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# The Air-puff Evoked Escape Behavior of the Cricket *Gryllus bimaculatus* and its Compensational Recovery after Cercal Ablations

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**ABSTRACT**—The air-puff evoked escape behavior of the cricket, *Gryllus bimaculatus*, was investigated. Crickets almost always escaped away from the stimulus source. In an optimal condition, the mean escape direction was 162° opposite to the stimulus source. Stronger (higher velocity) air-puff elicited an escape in larger number of crickets. However, the escape direction became incorrect when the stimulus was too strong.

Crickets with bilateral cercal ablation did not show any escape to an air-puff, while unilaterally ablated ones did respond to the same stimulus with an escape. However, the response rate of animals with unilateral cercal ablation was lower than that in intact animals. Although the mean escape direction of the crickets with unilateral cercal ablation was still opposite to the stimulus source, the direction was not so accurate as in intact animals.

About 6 days after the unilateral cercal ablation, the response rate showed a statistically significant compensational recovery. On the other hand, 14 days were necessary for the recovery of the escape direction. Information which regulating the response rate and the behavioral orientation is likely being processed in different neural pathways.

## INTRODUCTION

The cercus to giant interneuron system of crickets and cockroaches are known to be responsible for mediating a wind-evoked escape behavior. Although the neural systems for eliciting the escape behavior are not completely identical in either animals, each has been used as a model system to explore the neural basis of insect behavior (Bentley, 1975; Camhi and Tom, 1978; Camhi *et al.*, 1978; Gras and Hörner, 1992; Hörner, 1992; Tauber and Camhi, 1995).

In the cockroach, *Periplaneta americana*, neurophysiological studies including sensory physiology of cercal filiform sensilla and directional characteristics of seven pairs of giant interneurons have revealed many significant aspects of sensory mechanisms of the neural system (e.g. Westin *et al.*, 1977; Westin, 1979; Vardi and Camhi, 1982a, b; Comer and Dowd, 1987; Volman and Camhi, 1988). Some of the studies were appropriately coupled with behavioral investigations and could clarify the role of the neural system for mediating the wind-evoked escape behavior. In crickets, physiological characteristics of cercal filiform sensilla and the organization of receptive fields of giant interneurons (GIs) have also been investigated by many researchers (Edwards and Palka, 1974;

Murphey *et al.*, 1976, 1977; Palka and Olberg, 1977; Matsumoto and Murphey, 1977; Tobias and Murphey, 1979; Levine and Murphey, 1980; Gnatzy and Tautz, 1980; Kanou and Shimosawa, 1984; Shimosawa and Kanou, 1984a, b; Jacobs *et al.*, 1986; Kanou *et al.*, 1988, 1989; Miller *et al.*, 1991; Kanou, 1991, 1996; Matsuura and Kanou, 1998a). In addition, it has also been clarified how the information of air disturbance was reflected to the motor outputs (Kanou and Shimosawa, 1985). However, in spite of accumulation of knowledges about physiological natures of constituting elements of the neural system, the number of behavioral study of the cricket escape was very limited (Tauber and Camhi, 1995; Gras and Hörner, 1992). The first aim of the present study was to add better documentation of quantitative aspects of wind-evoked escape behavior in crickets. We investigated the effect of air-puff velocity on the release of the escape behavior and the behavioral change right after the unilateral cercal ablation.

Furthermore, we focused on a plasticity of the wind-evoked escape behavior. A recent neurophysiological investigation revealed that some of the response properties of cricket GIs to an air current stimulus showed compensational recoveries after a unilateral cercal ablation (Matsuura and Kanou, 1998b). Such functional changes in the interneurons must be reflected in some way to the released behaviors. The second aim of the present study was to explore the compensational recoveries of the escape behavior after cercal ablations quan-

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tatively.

## MATERIALS AND METHODS

### Animals

Adult female crickets (*Gryllus bimaculatus*) 1 week after the imaginal molt were used. They were collected from a breeding colony in our laboratory. The temperature of the breeding room was kept at 28–30°C and the LD cycle was 12:12. All the experiments were performed during the subjective daytime. Details were the same as in the previous paper (Kanou, 1996).

