schafer and Sanchez, 1973) or 15–60 µm long (Toh, 1981). A small V-shaped protuberance of cuticle occurs

at each hair base, and this opens distally and closes at the proximal side of the hair base (not shown). This structure limits the hair's deflection proximally and may constrain its optimal sensitivity to the distal direction, as shown for the hair plate sensillum of honeybees (Thurm, 1963). The joint membrane between the scape and the head can be divided into three parts, each of which corresponds to one of the three S-HP subgroups (Fig. 1). This structural partition of the joint membrane arises
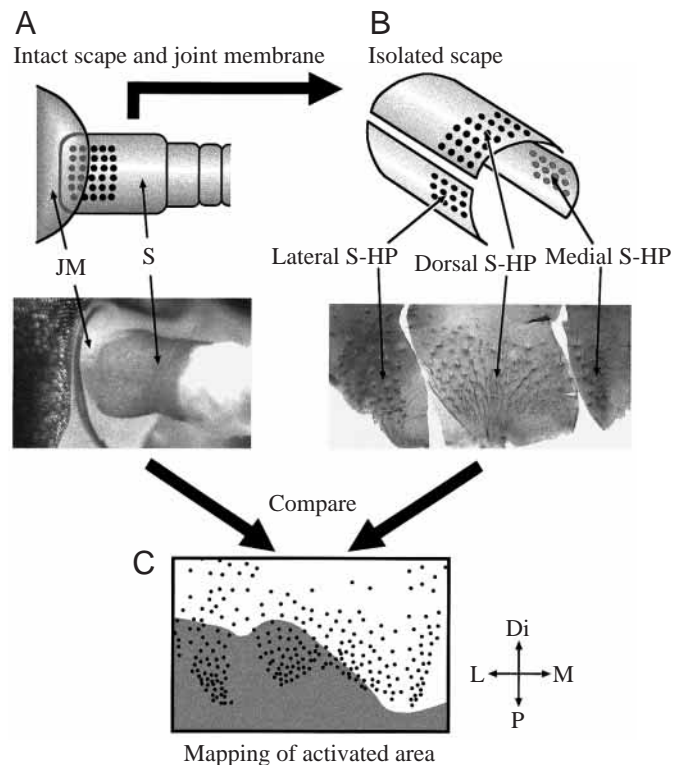

Fig. 2. The method used to map the activated area of the scapal hair plate (S-HP). (A) The S-HP and its adjacent joint. (B) The isolated and flattened scapal exoskeleton. (C) A map of the activated area. By comparing the S-HP area lying under the joint membrane (A) with the mapped sensillar pattern (B), the area of the S-HP activated for a given direction of joint movement was identified (shaded region). JM, joint membrane; S, scape; Di, distal; L, lateral; M, medial; P, posterior.
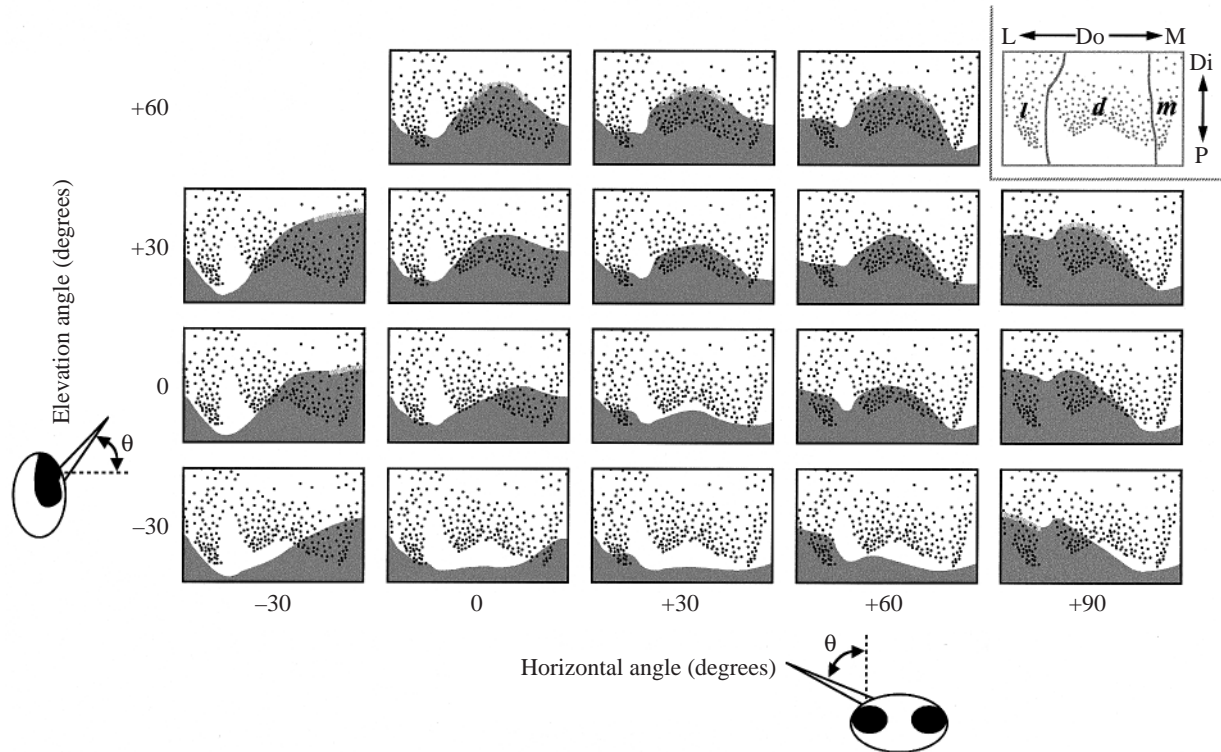
Fig. 3. The area of the scapal hair plate (S-HP) (left antenna) activated at various angles in the horizontal and vertical planes. Shaded areas indicate the activated region located under the joint membrane. The narrow boundaries of pale shading show a region for which it was difficult to determine the margin of the joint membrane exactly. The inset at the top right shows the geometry of the flattened scape and the boundaries of three subgroups of the S-HP. Insets at the bottom and left are dorsal and lateral views, respectively, of the head and an antenna, showing how the horizontal and elevation angles (θ), respectively, were determined. Di, distal; Do, dorsal; L, lateral; M, medial; P, posterior; *d*, dorsal S-HP; *l*, lateral S-HP; *m*, medial S-HP.

