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Authors: Okada, Jiro, Kanamaru, Yoshio, and Toh, Yoshihiro

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Jiro Okada*, Yoshio Kanamaru and Yoshihiro Toh

Department of Biology, Graduate School of Sciences, Kyushu University, Fukuoka 812-8581, Japan

ABSTRACT—The voluntary movement of antennae of blinded cockroaches was examined in the tethered-walking condition. An object of metal plate was presented to a tip of a single antenna in order to induce tactile orientation behavior. Horizontal movements of the antenna before and during the object presentation were analyzed both before and after ablation of a mechanosensory organ, the scapal hair plate (S-HP), at the base of antenna. The resting antennal position shifted outwardly by about 20° after the S-HP ablation. Spontaneous antennal movements in ablated animals became stiff and wider ranged. The tactile object was set at two different horizontal positions, 45° and 90° clockwise to the head, for the right side antenna. The number of contacts in a constant test period was significantly decreased in the tests at 45° after ablation. Trajectories of antennal movements before and after contacts were categorized into four patterns. In the case that an antenna made contact with the object during its abduction (outward) movement, it then passed the object outwardly or withdrew inwardly. These were termed "outward-pass (O-P)" and "outward-withdrawal (O-W)" patterns, respectively. Similarly, contacts during the adduction (inward) movement were divided into "inward-pass (I-P)" or "inward-withdrawal (I-W)" pattern. Significant effects of the S-HP ablation appeared in the tests at 90°: the I-P pattern mostly disappeared and was replaced by the I-W pattern. The results strongly suggest that the S-HP has crucial roles for controlling both spontaneous and stimulated movements of the cockroach antenna.

Key words: cockroach, antenna, hair plate, mechanoreceptor, tactile sense

INTRODUCTION

The antenna of insects functions as a multimodal sensor responsive to various chemical and physical stimuli (Schneider, 1964, and many others). Information perceived at the antenna is conveyed primarily to particular substructures in the brain such as the antennal and dorsal lobes, and processed there for expression and regulation of appropriate behaviors (Rospars, 1988; Homberg *et al.*, 1989). The importance of chemical sense derived mainly from the antennae has been described repeatedly for various resource finding behaviors (Baker, 1985). The mechanical sense derived from the antennae is also essential in knowing the physical environment, especially for nocturnal insects because they are more active when vision is not possible, i.e. during the night. It is so far known that mechanical stimuli of antennae cause some orientation behaviors in nocturnal cockroaches, such as a wind/touch-induced escape response (Comer and Dowd, 1993), a

mate-induced aggressive or escape response (Bell, 1978) and a stationary object-guided approach during searching (Okada and Toh, 2000).

A conspicuous behavior in some nocturnal insects is the antennal scanning in which a pair of antennae actively moves to probe the surroundings (Bell, 1991). Though the mode of movements differs among species, the insect antenna is most commonly mobile at the basal joints. In the cockroach *Periplaneta americana*, used in the present study, the antenna consists of two basal mobile segments, the scape and the pedicel, and more distal homologous 150-170 segments, correctively called the flagellum. The pedicel is mobile only in the vertical plane at the scape-pedicel joint. By contrast, the scape is moveable in any direction at the scape-head joint. Thus, *P. americana* exhibits a typical antennal scanning.

We have developed a new behavioral paradigm for exploring tactile perception by the active antenna of insects, utilizing the thigmotactic nature of the nocturnal cockroach *P. americana* (Okada and Toh, 2000). A blinded cockroach tethered on a treadmill of a free-rotating ball exhibits searching behavior continually with active antennal scanning and

* Corresponding author: Tel. +81-92-642-2315;
FAX. +81-92-642-2645.
E-mail: jokadscb@mbox.nc.kyushu-u.ac.jp

frequent zigzag locomotion. When a stationary test object is presented to a tip of single antenna, the animal touches the object repeatedly with the antenna, and tries to approach it. A single antenna is sufficient to distinguish the angular position of an object in the horizontal plane. For the sense organ concerned with the tactile perception of object direction, a group of mechanosensitive hairs on the scape (scapal hair plate, S-HP) was shown to be important by its lesion experiments (Okada and Toh, 2000). The S-HP is a cluster of about 200 mechanosensitive hairs adjacent to the scape-head joint. Movement of the joint activates the S-HP because a portion of its hairs is deflected under the joint membrane. The activated area in the S-HP is antennal position dependent (Okada and Toh, 2001). Thus, the S-HP, a proprioceptor for monitoring antennal deflection, is mostly concerned with tactile orientation. However, roles of S-HPs in the antennal movement itself are still unknown.

We show here the effects of the ablation of the S-HP on both spontaneous and stimulated antennal movements of tethered cockroaches. Tactile behavior of cockroach antennae was recorded by the same experimental system as that reported in our previous paper (Okada and Toh,

2000). Horizontal movements of antennae were registered frame-by-frame from still video images. A preliminary report has appeared elsewhere (Okada *et al.*, 2001b).

MATERIALS AND METHODS

Animal

Adult male cockroaches (*Periplaneta americana*) hatched and reared in a laboratory culture were used. They were fed rodent pellets. Room temperature for the culture was kept at 27°C. Both the compound eyes and the ocelli in all animals used were occluded by an opaque black paint in order to eliminate all vision.

To remove the mechanosensitive hairs of S-HP, the animals were first immobilized using ice, and then as many of the hairs were shaved off as possible using a sharp razor blade, as well as a thin surface layer of cuticle. Experiments on treated animals were conducted at least 2 days later, to allow for recovery from the operation.