### Experimental setup and air-puff stimulation

A floor of the test arena was a round cork board (40 cm in diameter) and was surrounded by a wall made of wire mesh (15 cm in height). Before the stimulation, a cricket was placed at the center of a test arena under an inverted semi-transparent cup. The cup was lifted up slowly just before delivering the stimulus air-puff. Only the insects stayed immobile before the stimulation was subjected to the further experiments. An air-puff stimulus was presented to the insect from a nozzle made of aluminum tube (10 mm in inner diameter) placed 18 cm away from the insect (Fig. 1). The nozzle was set on the floor so as the air to flow parallel to the surface of the floor of the test arena. The test arena was equipped with three stimulus nozzles placed at intervals of 120° (Fig. 1; nozzle A, B and C). In each trial, one of the nozzles was randomly chosen for delivering the air-puff stimulus in order to change the stimulus direction and to avoid the insects learning the nozzle position, if any. A stimulus air-puff was a jet of air made by an air-compressor (Hitachi, BEBICON 0.2OP-5S). The air was guided to the nozzle via a 2-port (CKD, USB3-6-2) and a 3-port (CKD, USG3-6-2) solenoid valves (Fig. 1). A 2-port solenoid valve (e.g. A1 in Fig. 1) was opened just before the stimulation. At this moment, the

air was vented out through a port of the 3-port solenoid valve (a dashed arrow from A2 in Fig. 1) installed posterior to the 2-port valve. Then, the air was guided to the intended nozzle (e.g. nozzle A in Fig. 1) by closing the vent and letting the air flow through the 3-port valve toward the nozzle (a solid arrow from A2 in Fig. 1). This procedure eliminated uncontrollable initial surge of the air current by the pressure build up behind the 2-port valve.

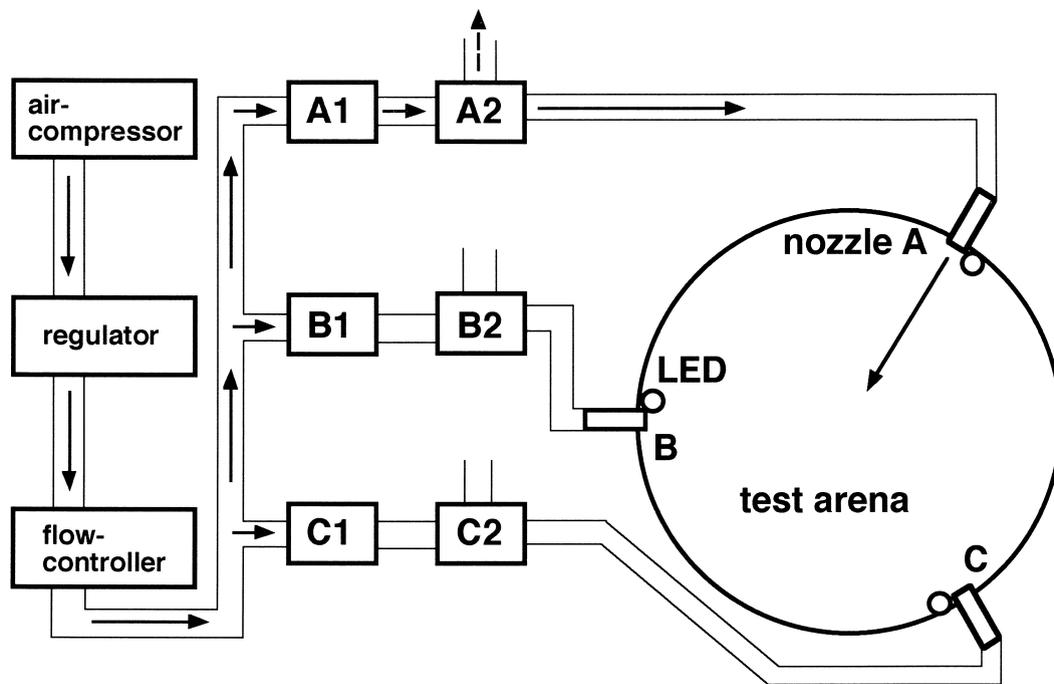
The stimulus duration, i.e. an opening time of the 3-port solenoid valve, was set by the duration of a rectangle electric pulse from an electric stimulator (Nihon Kohden, SEN-3201) applied to the valve. In the present study, the stimulus duration was 70 msec. The peak velocity of the stimulus air-puff was controlled by a flow-controller (KOFLOK, 2504FR). The velocity of the air-puff at the insect position (center of the test arena) was measured by a hot wire anemometer (Kanomax, 1010). In the present study, air-puffs with a peak velocity of 0.1, 0.9, 1.5, 3.0 and 3.9 m/sec were used.

The temperature of the experimental room was kept at 28–30°C.

### Analysis of the escape behavior

The behavioral response of a cricket to an air-puff was recorded with a video camera (SONY, AVC-D1) connected to a recorder (SONY, EVO-9500A), and later analyzed by displaying it on a CRT. An LED set above each nozzle (Fig. 1) was synchronously lightened with the air-puff in order to specify the used nozzle and the onset of the stimulus during the off-line analysis. The underneath of LED was covered with opaque tube to prevent the insects from seeing it.