from a thin exoskeleton spanning the antennal socket (not shown). Thus, each subgroup of the S-HP has its own subdivision of the joint membrane for mechanical activation.

Mapping the activated area of the S-HP

An example of the activated area of the left S-HP at various horizontal and elevation angles is shown schematically in Fig. 3. The antenna was moved from –30 to +90° horizontally and elevated from –30 to +60° vertically, in steps of 30°. Elevation preferentially activated the dorsal S-HP at all horizontal positions, and to a lesser extent the medial S-HP. The higher the elevation angle, the larger the area activated. The medial and lateral S-HPs were affected by horizontal movement of the antenna. When the antenna moved horizontally, the areas activated in the lateral or medial S-HPs changed in opposite directions.

Properties of the three subgroups of S-HP

The number of activated hairs was counted for 18 horizontal and elevation angles of the antenna (Fig. 4). The data are represented as the relative number of hairs deflected (R_N). The dorsal S-HP exhibited no consistent relationship between R_N and the horizontal angle at any elevation angle examined (Fig. 4A, dorsal S-HP). Conversely, consistently positive relationships were found for the dorsal group

between R_N and the elevation angle (Fig. 4B, dorsal S-HP). R_N values for the medial and lateral S-HPs showed, respectively, consistent negative and positive relationships for changes in horizontal angle (Fig. 4A, medial and lateral S-HPs). In particular, the lateral S-HP exhibited an almost linear relationship to the horizontal angle, with little scatter. In contrast, the R_N values of the medial and lateral S-HPs varied widely with horizontal position and were largely independent of elevation angle (Fig. 4B, medial and lateral S-HPs).

Response of the S-HP sensilla

The S-HP sensilla were usually silent in the resting state, but fired single-unit spikes in response to sustained deflections. In Fig. 5, the hair was deflected by 34° from its resting position and held for approximately 11 s, then released. This trapezoidal movement caused a transient high-frequency burst of spikes at the onset of deflection and a slower sustained discharge as long as the deflection was maintained. All sensilla responded similarly, suggesting a typical phasic-tonic receptor.