Experimental apparatus

The experimental setup used was the same as that in our previous report (Okada and Toh, 2000). Briefly, an animal was tethered to a free-moving Styrofoam ball to allow walking. An aluminum plate (1 cm width, 5 cm height) was presented to the flagellum of the right antenna at two different horizontal positions, at 45° and 90° clock-
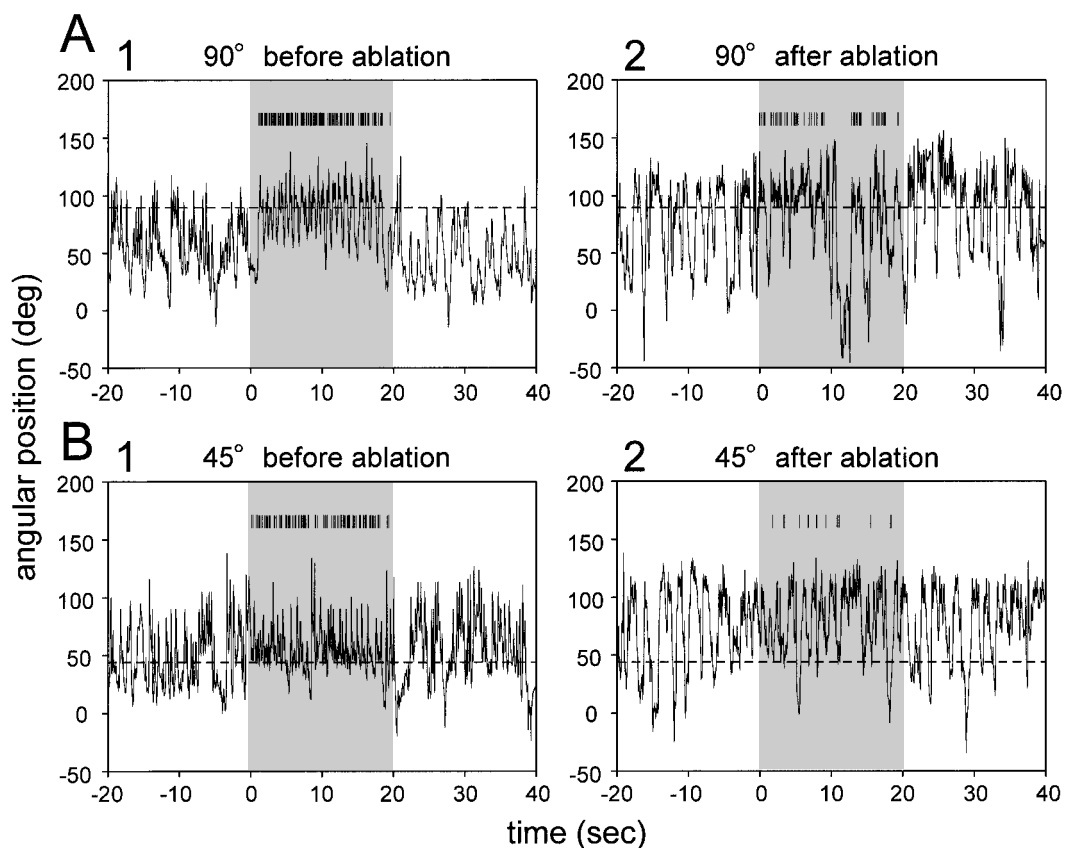

Fig. 1. Spontaneous and stimulated movements of an antenna before and after the S-HP ablation. A tactile object (a metal plate with 1 cm width and 5cm height) was presented to the right antenna at 90° (**A**) or 45° (**B**) clockwise to the head during the periods indicated by the shaded region (20 sec). Horizontal angular positions of the right antenna were registered frame-by-frame at 33 msec interval before (**1**) and after (**2**) the S-HP ablation. Vertical bars while the test object is present indicate the frames during which antennal contacts were observed. Horizontal broken lines show the angular position of the center of the presented object. After the ablation, amplitudes of antennal movements became wider, and the number of contacts was decreased particularly in the test at 45°. All data here were derived from the same animal.

wise to the head, for 20 sec, with the plate upright and facing the animal's head. The animals were allowed to touch the object with the distal most 3 mm of the antenna extended horizontally toward the object. Antennal movements were recorded by a video camera (frame rate, 30 Hz) positioned right above the animal.

Data analysis

Movements of antennae were measured by tracing their deflection on the still video images (for detail, see Okada and Toh, 2000). Horizontal angular positions of an antenna and its contacts with the test object were manually registered frame-by-frame at 33 msec intervals. The position was defined as measuring the angle of the flagellum with respect to the animal's midline. The origin for the antennal position was set at the center of the head capsule. The right of the midline was defined as positive, and the left as negative. The period of each test was for 40 or 60 sec: 20 sec before the object was presented, 20 sec while the object was present, and in some cases an additional 20 sec after that. Antennal contacts with the object could be recognized on the display either by the LED flashes of the contact monitor (Okada and Toh, 2000) or by the distortion of antennal tip.

Spectral analyses on rhythmic antennal movements were performed by using the fast Fourier transformation (FFT) function of waveform analysis software (Microcal Origin). 512 continuous data points of the horizontal antennal position, corresponding to a period of 16.9 sec, were sampled and processed by the FFT function. Ordinates of FFT spectra, indicating amplitude integrals during sampling periods, were normalized in order to compare data directly among spectrograms.

The effects of S-HP ablations were examined statistically by the Wilcoxon test. Significant difference was judged to be when $P<0.05$.

RESULTS

Antennal movements in intact animals

Horizontal movements of an antenna in an intact animal were examined in three successive stages: before, during and after the object was presented (for 20 sec each). Fig. 1 A1 and B1 are typical examples for movements of the right antenna, in which the test object was presented to the tip of flagellum at 90° and 45°, respectively. Before the object was presented, the antenna moved rhythmically in the range from −40° to 130°, centering around 40°. The direction of antenna corresponded roughly to the orientation of walking: rightward turns were accompanied by outward antennal deflections, and leftward turns by inward antennal deflections (data not shown).