In an earlier study of the wind-evoked cricket escape behavior, the responses were categorized into three groups, turn, jump and turn plus jump (Tauber and Camhi, 1995). In the present study, any body movement accompanied with at least one leg step was counted as a "response", and not categorized further. The main aim of the present study is to find the rate of response occurring and the direction of escape and does not necessitate any further classification of



**Fig. 1.** An experimental setup for the analysis of a wind-evoked escape behavior. The floor of the test arena was a round cork board and was surrounded by a fence made of wire mesh. A compressed air was guided to the stimulus nozzles set at the edge of the test arena via solenoid valves. The flow volume per a time was controlled by a flow-controller. A video camera was set right above the test arena. An LED set above each nozzle was synchronously lightened with the onset of an air-puff. A1, B1 and C1: 2-port solenoid valves. A2, B2 and C2: 3-port solenoid valves. See text for details.

responses; besides, the time resolution of our video recording system was not good enough to distinguish between the jump and the turn plus jump responses. Other types of responses such as a kicking (Dumpert and Gnatzy, 1977), a head stand (Gnatzy and Heißlein, 1986) or a cercal cleaning (Baba and Shimozawa, 1997) were not observed in the present investigation.

In the off-line analysis, the stimulus and the response angles (Fig. 2A, B) were measured on a CRT screen and were plotted (e.g. Figs. 2C, 3). A slope of a regression line of the plots was employed as an index to assess the mean escape direction. If crickets always escape toward  $180^\circ$  opposite direction from the air-puff, for example, the regression line will show a  $45^\circ$  slope ( $y = x$ ; Fig. 2C). A correlation coefficient ( $r$ ) was also employed to assess the consistency of the relation between stimulus and response angles.

### Sensory deprivation

In the experiment of sensory deprivation, a unilateral or a bilateral cercal ablation was done with a sharp razor blade. A cercus (or cerci) was (were) cut off at the base(s) with a special attention not to leave any mechanosensory filiform hairs. For the unilateral cercal ablation, the right side cercus was removed. In order to exclude the effect of surgical operation, the operated animals were rested for one day before starting the behavioral experiments. After the ablation, 5 or 6 crickets were reared together in a transparent polystyrene con-

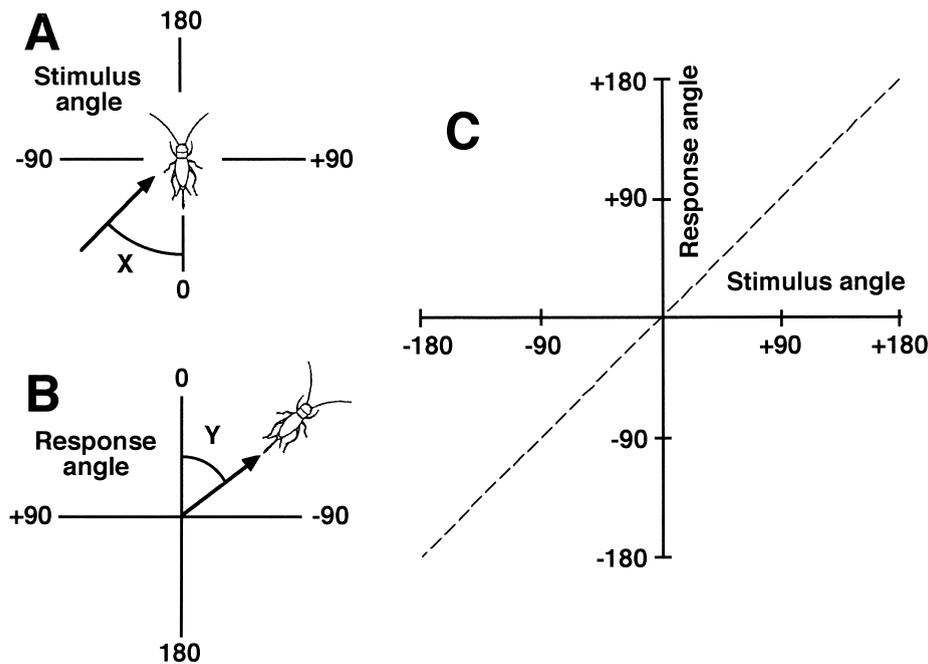
tainer ( $20 \times 20 \times 25$  cm).