The response to long-lasting deflections was examined in the hairs of the three subgroups. The deflection was held for 21 min at 25–40° for different hairs, and mean spike frequencies were calculated and plotted every 30 s (Fig. 6). The initial spike frequencies were 98, 99 and 132 Hz in hairs
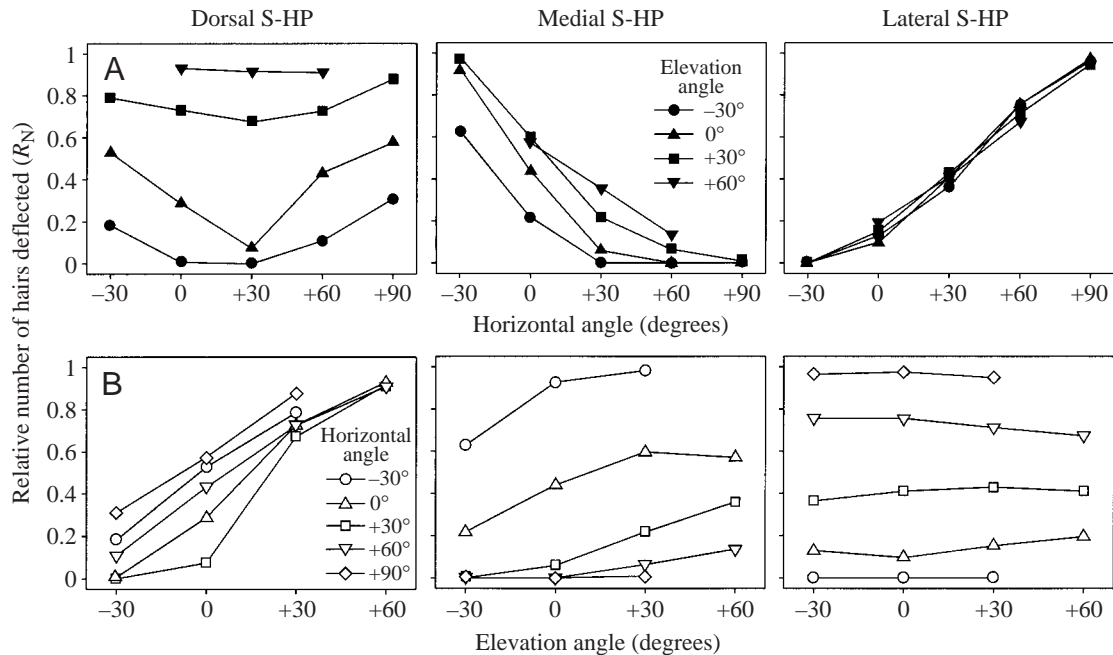
Fig. 4. Relationships between the relative number of hairs deflected (R_N) and antennal angle. Each normalized plot derived from seven animals indicates the fraction of the cumulative number of hairs deflected in a given antennal direction with respect to the cumulative maximal number of hairs deflected for all antennal directions. (A) Deflection in the horizontal plane. Note the almost linear relationships for the lateral scapal hair plate (S-HP), with little dispersion. (B) Deflection in the vertical plane (see text for detail).
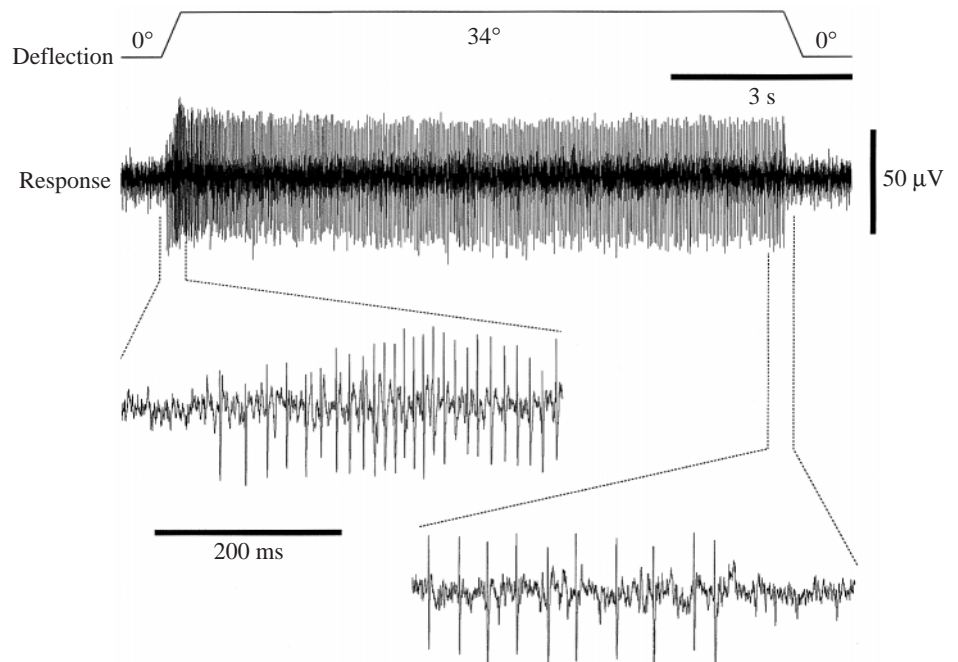

Fig. 5. Response of a sensillum of the right lateral scapal hair plate to artificial deflection. The hair was deflected distally by 34° from its resting position, held for 11 s, then released (top trace). Single-unit impulses continued for as long as the hair was deflected (second trace). In the dynamic phase of deflection, a transient burst was observed (see expanded region at the onset of deflection), with no additional off-discharge (see expanded region at the offset of deflection).