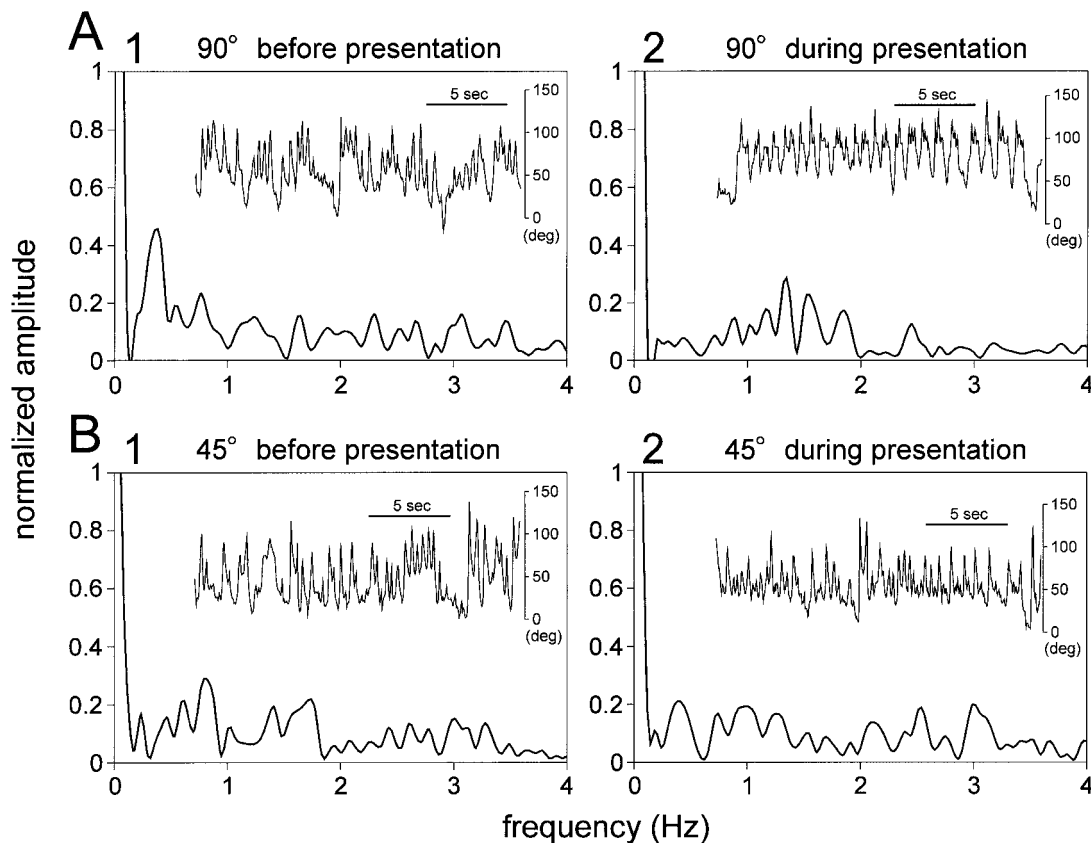When an object was presented at 90° to the antennae, they made the first contact with it by chance within a few

Fig. 2. Amplitude-frequency relationships of horizontal antennal movements in an intact animal. FFT spectra before (**1**) and during (**2**) object presentations at 90° (**A**) and 45° (**B**). The original data were derived from those shown in Fig. 1. Ordinates are shown in the normalized amplitude comparable through all spectrograms including those in Fig. 3. Insets in each graph are original waveforms before FFTs (extracted from Fig. 1 and expanded). During the object presentations both at 90° (**A2**) and 45° (**B2**), lower frequency components (<1 Hz for 90°, 0.3–2 Hz for 45°) decreased, while higher ones (1–2 Hz for 90°, 2-3 Hz for 45°) increased. Data points in the FFT spectra were connected with spline curvature methods.

seconds in most cases. Antennal oscillation shifted suddenly around 90° to probe the object. The angular range was concentrated, as long as the object was there. The animals continued to orient towards the test object because of their thigmotactic nature (data not shown). In the example of Fig. 1 A1, the animal made 68 contacts in the 20 sec. Antennal oscillation returned to normal range after the object was removed, and the zigzag walking resumed. Similar responses of antenna were observed when the object was presented at 45°. The range of antennal movement was concentrated around 45° to make contacts (n=65 in Fig. 1 B1). The positive tactile orientation of the body was also observed (data not shown).

To investigate differences between the antennal movements before and during the test in more detail, FFTs were performed on the horizontal antennal movements. Fig. 2 shows the FFT spectra for amplitude-frequency relationships before (1) and during (2) the tests at 90° (A) and 45° (B). The results were derived from the data shown in Fig. 1 A1 and B1. Before the object was presented, the antennal oscillations were distributed over wide range of frequency of 0–4 Hz in both cases (Fig. 2 A1, B1). Lower frequency movements at less than 1 Hz were relatively conspicuous in all animals examined (n=10). During the test at 90°, the

antenna showed a regular pattern of movement which consisted of a repetition of a wave composed of a single large wave and a few small ones (see inset of Fig. 2 A2). Such regularity also appeared in the test at 45° (compare the inset of Fig. 2 B2 with that of B1). These changes of the movement pattern were also shown in the amplitude spectra. In the test at 90°, the low frequency component at less than 1 Hz decreased, and the higher frequency component at a particular frequency band (1–2 Hz) became remarkably large (Fig. 2 A2). Similar changes in amplitude spectra were observed in the test at 45° (note a decrease of amplitudes at 0.3–2 Hz and an increase at 2–3 Hz in Fig. 2 B2). Though frequency bands differed, similar changes of the spectral pattern in both 90° and 45° tests were observed in 5 animals out of 10. The other 5 animals showed different changes: decreases of the lower frequency component or increases of the higher one.