In the cercal ablation experiment, a small amount of body fluid was inevitably lost from the wound. As the bleeding might affect the behavioral response, we investigated the effect by a sham operation. In order to deprive an almost equivalent volume of body fluid with those lost in a bilateral cercal ablation, a small cut was made on a pleural membrane of the 3rd or the 4th abdominal segment of a cricket with a razor blade. Until the 3rd day after the operation, the escape behavior of the treated animals were investigated every day. During the 3 days, the response rate and the directional properties of the escape (the slope of the regression line and the correlation coefficient) were almost identical with those in intact animals. The bleeding due to the cercal ablation, therefore, did not seem to have any effect in the escape behavior.

## RESULTS

### Effects of air-puff velocity

Escape behaviors were investigated by changing the peak velocity of the air-puff (0.1, 0.9, 1.5, 3.0 and 3.9 m/sec). In normal adults, the response rate became higher with the increase of the stimulus velocity (Table 1). The maximum re-



**Fig. 2.** Conventions for measuring stimulus (A) and response (B) angles. (C) a coordinate on which a response angle (ordinate) was plotted against the stimulus angle (abscissa). Dashed line ( $y=x$ ) is an ideal regression line when the averaged response direction was toward  $180^\circ$  opposite to the stimulus source.

**Table 1.** Effect of peak velocity of an air-puff on the escape behavior

Peak velocity of air-puff (m/sec)	Response rate (%)	Slope of regression line	Correlation coefficient ( $r$ )
0.1	0.7	—	—
0.9	1.3	—	—
1.5	6.0	0.92	0.88
3.0	51.3	0.89	0.89
3.9	56.0	0.69	0.81

Sample size at each peak velocity was 150 (6 crickets  $\times$  25 trials)

sponse rate obtained was 56% when the stimulus velocity was 3.9 m/sec (Table 1). At the stimulus velocities of 1.5 and 3.0 m/sec, most escapes were triggered to opposite to the stimulus direction, i.e. the slope of regression lines were 0.92 and 0.89 with the correlation coefficients of 0.88 and 0.89, respectively (Table 1: sample numbers at 0.1 and 0.9 m/sec stimulation were too small for the analysis because of the small response rates). However, at 3.9 m/sec, both the slope of a regression line and the correlation coefficient were smaller than those at 1.5 or 3.0 m/sec (Table 1), i.e. the sensory system could not encode the direction of an air-puff accurately when the stimulus was extremely strong (see DISCUSSION).

The 3.0 m/sec air-puff resulted in relatively high response rate and well oriented escapes. We used the 3.0 m/sec air-puff in all the following investigations as a "standard stimulus".

### The escape behavior of normal adult crickets

By using the standard stimulus, we investigated the escape behavior of normal adult crickets in larger number of animals. The response rate obtained from 9 groups of crickets was  $53.7 \pm 5.0\%$  (mean  $\pm$  SD). Each group consisted of more than 10 individuals and the total trial number in one group ranged from 76 to 384.

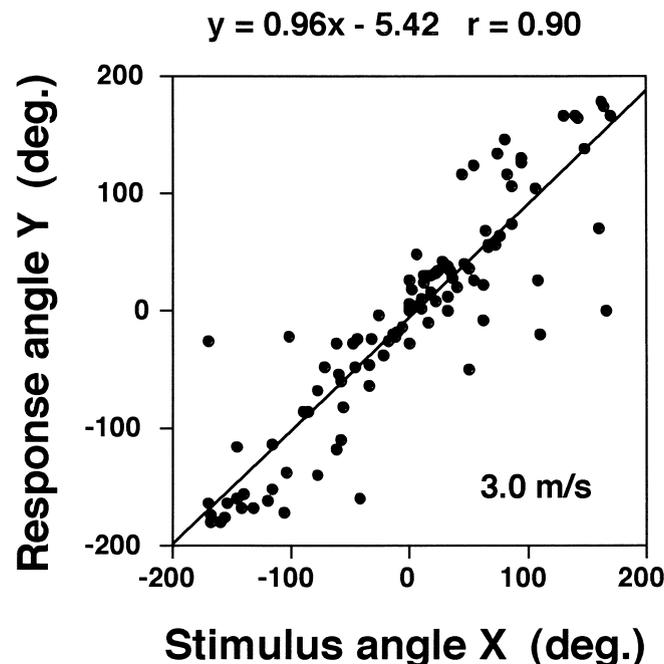
Directional characteristics of the escape were investigated in 7 groups of normal adults by using the standard stimulus (Table 2). The mean escape direction was toward  $162^\circ$  opposite to the stimulus source (the mean slope of the regression lines was 0.90) and the mean Y-intercept was -1.03. The mean correlation coefficient was 0.87. Thus, the cricket sensory system can detect the direction of the stimulus source accurately and the motor system is designed to make an escape away from the stimulus source.