from the medial, dorsal and lateral S-HPs, respectively. The spike frequencies decreased strongly during the first 2 min, then continued to adapt slowly. However, a substantial spike discharge remained even at the end of the 21 min recording for each hair. In some hairs, high-frequency discharges were maintained at 10–30 Hz throughout the stimulus period (see hairs of the medial and lateral S-HPs in Fig. 6). We detected

no consistent differences among the three subgroups. The decay times were not analysed quantitatively since the sample number was too small. Long-term analysis was difficult to maintain mainly because of the frequent electromyographic impulses picked up from antennal muscles in the scape. All eight hairs tested showed spike discharges that were sustained for at least 10.5 min.
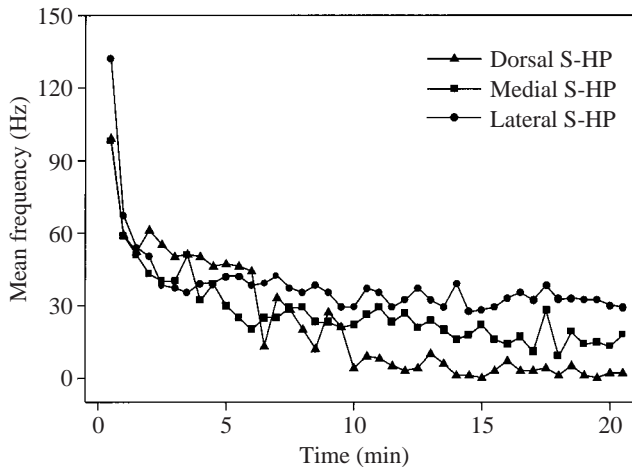
Fig. 6. Responses of representative hairs from the three different parts of the scapal hair plate (S-HP) to a long-lasting (21 min) deflection. Each point represents the mean number of spikes in a 0.5 min sample. Although the frequencies varied, these sensilla maintained their excitability for at least 21 min.

Properties of the phasic and tonic components of the sensillar response

The responses of sensilla could be categorized into phasic and tonic components. The relationships between these components and two parameters characterizing deflection amplitude (angle) and velocity were analyzed. The time courses of spike frequency (peri-stimulus time histograms, PSTHs) are shown in Fig. 7. The following two experiments were performed: (i) altering the angle at a constant angular velocity (Fig. 7A) and (ii) altering the velocity at a constant angular displacement (Fig. 7B). As the deflection angle increased from 12 to 60° at a constant deflection velocity ($60.1\,°\,s^{-1}$), both the transient-phase frequency (TPF) and the sustained-phase frequency (SPF) increased in a stimulus-dependent manner from 22 to 250 Hz and from 0 to 140 Hz, respectively (Fig. 7A). When, conversely, the deflection velocity was altered from 24 to $245\,°\,s^{-1}$ at a constant deflection angle (37°), the TPF increased from 118 to 166 Hz, but the SPF did not change (Fig. 7B).

We recorded responses from 24 hairs to alterations in the angle and velocity of deflection (Fig. 8). Data were obtained from nine dorsal, eight medial and seven lateral S-HP hairs, which ranged in length from 20.3 to $54.7\,\mu m$ ($38.4\pm8.7\,\mu m$, mean ± s.d., N=24 hairs). All sensilla were silent in the resting position and began to discharge when deflected by more than their threshold angle, which ranged between 1.8 and 13.0° from the resting position: the mean deflection was $5.9\pm2.8\,°$ for a deflection velocity averaging $102.0\pm15.2\,°\,s^{-1}$ (means ± s.d., N=24). The transient and sustained response phases were analyzed with respect to the deflection angle and velocity (Fig. 8). The SPF was clearly dependent on the deflected angle in all hairs (Fig. 8Ai). Although each hair was deflected to the maximum extent possible mechanically (46–72°), the SPF still did not attain saturation in most cases. The maximum SPF
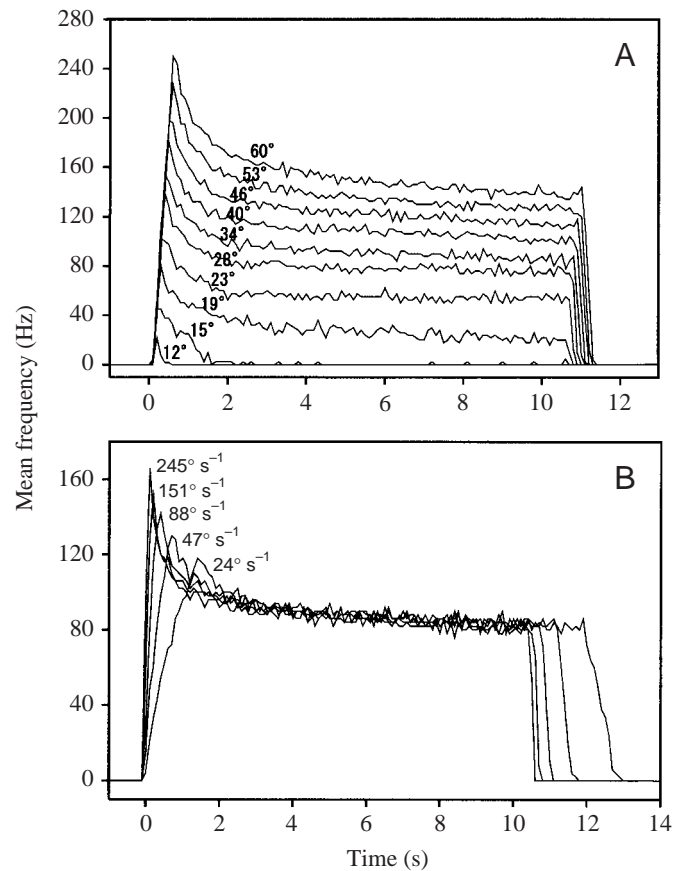