Effects of S-HP ablation on antennal movements

Antennal movements in the horizontal plane were examined after ablation of the S-HP, using the same behavioral procedure as described above (Fig. 1 A2, B2). Spontaneous antennal movements occurred in wider arcs within the range –50° to 150°. The resting position of the ablated
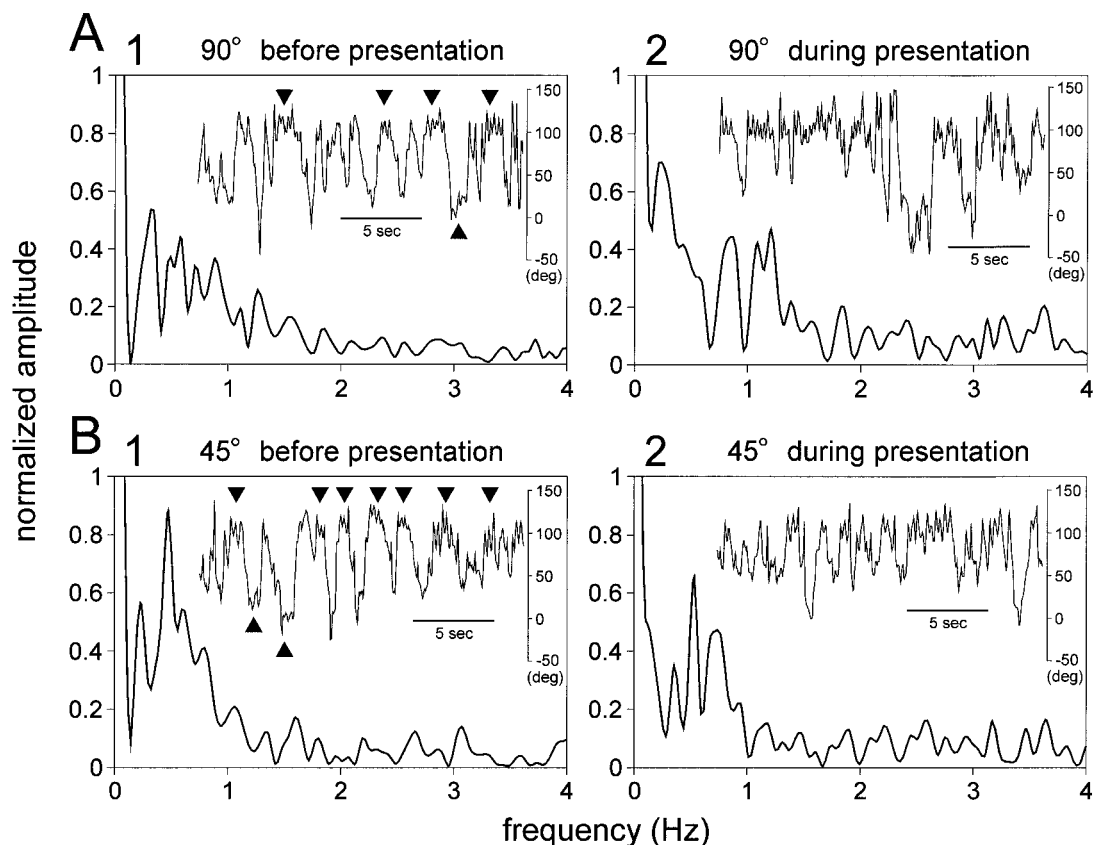

Fig. 3. Amplitude-frequency relationships of horizontal antennal movements after the S-HP ablation. FFT spectra before (**1**) and during (**2**) object presentations at 90° (**A**) and 45° (**B**). The original data were derived from those shown in the Fig. 1. The "over-swing" movements of treated antenna are represented clearly by increases in low frequency (<1 Hz) components in all four spectrograms (compare with the spectra in Fig. 2). Arrowheads in insets show small tremble-like cycles around the extreme positions.

antenna shifted to a more posterior (abducted) position around 60° (data not shown). Moreover, the reverse of antennal movements (transition from adduction to abduction or vice versa) became stiff. This was characteristic in cycles of small tremble-like movements intermixed with large movements at the extreme positions (see arrowheads in the insets of Fig. 3 A1 and A2). The trembles continued up to several seconds, resulting in the stiff movement of the antenna. These effects on horizontal antennal movements were caused after the S-HP ablation in all 10 animals examined. As far as we could observe from the video images, walking behavior itself was not affected by the ablation.

Effects of the S-HP ablation on antennal movements appeared clearly during tests at both 90° and 45° (Fig. 1 A2 and B2, respectively). In the test at 90° (Fig. 1 A2), the antenna made the first contact immediately after the object was presented, and concentrated its position around the object for the first half of stimulus period. But it then moved away from the object afterwards in this example. For the test at 45° (Fig. 1 B2), the arcs of antennal oscillation were slightly narrower than those before the test. However, their range was apparently wider than that before ablation. In the example of Fig. 1, the positive body orientation to the test object was apparently impaired (data not shown), and the number of contacts was decreased to 46 and 12, for tests at 90° and 45°, respectively, as our previous data (Okada and Toh, 2000).

FFT analyses for amplitude-frequency relationships clearly showed differences between the spectral patterns before and after ablation (Fig. 3). A common effect of the ablation in both control and stimulation stages was a wider range of the horizontal antennal movements, which was characterized by increases of the low frequency components (compare the corresponding spectra at <1 Hz between Fig. 2 and 3). In Fig. 3, although differences at low frequency were rather obscure between the spectra before and during the object's presence, higher frequency (> 1 Hz) components were slightly increased. The increase of higher frequencies in both tests at 90° and 45° was observed in 4 animals out of 10 and in additional 2 animals for one of two tests, although the frequency bands differed among individuals.