Fig. 3 shows an example of the directions of stimulus vs.

**Table 2.** Directional characteristics of the escape behavior of normal adult crickets

Group	Slope of regression line	Y-intercept (deg.)	Correlation coefficient (r)	Number of samples
1	0.99	-1.01	0.94	145
2	0.89	-3.25	0.86	145
3	0.88	-5.72	0.84	115
4	0.91	-1.74	0.84	384
5	0.96	-5.24	0.90	93
6	0.79	+7.28	0.85	104
7	0.89	+2.63	0.89	76
Mean	0.90	-1.03	0.87	-

Each group contains more than 10 crickets.



**Fig. 3.** An example of directions of stimulus vs. response angles in normal adult crickets investigated with a standard air-puff (3.0 m/sec). The slope of the regression line (0.96) and the correlation coefficient ( $r = 0.90$ ) show that the escape is triggered to almost opposite direction from the stimulus source.

response angles of a group of crickets (group 5 in Table 2).

### Effects of cercal ablations

When both cerci were ablated (bilateral cercal ablation), the 46.0% response rate of a group of intact crickets dropped to 0% (Table 3). When one of a pair of cerci was ablated (unilateral cercal ablation), the 48.1% response rate in intact crickets dropped to 5.5% (Table 3). Although the response rate showed a significant decrease after the unilateral cercal ablation, the operated insects could still respond to an air-puff to some extent. These results again suggest that the inputs from mechanosensory filiform hairs on the cerci are responsible for the elicitation of an escape behavior as have been suggested in earlier studies (e.g. Bentley, 1975).

Directional characteristics of the escape were also investigated in a group of crickets after a unilateral (right side) cercal ablation. By the ablation, the response angles became small and were biased to the right side, i.e. the slope of the regression line changed from 0.82 (intact) to 0.72 and the Y-intercept changed from  $-2.6^\circ$  (intact) to  $-19.25^\circ$  (Table 3). Furthermore, the direction of escape showed a large variation after the ablation, i.e. the correlation coefficient changed from 0.85 (intact) to 0.80 (Table 3). Thus the number of incorrect escape increased after the unilateral cercal ablation.

Although the unilateral cercal ablation caused an increase of incorrect orientation, some escapes were still directed toward opposite to the stimulus source. Therefore, the input from filiform hairs on a single cercus is enough for the crickets to recognize the rough direction of an air current (see discussion).

### Behavioral recovery after cercal ablations

After a bilateral or a unilateral cercal ablation, the response rate, the slope of the regression line and the correlation coefficient were traced in order to explore the time course of a compensational recovery.

#### *Bilateral cercal ablation*

In case of bilateral cercal ablation, the 46.0% response rate of a group of intact crickets dropped to 0% as mentioned before (Table 3). The response rate was traced every 7 days until 29 days after the treatment. All the response rates obtained during the period were between 1 and 1.5%, i.e. no recovery was observed. As there was no regeneration of a cercus or cercal filiform hairs during the period, non-cercal

inputs are supposed to have no or only a minor role in the elicitation of an air-motion evoked escape behavior. The non-cercal neural pathway, if any, showed no compensational recovery after the cercal ablation.

#### *Unilateral cercal ablation*

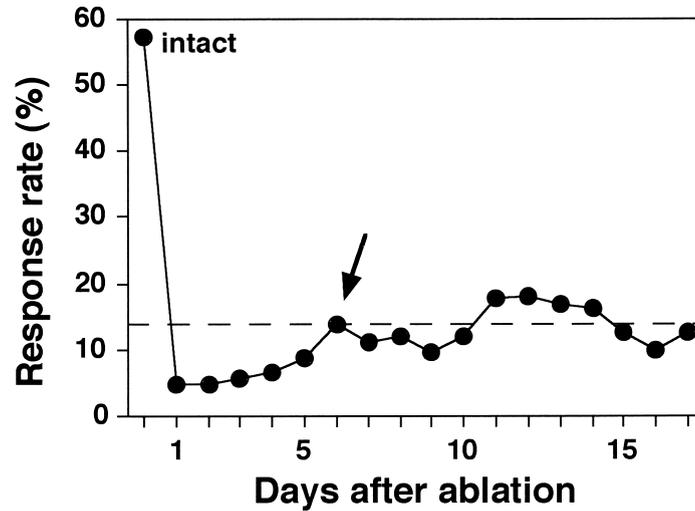
In case of unilateral cercal ablation, the 48.1% response rate of a group of intact crickets dropped to 5.5% as mentioned before (Table 3). We investigated the recovery time course of the response rate in another group of crickets. In the group, a 57.4% response rate dropped to 4.8% 1 day after the unilateral cercal ablation (Fig. 4). The response rate gradually became larger and showed a statistically significant recovery ( $P < 0.01$ ) on the 6th day after the ablation (Fig. 4, arrow). We traced the change in response rate until 29th day after the ablation. Although the response rate after the 6th day showed a small fluctuation (Fig. 4), all those measured during the 6th to 29th day were significantly higher than that of animals 1 day after the ablation. The response rate after the maximum recovery was, however, lower than that of intact animals (see discussion).