Fig. 7. The time courses of averaged spike frequencies depend on the deflection angle (A) and the deflection velocity (B). (A) An example from a hair of the lateral scapal hair plate (S-HP); deflection angle was increased from 12 to 60° at a constant deflection velocity ($60.1\,°\,s^{-1}$). (B) An example from a hair of the medial S-HP; deflection velocity ($24–245\,°\,s^{-1}$) was increased at a fixed angle (37°). Sample bin width, 0.1 s (A,B).

ranged from 86.5 to 143.8 Hz in different hairs. The TPF was also dependent on the deflection angle (Fig. 8Aii) and again failed to reach an asymptote in most cases. The maximum TPF ranged from 146.7 to 290 Hz when each hair was deflected maximally (46–72°) at $60.1–123.4\,°\,s^{-1}$ ($88.8\pm19.4\,°\,s^{-1}$; mean ± s.d., N=24). Although deflection velocities for a constant angular displacement (18–37° for different hairs) were explored from $16.9–32.4\,°\,s^{-1}$ up to $172.5–331.0\,°\,s^{-1}$ in different hairs, the SPFs remained almost constant irrespective of stimulus (Fig. 8Bi). The TPF had a slight initial positive relationship with the deflection velocity for most hairs (Fig. 8Bii). In some hairs, the TPF first saturated and then dropped slightly at the highest velocities.