Contact patterns of antenna before and after S-HP ablation

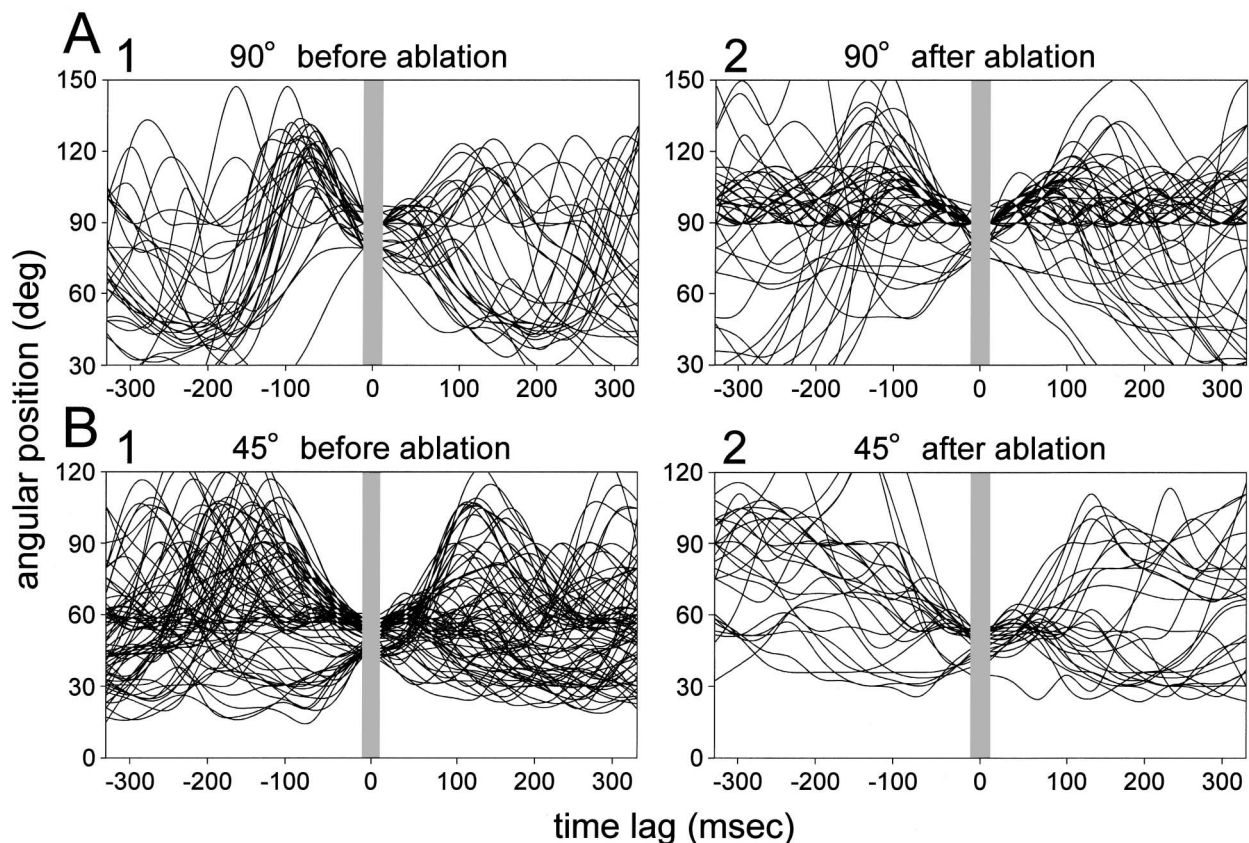Intact animals searching on the treadmill probed the

Fig. 4. Trajectories of horizontal antennal movements before and after contacts with test objects. Time zero means the instant of antennal contact. **A**. Superimposed trajectories before (**1**) and after (**2**) the S-HP ablation in the object presentations at 90° for 20 sec. After the ablation, the I-P pattern almost disappeared. Number of contacts: 31 before the ablation, 47 after the ablation. **B**. Superimposed trajectories in the object presentations at 45° for 20 sec. Though the number of contacts decreased from 77 (before ablation) to 26 (after ablation), the contact patterns themselves did not basically change. Data points for the trajectories were connected with spline curvature methods.

presented tactile object frequently with their antennae, and tried to approach it. The ablated animals could still make contacts with objects at reasonable frequencies (see following for detail), but their ability of orientation was significantly impaired (cf. Okada and Toh, 2000). We next investigated changes in the contact pattern by means of the frame-by-frame tracing of antennal movements. The trajectory for the contact patterns consisted of 22 data points ($\approx$ 660 msec): 11 continuous points before and at contact, and 11 points at and after leaving the object. Thus, the data points for the contacts themselves were omitted in the trajectories. Fig. 4 shows typical examples of the superimposed trajectories observed in each 20 sec test. Variations of the antennal angular position at time 0 are due to the width of the test object (1 cm). Contacts were classified logically into four patterns. Suppose that a horizontally moving antenna makes contacts with an object during its abduction (outward) movement. It will pass outwardly or withdraw inwardly in the next movement. The former was termed the outward-pass (O-P) pattern, and the latter the outward–withdrawal (O-W) pattern. Conversely, in cases of the adduction

(inward) movements, contacts were categorized into the inward-pass (I-P) pattern or the inward-withdrawal (I-W) pattern.

When the test object was presented to the antenna of an intact animal at 90°, the antenna made contacts during its inward movement in almost all cases, and then left the object inwardly (I-P pattern) or outwardly (I-W pattern) (Fig. 4 A1). Ratios of the I-P and I-W patterns were approximately same in this case, but not consistent through individuals. In most of animals (8 out of 10), approaches of antenna toward the object at 90° were observed mainly during the inward (adduction) movement. This specific approaching pattern may result from the coordination of horizontal and vertical movements of the antenna. For the test at 45°, the I-W pattern was the most dominant (Fig. 4 B1). This was noted in 9 animals out of 10. When an antenna made contact with the object at 45° during its outward (abduction) movement, it passed the object mostly irrespective of the S-HP ablation. This was the same for all 10 animals examined.