Directional characteristics of the escape were also investigated after a unilateral cercal ablation. Although the slope of the regression line occasionally showed normal values (i.e. similar to that in intact crickets) during the recovery period (e.g. 5th, 11th and 12th days in Fig. 5A), it fluctuated widely before the 14th day. After the 14th day, the slope of regression line has been fixed to almost identical with that in intact animals, and that was maintained until at least 29th day after the ablation (data are not shown). The correlation coefficients also occasionally showed normal values during the recovery period (e.g. 4th and 5th days; Fig. 5B). However, it fluctuated widely before the 10th day. After the 10th day, the correlation coefficient was fixed to almost identical with that in intact animals and was maintained until at least 29th day after the ablation. From these facts, it was revealed that at least 14 days were necessary for the complete correction of the escape direction.

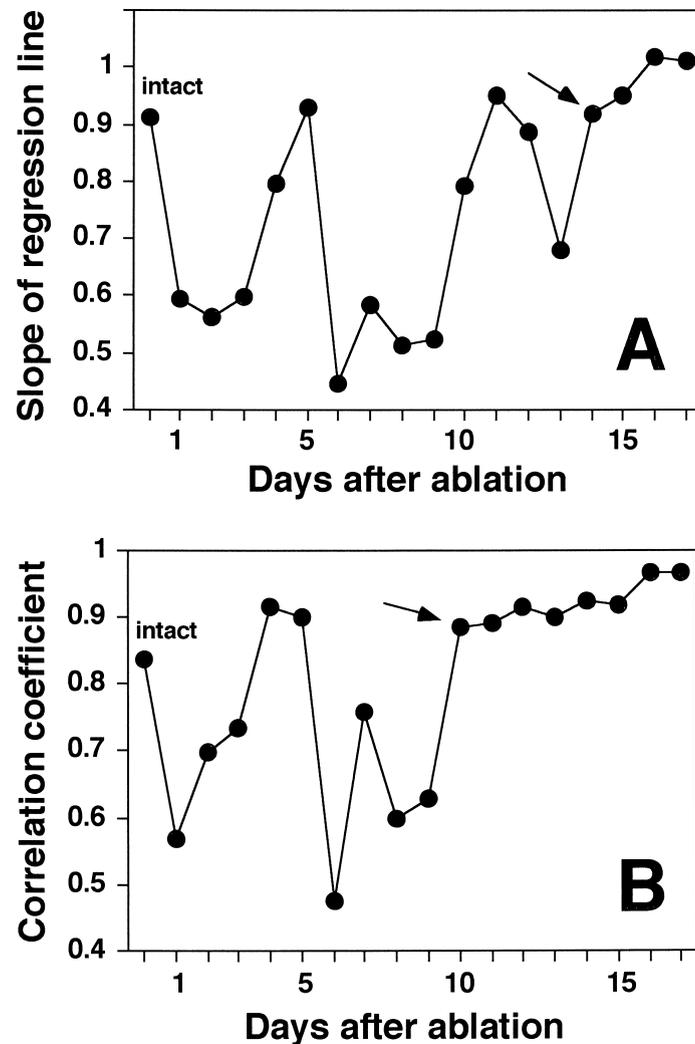
The Y-intercept of the regression line in animals 1 day after the ablation was  $-19.25^\circ$  as mentioned before (Table 3). It also showed changes with the laps of time, and those on the 8th, 15th, 22nd and 29th day were  $-9.56^\circ$ ,  $+9.80^\circ$ ,  $+8.14^\circ$  and  $-6.73^\circ$ , respectively (see DISCUSSION).

**Table 3.** Changes in the escape behavior after cercal ablations

	Response rate (%)	Slope of regression line	Y-intercept (deg.)	Correlation coefficient (r)	
Intact	46.0	48.1	0.82	-2.6	0.85
1 day after a bilateral cercal ablation	0	-	-	-	-
1 day after a unilateral cercal ablation	-	5.5	0.72	-19.25	0.80



**Fig. 4.** Changes in the response rate after unilateral cercal ablation. The response rate showed a large decrease just after the ablation (1st day). A statistically significant recovery ( $P < 0.01$ ) was first observed on the 6th day after the ablation (arrow).