Discussion

Activation of the S-HP by two-dimensional movements of the antenna

The peripheral representation of the direction of a movable joint has been morphologically described for the antennal
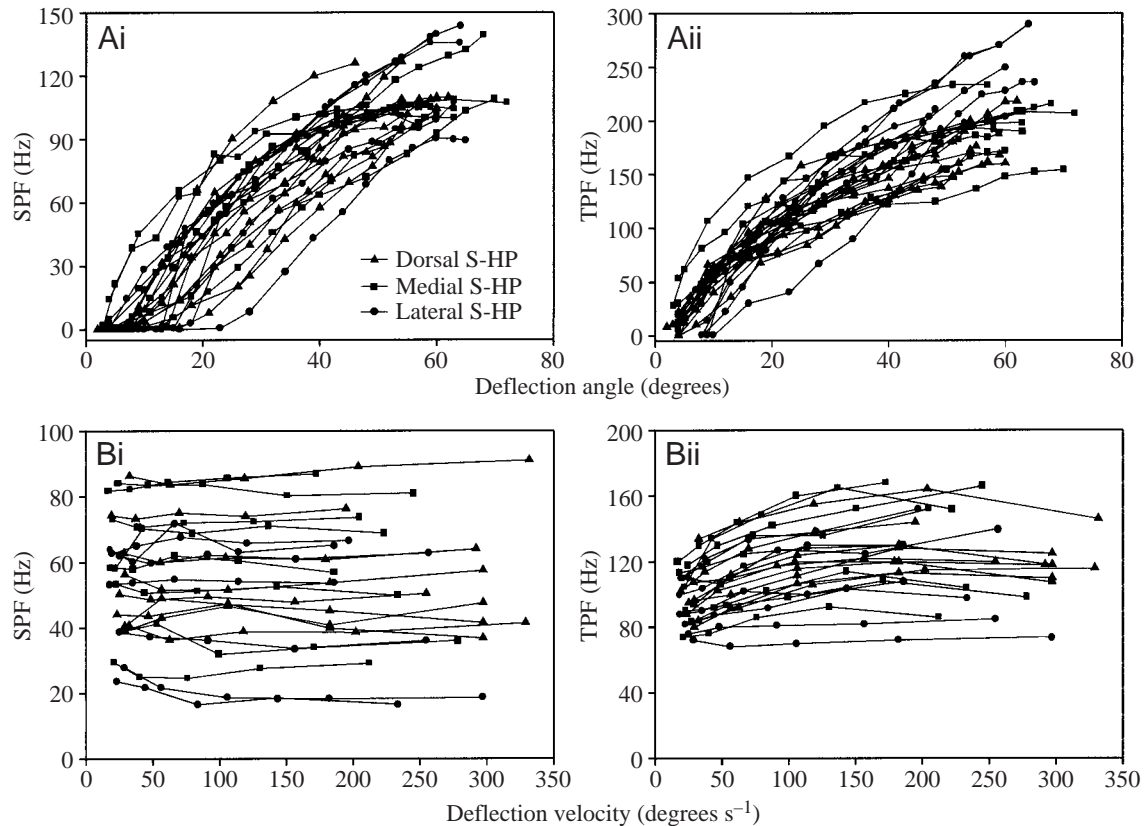
Fig. 8. Sustained-phase frequency (SPF) and transient-phase frequency (TPF) in response to different hair deflection angles (A) and velocities (B). The data are from nine dorsal, eight medial and seven lateral hairs. There were no apparent difference in SPFs and TPFs among the three scapal hair plate (S-HP) subgroups. (Ai) Relationship between SPF and hair deflection angle. (Aii) Relationship between TPF and hair deflection angle. These two relationships clearly exhibited angle-dependency. (Bi) Relationship between SPF and hair deflection velocity. (Bii) Relationship between TPF and hair deflection velocity. Positive relationships were observed for most hairs in Bii, but not in Bi.

hair plates of cockroaches. The activated area, where mechanosensitive hairs would be deflected under a joint membrane, was mapped for two-dimensional movements of the antenna. This is the first report of precise mapping of the activated area for hair plates in this two-dimensionally movable joint. The three subgroups of hairs comprising the S-HP were characterized quantitatively by examining the relative number of hairs deflected (R_N). These analyses showed that the lateral subgroup of S-HPs may provide the most reliable information about the horizontal component of antennal position and did not depend on vertical position. In contrast, the vertical component of antennal position could be relatively well-encoded by the dorsal subgroup of S-HPs. The medial S-HP exhibited intermediate coding characteristics for both components. These differences may arise from the subgroup-specific relationships between the distribution of hairs and the corresponding topography of the joint membrane.

We have developed a behavioural paradigm for testing tactile detection by antennation utilizing the thigmotactic nature of cockroaches (Okada and Toh, 2000). This behavioural test showed that the S-HPs may be important for detecting the horizontal position of objects precisely, relative to the animal itself. The S-HP would be a good subject for

studying the mechanosensory system of insects, because it consists of a relatively small number (approximately 200) of sensory cells and can be deprived of its function simply by shaving off the hairs without further surgical intervention. The present results for the S-HP supply the basic information necessary for further physiological studies on the central processing of tactile perception.

Mechanoreceptors within the antennal base have been described, for various insects, as hair plates, chordotonal (Janet's) organs, Johnston's organs and campaniform sensilla (Hicks' organs). These mechanoreceptors are generally regarded as the proprioceptors for antennal movements. In *P. americana*, of the mechanoreceptors known so far, only the S-HP seems to perceive the horizontal component of antennal position (Okada and Toh, 2000). Resolution of the vertical component of antennal position may be a function of the hair plates at the scape–pedicel joint (pedicellar hair plates) and of the chordotonal organ in the pedicel, as well as the S-HP. Mapping of the area activated in the pedicellar hair plate and recording the physiological responses of the chordotonal organ and the pedicellar hair plates would be essential further steps in a systematic study of the peripheral representation of antennal orientation.

Response properties of the S-HP sensilla

The properties of mechanoreceptors of the S-HP were investigated using a pull-and-hold type of stimulation. These trapezoidal stimuli may mimic natural movements of hairs better than ramps or sinusoids. The sensilla were silent in their resting position and began to fire when their deflection angle exceeded approximately 6° from the resting position. Spike frequency reached its maximum immediately after the cessation of the dynamic phase and then gradually decreased to a steady tonic firing rate, although even this level of firing was not constant when examined carefully, but continued to adapted (Fig. 6). Responses in both the transient and sustained phases were clearly dependent on the deflection angle in all hairs (Fig. 8A). The transient-phase response also showed a positive relationship with the deflection velocity for most stimulus ranges examined, but this was not the case for the sustained-phase response (Fig. 8B). All the sensilla showed typical phasic-tonic responses to hair deflections. Firing of single-unit spikes was consistent with previous histological results on the mechanoreceptors of antennal hair plates in *P. americana*, which revealed a single bipolar mechanoreceptor per hair (Schafer and Sanchez, 1973; Toh, 1981). We could detect no qualitative or quantitative differences between the physiological responses of the three subgroups of S-HP.