The S-HP ablation caused changes of contact patterns especially in the test at 90° (Fig. 4 A2). Before the lesion,
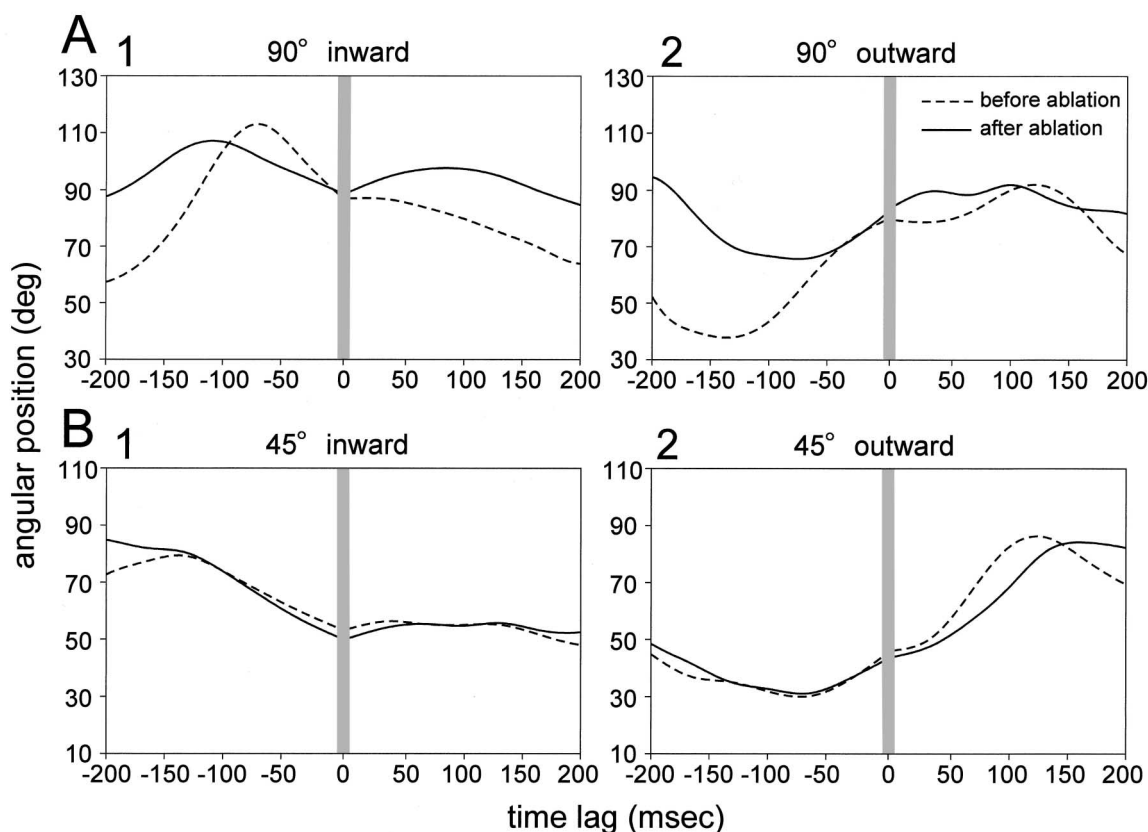

Fig. 5. Averaged trajectories before and after the S-HP ablation. Antennal trajectories were classified into two groups according to the approaching pattern toward object, the inward (**1**) and outward (**2**) groups, and averaged. The data derived from Fig. 4 clearly show the effects of the S-HP ablation. **A.** Averaged trajectories before (broken lines) and after (solid lines) the ablation in the presentations at 90°. In the inward group (**1**), the I-P pattern in intact antenna almost disappeared after the ablation, and was replaced by the I-W pattern. There was no remarkable change in the outward group (**2**). Number of trajectories averaged: 29 (before ablation) and 40 (after ablation) in the inward group, 2 (before) and 7 (after) in the outward group. **B.** Averaged trajectories before and after the ablation in the presentations at 45°. No change occurred in the basic contact pattern in both groups (**1** and **2**). Number of trajectories averaged: 59 (before) and 21 (after) in the inward group, and 18 (before) and 5 (after) in the outward group.

both the I-P and I-W patterns were present (Fig. 4 A1). While after the lesion, the I-P pattern was considerably reduced, and the I-W patterns became dominant (Fig. 4 A2). In contrast, in the test at 45°, the contact pattern itself was not significantly changed after the lesion, though the number of contacts was greatly decreased. Fig. 5 shows averaged trajectories of antennal movements before and after the S-HP (data derived from Fig. 4). Trajectories in each test were divided into two groups according to the direction of approach towards the object, i.e. "inward" and "outward" groups. The most remarkable change in contact pattern appeared in the inward group at 90° (Fig. 5 A1). The inward group at 45° (Fig. 5 B1) and the outward groups at 90° (A2) and 45° (B2) were not affected by the ablation in the basic contact pattern.

Effects of S-HP ablation on the contact pattern were examined statistically. The total numbers of contacts before and after ablations in 10 animals were 403 and 353 for 90° tests, and 531 and 235 for 45° tests, respectively (data from one 90° and one 45° tests for each animal). Statistical tests

resulted in a significant difference of the number of contacts in the pair of 45° tests ($P < 0.01$, Wilcoxon test), but not in the pair of 90° tests ($P > 0.05$). The decrease in number of contacts at 45° may be due to the shift of the horizontal center for antennal oscillation to more a distant (outward) position by approximately 20°.

Ratios of the 4 contact patterns (I-P, I-W, O-P and O-W patterns) to the total number of contacts in all 10 animals are shown in Fig. 6A. Remarkable changes of the contact pattern after the ablation were caused in the I-P and I-W patterns at 90° tests: an increase in ratio of the I-W pattern and a decrease in that of the I-P pattern. To compare numbers of contact patterns between intact and ablated animals by the Wilcoxon test, the total number of contacts before and after the ablation must be the same in each animal. Thus, the total number of contacts was adjusted to the smaller one in both intact and ablated trials. Because there was no tendency for temporal changes in the contact pattern during tests, the sampling from the larger group was made from the first contact. As changes in number of contacts in 10 individuals are shown in Fig. 6B, 9 animals out of 10 exhibited decreases in the I-P pattern (Fig. 6 B1), and increases in the I-W pattern (Fig. 6 B2). Significant differences were detected in both the I-P and I-W patterns ($P < 0.05$ and < 0.01, respectively). Similarly, O-P and O-W patterns at 90° and all 4 patterns at 45° were analyzed for both intact and treated animals, but no significant difference was detected in those pairs.
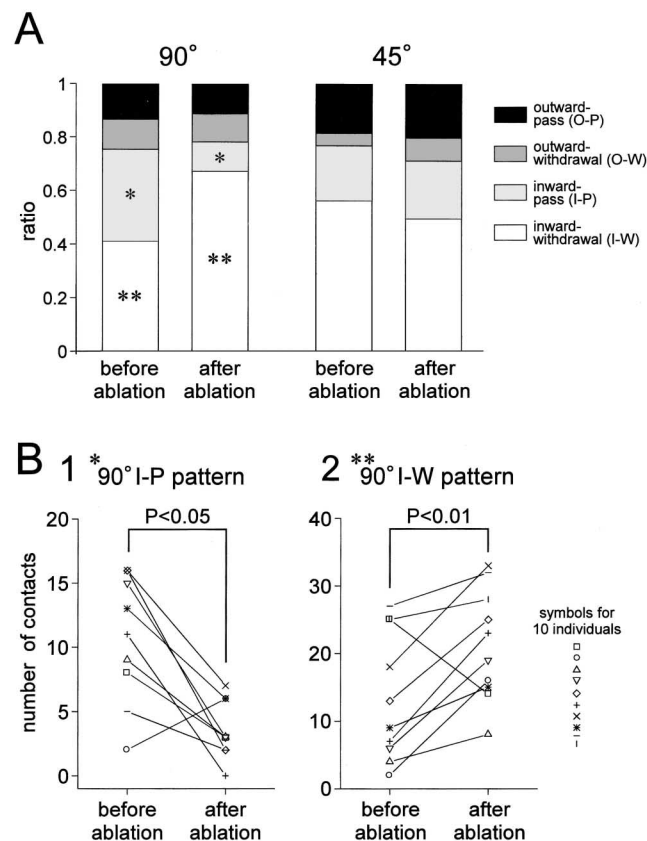
DISCUSSION