**Fig. 5.** Changes in the slope of the regression line (A) and the correlation coefficient (B) measured after the unilateral (right side) cercal ablation. The slope of regression line became smaller just after the ablation and showed a fluctuation during the recovery period. It was fixed after the 14th day. The correlation coefficient also became smaller just after the ablation and showed a fluctuation. It was fixed after the 10th day. See text for details.

## DISCUSSION

### Sensory inputs for triggering the wind-evoked escape behavior

Ablation experiments revealed that the cercal input was essential to trigger the wind-evoked escape behavior of the cricket. However, we could not completely exclude the possibilities of other sensory inputs mediating the escape behavior because a small number of response to an air-puff was still observed even after the bilateral cercal ablation. Those responses were likely being mediated by the input from mechanoreceptors on the body surface other than cerci because it was carefully avoided to give any visual or chemical cues along with the air-puff. However, the role of such mechanoreceptors, if any, were considerably smaller than those in the cockroach, *Periplaneta americana*. In the cockroach, about 50% of wind-evoked escape behavior is triggered by the input from mechanoreceptors other than cercal filiform hairs (Stierle *et al.*, 1994). In the present experiments, the 46.0% response rate of a group of crickets dropped to 0% after the bilateral cercal ablation, and the response rate was 1 or 1.5% over the 29 days after the ablation. In an preliminary investigation, we once observed that a 58.1% response rate dropped to 4.5% after the bilateral cercal ablation (data are not shown). Therefore, the contribution of mechanoreceptor other than cercal filiform hairs for triggering the escape behavior seems less than 10% ( $< 4.5/58.1$ ) in *Gryllus*, if any.

In terms of response eliciting, the degree of contribution of filiform hairs on a single cercus of crickets was largely different from that in cockroaches. In crickets, the 57.4% response rate in intact animals dropped to 4.8% after the unilateral cercal ablation, and was about 15% even after a maximum recovery (Fig. 4). This suggests that, for the elicitation of a cricket escape, a contribution of inputs from filiform hairs on a single cercus is rather small. In intact crickets, therefore, the inputs from filiform hairs on one cercus must work facilitatively in combination with the inputs from filiform hairs on the other cercus. In case of the cockroach, *Periplaneta americana*, the response rate to a 1.8 m/sec air-puff was 96.9% when the air-puff was applied from the left side and 98.4% from the right side. After the left cercus ablation, the response rate was 81.6% when the air-puff was presented from the left side and 85.7% from the right side (Comer and Dowd, 1987). The contribution of mechanical inputs other than cercal inputs is relatively large in the cockroaches as mentioned above, and the effect of unilateral cercal ablation on the elicitation of escape behavior is rather small when compared to that of crickets. This suggests that, in terms of response eliciting, contribution of sensory inputs from a single cercus in cockroaches is larger than that in crickets.

### Effects of air-puff velocity on the escape behavior

The response rate and the directional characteristics of the wind-evoked escape behavior changed according to the change of the stimulus velocity. An air-puff with higher peak velocity resulted in a higher response rate (Table 1). How-

ever, the strongest air-puff used in the present study resulted in a larger number of incorrect orientation in the escape (Table 1).

The wind sensitive cercal filiform hairs have their own directionality (Edwards and Palka, 1974; Bacon and Murphey, 1984), and at least 8 classes of filiform hairs with different directionality have been reported in *Acheta* (Landolfi and Jacobs, 1995). Such a directional property of sensory apparatus must be a basis for the cricket neural system to encode the direction of air-motion accurately (Kanou, 1991, 1996; Matsuura and Kanou, 1998a). Therefore, an irregular motion of cercal filiform hairs must be a main reason for the incorrect orientation in the escape. In an experiment using a tone stimulus, Gnatzy and Tautz (1980) observed that the directional hairs began to make irregular vibrations under an extremely strong stimulus condition. The main reason of the irregular vibration must be a disagreement of the preferential plane of hairs and the direction of stimulus air-motion. In addition to this reason, a turbulence in the air-puff might be another reason for the increase of incorrect orientation observed in the present study. Although we did not make a detailed investigation of air-particle motion in the puff used in the present study, an air-puff might basically cause a traveling air vortex ring as is produced during the wing flicks of a cricket (Heinzel and Dambach, 1987), because the profile of the air-motion in a puff might be more similar to that of an air pushed by flicking wings rather than that of continuous flow. One difference is that our air-puff slides the surface of the floor and a perfect vortex ring may not be generated. According to Heinzel and Dambach (1987), the critical Reynolds number between a stable vortex ring and a turbulence was 1,600 for a large wing pair and 1,333 for a small wing pair. The Reynolds numbers of the air-puff used in the present study were 949, 1897 and 2467 for 1.5, 3.0 and 3.9 m/sec stimulation, respectively. We are not sure if a comparison of Reynolds number is available for estimating the similarity of air-motion because it is difficult to compare the values when the definition of characteristic length and speed are different (Heinzel and Dambach, 1987). However, turbulence might possibly take place at the 3.9 m/sec air-puff because of the extremely large Reynolds number, i.e. 2467.