The response properties of hair-plate sensilla have been reported for different joints in various insects (Pringle, 1938; Haskell, 1959; Thurm, 1963; Schafer, 1971; French and Wong, 1976, 1977; Wong and Pearson, 1976; Liske, 1982; Kuenzi and Burrows, 1995; Newland et al., 1995) and also in a crustacean (Vedel, 1986). Although the responses of the hairs vary widely, they can be categorized into phasic or phasic-tonic types. Our results closely resembled those described previously for phasic-tonic mechanosensitive hairs. Long-term continuity of tonic activity has not been reported so far, except by Thurm (1963), who showed that the hair-plate sensilla at the head–thoracic joint were able to generate spikes for more than 4 min. We have demonstrated here that the S-HP hairs can be activated for even longer, at least 10–20 min. Cockroaches often freeze for a few seconds in response to external stimuli (vibration of the substratum, wind, touch to the body) if the stimulus is weak. In response to strong stimuli, escape behaviour may occur, and this continues until a safe zone such as dark place is found (Meyer et al., 1981; Okada and Toh, 1998). When cockroaches cease this escape behaviour, they tend to 'freeze' for up to several minutes (J. Okada and Y. Toh, unpublished observation). The slowly adapting nature of S-HP sensilla could contribute to continuous proprioceptive monitoring of the precise position of the antennae, even in such a situation. This would allow the animals to be ready to escape in an appropriate direction (away from the origin of the stimulus) if an additional attack from a predator were detected by the antennae.

The ultimate goal of this study was to elucidate the representation in the central nervous system of the tactile world by the antennae. A knowledge of the central anatomy of the S-HP afferents will be one of the important steps towards achieving this aim. The central morphologies of the antennal hair-plate neurons have been described in the moth (Hildebrand et al., 1980), the locust (Bräunig et al., 1983), the honeybee (Maronde, 1991) and the ant (Ehmer and Gronenberg, 1997). The axons from these hair plates extend primarily to the dorsal lobe of the deutocerebrum, where they arborize. This region also includes antennal motor neurons that can interact with mechanosensory afferents from the antennae (for reviews, see Rospars, 1988; Homberg et al., 1989). In addition, some mechanosensory afferents from each flagellum may also project to the ipsilateral dorsal lobe, instead of the antennal lobe (Suzuki, 1975; Hildebrand et al., 1980; Koontz and Schneider, 1987; Kloppenburg, 1995; Nishikawa et al., 1995; Staudacher and Schildberger, 1999). Tactile information from mechanoreceptors on the flagellum would be integrated in the central nervous system with directional information from the proprioceptors in the antennal base to generate a tactile picture of local space. The most likely location for the first step of this integration mechanism is the dorsal lobe.

References

Bell, W. J. (1991). *Searching Behaviour: The Behavioural Ecology of Finding Resources*. London: Chapman & Hall.
Bräunig, P., Pflüger, H. J. and Hustert, R. (1983). The specificity of central nervous projections of locust mechanoreceptors. *J. Comp. Neurol.* **218**, 197–207.
Comer, C. M. and Dowd, J. P. (1993). Multisensory processing for movement: antennal and cercal mediation of escape turning in the cockroach. In *Biological Neural Networks in Invertebrate Neuroethology and Robotics* (ed. R. D. Beer, R. E. Ritzmann and T. Mckenna), pp. 89–112. New York: Academic Press.
Ehmer, B. and Gronenberg, W. (1997). Proprioceptors and fast antennal reflexes in the ant *Odontomachus* (Formicidae, Ponerinae). *Cell. Tissue Res.* **290**, 153–165.
French, A. S. and Wong, R. K. S. (1976). The responses of trochanteral hair plate sensilla in the cockroach to periodic and random displacements. *Biol. Cybern.* **22**, 33–38.
French, A. S. and Wong, R. K. S. (1977). Nonlinear analysis of sensory transduation in an insect mechanoreceptor. *Biol. Cybern.*#**26**, 231–240.
Haskell, P. T. (1959). Function of certain prothoracic hair receptors in the desert locust. *Nature* **183**, 1107.
Hildebrand, J. G., Matsumoto, S. G., Camazine, S. M., Tolbert, L. P., Blank, S., Ferguson, H. and Ecker, V. (1980). Organisation and physiology of antennal centres in the brain of the moth *Manduca sexta*. In *Insect Neurobiology and Pesticide Action*, pp. 375–382. London: Society of the Chemical Industry.
Homberg, U., Christensen, T. A. and Hildebrand, J. G. (1989). Structure and function of the deutocerebrum in insects. *Annu. Rev. Entomol.*#**34**, 477–501.
Kloppenburg, P. (1995). Anatomy of the antennal motoneurons in the brain of the honeybee (*Apis mellifera*). *J. Comp. Neurol.* **363**, 333–343.
Koontz, M. A. and Schneider, D. (1987). Sexual dimorphism in neuronal projections from the antennae of silk moths (*Bombyx mori*, *Antheraea polyphemus*) and the gypsy moth (*Lymantria dispar*). *Cell Tissue Res.* **249**, 36–50.
Kuenzi, F. and Burrows, M. (1995). Central connections of sensory neurons