Antennal movements of cockroaches

Antennal movements in searching cockroaches examined in the present study could be classified into two modes; spontaneous and stimulated. In the spontaneous mode, horizontal antennal deflection corresponded roughly with the direction of walking: rightward turns were accompanied with outward and inward deflections of the right and left antennae, respectively, and vice versa for leftward turns. This suggests that the antennal motor system and the steering system for walking are coupled functionally in the CNS. In the stimulated mode, the antenna shifted quickly and pointed around the test object to make frequent contacts. Spectral analyses showed that the stimulated movement of antenna included more components at higher frequency than spontaneous movement. This is sound because antennal movements in the stimulated mode mainly consist of repetitions of small and rapid strokes.

The antenna of an insect usually includes two mobile segments (scape and pedicel) at its base. These segments have different rotation axes to each other in many cases, indicating that the distal part of antenna (flagellum) is mobile 3-dimensionally. On the other hand, movements of the head capsule could also account for 3-dimensional movements of the flagellum. In *P. americana*, the joint between scape and pedicel is mobile only in almost the vertical plane, and that

Fig. 6. Effects of the S-HP ablation on the antennal contact pattern. **A**. Ratios of 4 contact patterns to the total number of contacts in 10 animals (one 90° and one 45° tests for each animal). Remarkable changes were observed after the ablation in the I-P (*) and I-W (**) patterns in tests at 90°. **B**. Effects of the S-HP ablation on number of contacts for the I-P pattern (**1**) and the I-W pattern (**2**) in 90° tests in each of 10 individuals. Differences of the I-P (*) and I-W (**) patterns were significant between trials before and after the ablation (Wilcoxon test, $P < 0.05$ and < 0.01 respectively).

between head and scape in any direction. These suggest that the horizontal component of antennal movements seems to derive mainly from both the head-scape joint and the neck. Our preliminary study (Okada *et al.*, 2001a) in searching cockroaches showed that yaw movements of the head capsule were at most ±30°, suggesting that the major source for the horizontal component of antennal movement (in the range −40° to 130°) may be in the head-scape joint. This joint is operated by three musculatures, a single levator and a pair of adductor and abductor, connecting three different attachments at the proximal edge of the scape with the tentorium in the head. Reciprocal activities of the abductor and adductor muscles are most likely to produce the horizontal movement of flagellum. But the horizontal component could also be explained by a combination of movements of the free-moving neck and the vertically-moving scape-pedicel joint, even if the head-scape joint could not move at all. 3-D analyses for the mobile three parts (scape, pedicel, head capsule) would be necessary to determine to what extent these parts contribute to the horizontal antennal movement.

The voluntary movement of antenna has been described in some insects, flies (Horn and Kessler, 1975), crickets (Honegger, 1981; Horseman *et al.*, 1997), locusts (Saager and Gewecke, 1989), bees (Erber *et al.*, 1993), beetles (Pelletier and McLeod, 1994), ants (Ehmer and Gronenberg, 1997a, b) and stick insects (Dürr *et al.*, 2001), and also for crustacean crayfishes (Sandeman and Wilkens, 1983; Zeil *et al.*, 1985), in relation with their specific behaviors. In the cockroach *P. americana*, antennal deflections induced by the sex and aggregation pheromones have been examined (Rust *et al.*, 1976), where both antennae first responded to the pheromones with outward deflections regardless of the direction of odor source, and then turned antennae toward the source mainly by the head movement. Our present study added a new example to the repertoire for voluntary antennal movements in insects.