### Directional characteristics of the escape behavior

Normal intact crickets showed a highly directional escape to an air-puff. The sensory-to-motor system of the cricket is designed to make an escape further away from the stimulus source. The system must ensure a high survival rate for crickets from attacks of their predators. Such a behavioral directionality must be underlain by distinctive directional sensitivities of GIs (GIs 8-1, 9-1, 9-2, 9-3, 10-2 and 10-3) (Tobias and Murphey, 1979; Miller *et al.*, 1991; Kanou, 1991, 1996; Matsuura and Kanou, 1998a).

In the present study, we have revealed that a cricket could still make a directional escape even right after the ablation of one of a pair of cerci (Table 3). Our previous electrophysiological study revealed that the response magnitude of GIs

(GIs 8-1, 9-1, 9-2 and 9-3) to an air current stimulus was largely affected by a unilateral cercal ablation, however, the most sensitive directions of some GIs were still identical with those in intact animals even after the ablation (Matsuura and Kanou, 1998a). Therefore, the high preservation of a behavioral directionality must be supported by such directional characteristics of such GIs. Although the orientation of the escape was not so accurate as in intact animals, such a mechanism must be essential for crickets to survive because an injury on sensory apparatus must frequently occur in natural environments.

### Behavioral compensation after a unilateral cercal ablation

The response rate showed a statistically significant recovery 6 days after the unilateral cercal ablation. However, the response rate was still lower than that in intact animals even after a maximum recovery (Fig. 4). It suggests that the response rate is basically regulated by the total amount of sensory input or the number of filiform hairs. On the other hand, unlike response rate, the direction of escape expressed with the slope of regression line was almost perfectly compensated 14 days after the unilateral cercal ablation (Fig. 5A). The time course of the compensation of behavioral direction seems rather short when compared to that in cockroaches. In adult cockroaches, *Periplaneta americana*, the turning direction was not perfectly compensated even 49 days after a unilateral cercal ablation (Vardi and Camhi, 1982a).

Although the Y-intercept of the regression line measured 15 days after the ablation ( $+9.80^\circ$ ) was slightly larger than that in intact animals (mean =  $-1.03^\circ$ , varied from  $-5.72^\circ$  to  $+7.28^\circ$ ; Table 2), the difference between those in the 15th-day animals ( $+9.80^\circ$ ) and the nearest one in the intact animals ( $+7.28^\circ$ ) was only  $2.52^\circ$ . The Y-intercept during the recovery period showed an irregular fluctuation, i.e. those on the 8th, 15th, 22nd and 29th day were  $-9.56^\circ$ ,  $+9.80^\circ$ ,  $+8.14^\circ$  and  $-6.73^\circ$ , respectively. The large absolute values of the Y-intercept in the early period are likely due to small correlation coefficients, i.e. large variations in the escape direction. Therefore, we were not sure whether the escape direction of the crickets 15 days after the right cercus ablation were really biased to the right side or not. However, as the absolute value of the Y-intercept of the treated animals gradually became small, the change might show one aspect of the recovery rather than a simple variation. If it is true, a longer period might be necessary for the compensational recovery of the escape direction than we have assumed.

As we used adult crickets in the present study, there was no cercal hair regeneration after cercal ablations. However, it has been revealed that some of the GIs in adult crickets showed compensational functional changes after a unilateral cercal ablation (Matsuura and Kanou, 1998b). Therefore, the behavioral compensations were likely to be caused by functional changes occurred somewhere in the neural circuit rather than a reinnervation of newly emerged sensory afferents with postsynaptic neurons. Probably, changes in a synaptic strength between particular cercal filiform hairs on the remained cer-

cus and some GIs caused functional changes of the GIs and resulted in the behavioral compensations.

The information regulating the response occurring and the escape direction must be processed independently and in parallel because there was a large difference between the recovery time course of them. In other words, they are likely being processed in different neural circuits. As a longer period was needed for the compensational change of the escape direction, it can be speculated that the neural circuit dealing the information to determine the direction of the escape must be more complicated than that of triggering the escape.

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