from a hair plate proprioceptor in the thoraco-coxal joint of the locust. *J. Exp. Biol.* **198**, 1589–1601.

Liske, E. (1982). Proprioceptive control of head position and head movement in the praying mantis. *Naturwissenschaften* **69**, 452–453.

Maronde, U. (1991). Common projection areas of antennal and visual pathways in the honeybee brain, *Apis mellifera*. *J. Comp. Neurol.* **309**, 328–340.

Meyer, D. J., Margiotta, J. F. and Walcott, B. (1981). The shadow response of the cockroach *Periplaneta americana*. *J. Neurobiol.* **12**, 93–96.

Newland, P. L., Watkins, B., Emptage, N. J. and Nagayama, T. (1995). The structure, response properties and development of a hair plate on the mesothoracic leg of the locust. *J. Exp. Biol.* **198**, 2397–2404.

Nishikawa, M., Yokohari, F. and Ishibashi, T. (1995). Central projections of the antennal cold receptor neurons and hygroreceptor neurons of the cockroach, *Periplaneta americana*. *J. Comp. Neurol.* **361**, 165–176.

Okada, J. and Toh, Y. (1998). Shade response in the escape behavior of the cockroach, *Periplaneta americana*. *Zool. Sci.* **15**, 831–835.

Okada, J. and Toh, Y. (2000). The role of antennal hair plates in object-guided tactile orientation of the cockroach (*Periplaneta americana*). *J. Comp. Physiol. A* **186**, 849–857.

Pringle, J. W. S. (1938). Proprioception in insects. III. The function of the hair sensilla at the joints. *J. Exp. Biol.* **15**, 467–473.

Rospars, J. P. (1988). Structure and development of the insect antennodeutocerebral system. *Int. J. Insect Morphol. Embryol.* **17**, 243–294.

Schafer, R. (1971). Insect mechanoreceptors: Information content in responses of antennal sensilla chaetica (Abstract). *Proc. Int. Union Physiol. Sci.* **9**, 497.

Schafer, R. and Sanchez, T. V. (1973). Antennal sensory system of the cockroach, *Periplaneta americana*: Postembryonic development and morphology of the sense organs. *J. Comp. Neurol.* **149**, 335–354.

Seelinger, G. and Tobin, T. R. (1981). Sense organs. In *The American Cockroach* (ed. W. J. Bell and K. G. Adiyodi), pp. 217–245. London: Chapman & Hall.

Staudacher, E. and Schildberger, K. (1999). A newly described neuropile in the deutocerebrum of the cricket: Antennal afferents and descending interneurons. *Zoology* **102**, 212–226.

Suzuki, H. (1975). Antennal movements induced by odour and central projection of the antennal neurones in the honey-bee. *J. Insect Physiol.* **21**, 831–847.

Thurm, U. (1963). Die Beziehungen zwischen mechanischen Reizgrössen und stationären Erregungszuständen bei Borstenfeld-Sensillen von Bienen. *Z. Vergl. Physiol.* **46**, 351–382.

Toh, Y. (1981). Fine structure of sense organs on the antennal pedicel and scape of the male cockroach, *Periplaneta americana*. *J. Ultrastruct. Res.* **77**, 119–132.

Vedel, J. P. (1986). Morphology and physiology of a hair plate sensory organ located on the antenna of the rock lobster *Palinurus vulgaris*. *J. Neurobiol.* **17**, 65–76.

Wong, R. K. S. and Pearson, K. G. (1976). Properties of the trochanteral hair plate and its function in the control of walking in the cockroach. *J. Exp. Biol.* **64**, 233–249.