Function of the S-HP in controlling antennal movement

Removal of mechanosensitive hairs of the S-HP resulted in the wide-ranged and stiff movement of antenna. The resting position of the ablated antenna was shifted outwardly. These results implicate a feedback mechanism from the S-HP to the antennal motor system for horizontal movements (Fig. 7). The feedback seems to have a negative effect directed toward the neutral position, i.e. the center of the horizontal arc. Its strength may also depend on antennal position, i.e. the larger in antennal deflection, the greater the strength. Thus, the putative feedback limits the extreme position for reverse. Consequently, it may contribute to the smooth rhythmic movement of antennae (Fig. 7A before ablation). If the negative feedback were removed by the S-HP ablation, the antenna would over-swing and it would become difficult to reverse its on-going movement smoothly at the extreme position (Fig. 7A after ablation). The negative feedback loops from the hair plates in the legs to their motor
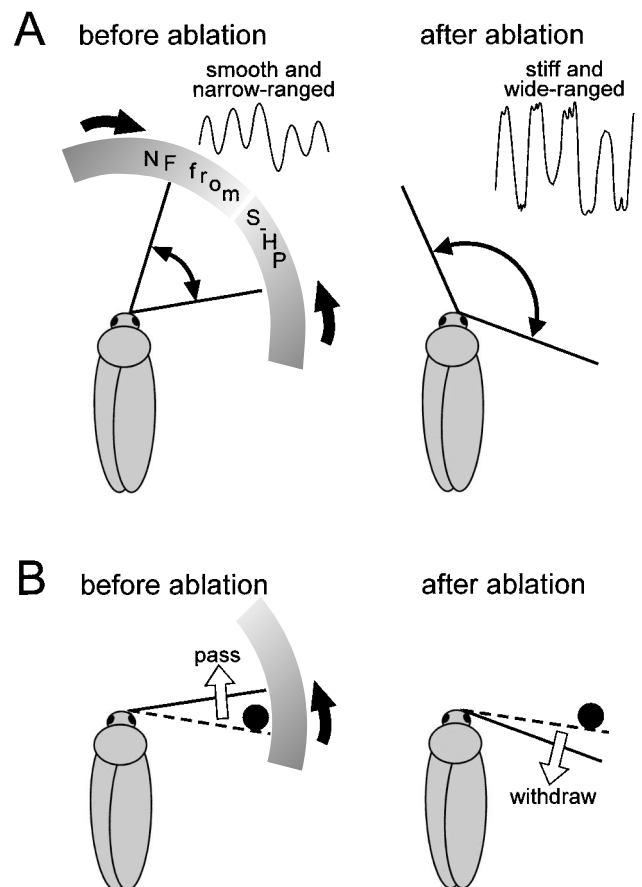

Fig. 7. Possible roles of the S-HP in horizontal antennal movements. **A**. Spontaneous movements of antenna before and after the S-HP ablation. Before the ablation, the antennal movement was smooth and narrow-ranged. The shaded arc indicates the negative feedback (NF) from the S-HP to the antennal motor system for horizontal movement, and the NF's strength is depicted by density. Thick arrows along the NF arc show direction of the force. After the ablation, the movements became stiff and wide-ranged. **B**. Effects of the S-HP ablation on the contact pattern. In tests at 90°, the I-P pattern, one of two major patterns before the ablation, was replaced by the I-W pattern after that. Broken lines; contacting antenna. Solid lines; leaving antenna. Filled circles; presented object. Open arrows; direction of antennal movement.

neurons have been shown physiologically in cockroaches (Pearson *et al.*, 1976) and locusts (Kuenzi and Burrows, 1995). Similar physiological studies on neural connections between the S-HP and the antennal motor neurons would confirm the presence of the putative feedback and give further understanding on the mechanosensory control of antennal movements in cockroaches.

The S-HP ablation affected the contact pattern of antenna in the test at 90°. Before the ablation, both the I-P and I-W patterns were present, but the I-P pattern was mostly replaced by the I-W pattern after the ablation (Fig. 7B). This change also could be explained by the negative feedback loop being more effective at a largely deflected position. Insect antennae, especially in the resting state, generally tend to withdraw right after contact with the object.

This reflexive movement, often called the avoidance reflex, may protect antennae from excessively intense stimuli (cf. Saager and Gewecke, 1989). But in a largely abducted position, the abducting force originating from the avoidance reflex probably gives way to the opposite adducting force from the S-HP feedback. If so, the antenna will pass and leave the object inwardly (Fig. 7B before ablation). On the other hand, when the force from S-HP was deprived by its ablation, the antenna may repeat the I-W pattern irrespective of its position due to the nature of avoidance reflex (Fig. 7B after ablation).

Intact antennae in the adduction (inward) movements tented to withdraw after contacts with the object at 45°, whereas in the abduction (outward) movements, antennae mostly passed the object at 45°. These I-W and O-P patterns were unchanged even after the S-HP ablation. The passing movement of antenna against external tactile stimuli is similar to the resistance reflex such as the antennal positioning behavior against air force during insect flight (cf. Saager and Gewecke, 1989). Thus, the mode of antennal reflex (avoidance/resistance) in searching cockroaches is phase-dependent. The phase-dependency would be attributable to the central program, but is so far completely unknown.

The present behavioral experimental system was rather unnatural because the presented tactile object was stationary in spite of animal's locomotion. However, this system made quantitative analyses possible, and consequently provided some suggestions about the mechanosensory control of antennal movements. The S-HP in *P. americana* has been described in our previous study as a mechanosensory organ involved in the tactile detection of an object's location by antennae (Okada and Toh, 2000). The present study focused on both the spontaneous and stimulated antennal movements, and examined contribution made by the S-HP. The hair plates in insects occur in various segments, and may give directional information about joint movements. Hair plates in legs and body joints function as gravity sensors in honeybees (Lindauer and Nedel, 1959; Thurm, 1963) and ants (Markl, 1962). The physiological role of hair plates in leg motor control was described in the case of the cockroach (Wong and Pearson, 1976; Pearson *et al.*, 1976) and the locust (Kuenzi and Burrows, 1995), and the behavioral role in the case of the stick insect (Wendler, 1966; Bässler, 1977). Hair plates in the neck of preying mantises are known to participate in distance estimation using "motion parallax" (Poteser *et al.*, 1998). These examples suggest that the reflex pathways from hair plates to motor systems play critical roles for the sensory and motor behaviors of insects.

Besides the S-HP, other mechanosensory organs, presumably monitoring antennal direction, are known in the pedicel of cockroaches, such as the chordotonal organ, the Johnston's organ, the campaniform sensilla and the hair plates (Toh, 1981; reviewed by Seelinger and Tobin, 1981). It is unlikely that these mechanoreceptors in the pedicel code the horizontal component of antennal position effectively because the pedicel moves in almost the vertical plane. However, the antenna could move horizontally by the combination of the free-moving neck and the vertically-moving pedicel, even if the head-scape joint were fixed. We always observe vigorous movements of both the head capsule and the pedicel during searching behavior. Further careful analyses for movements of all mobile parts (scape, pedicel and head capsule) may give clues as to whether mechanoreceptors in the pedicel and the neck participate in the coding of horizontal movements of antenna.

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