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Source: Zoological Science, 21(1) : 7-14

Published By: Zoological Society of Japan

URL: [https://doi.org/10.2108/0289-0003\(2004\)21\[7:FCOCGI\]2.0.CO;2](https://doi.org/10.2108/0289-0003(2004)21[7:FCOCGI]2.0.CO;2)

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# Functional Changes of Cricket Giant Interneurons Caused by Chronic Unilateral Cercal Ablation during Postembryonic Development

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**ABSTRACT**—One of a pair of cerci was ablated in the first-, fourth- and last-instar nymphs of the cricket, *Gryllus bimaculatus*. The insects were then reared until the final molt, after which the intensity-response (I-R) relationships for four giant interneurons (GIs) 8-1, 9-1, 9-2 and 9-3 with regard to a controlled air current stimulus were measured. In order to examine the functional changes during postembryonic development and the differences in the physiological plasticity of GIs between nymphs and adults, the obtained I-R curves for each GI were compared with those measured in intact and unilaterally cercus-ablated adult crickets. Each GI showed a distinctive change in response magnitudes after the long-term unilateral cercal ablation. In most cases, the I-R curves for each GI in the crickets ablated from nymphal periods were different from those in the adult crickets mentioned above. Moreover, the pattern of change in response magnitude was different from GI to GI. In contrast to these observations, it was reported that some important characteristics of the wind-evoked escape behavior such as relative occurrence and escape direction in unilaterally cercus-ablated crickets investigated after a long-term rearing were almost identical with those in intact crickets. Therefore, the results obtained in the present study suggest that functional changes occur not only in GIs but also in many other neural elements in the escape-eliciting system in order to maintain the features of wind-evoked escape behavior.

**Key words:** cricket, escape behavior, giant interneuron, compensation, plasticity

## INTRODUCTION

In natural environments, animals sometimes suffer from damage to their sensory apparatus. This is highly disadvantageous for the animals because they occasionally carry out incorrect behavior due to the misunderstanding of sensory information. Therefore, most animals compensate the evoked behavior in some other ways. Such behavioral compensation must be supported by changes that occur somewhere in the neural system. The plasticity of the neural system is therefore essential for animals to survive in changing environments.

Crickets exhibit escape behavior in response to an air disturbance stimulus (Gras and Hörner, 1992; Tauber and Camhi, 1995; Baba and Shimozawa, 1997; Kanou *et al.*,

1999, 2001). Air motion is first detected by a number of fili-form hairs on their cerci; a pair of appendages at the abdominal tip (Edwards and Palka, 1974; Bentley, 1975; Shimozawa and Kanou, 1984a, b), and then the information of air motion is integrated by some GIs (Murphey *et al.*, 1977; Kanou and Shimozawa, 1984; Miller *et al.*, 1991). These GIs carry the information of air motion to other parts of the body, and play an important role in eliciting escape behavior (Kanou and Shimozawa, 1984, 1985). After a unilateral cercal ablation, adult crickets, *Gryllus bimaculatus*, show compensational changes in their escape behavior (Kanou *et al.*, 1999, 2001, 2002). Some functional changes that occur in the GIs after the unilateral cercal ablation (Murphey and Levine, 1980; Levine and Murphey, 1980; Matsuura and Kanou, 1998b) are supposed to be the basis of behavioral compensations.

The aim of the present study was to investigate how the plasticity of the cercal sensory system changes during postembryonic development. Crickets are hemimetabolous insects and, similarly to adults, their nymphs also have cerci

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with filiform hairs (Kanou *et al.*, 1988). The nymphs also show wind-evoked escape behavior (Kanou *et al.*, 2001). Therefore, crickets are suited for studying the change in the plasticity of a neural network during postembryonic development.

## MATERIALS AND METHODS

### Animals

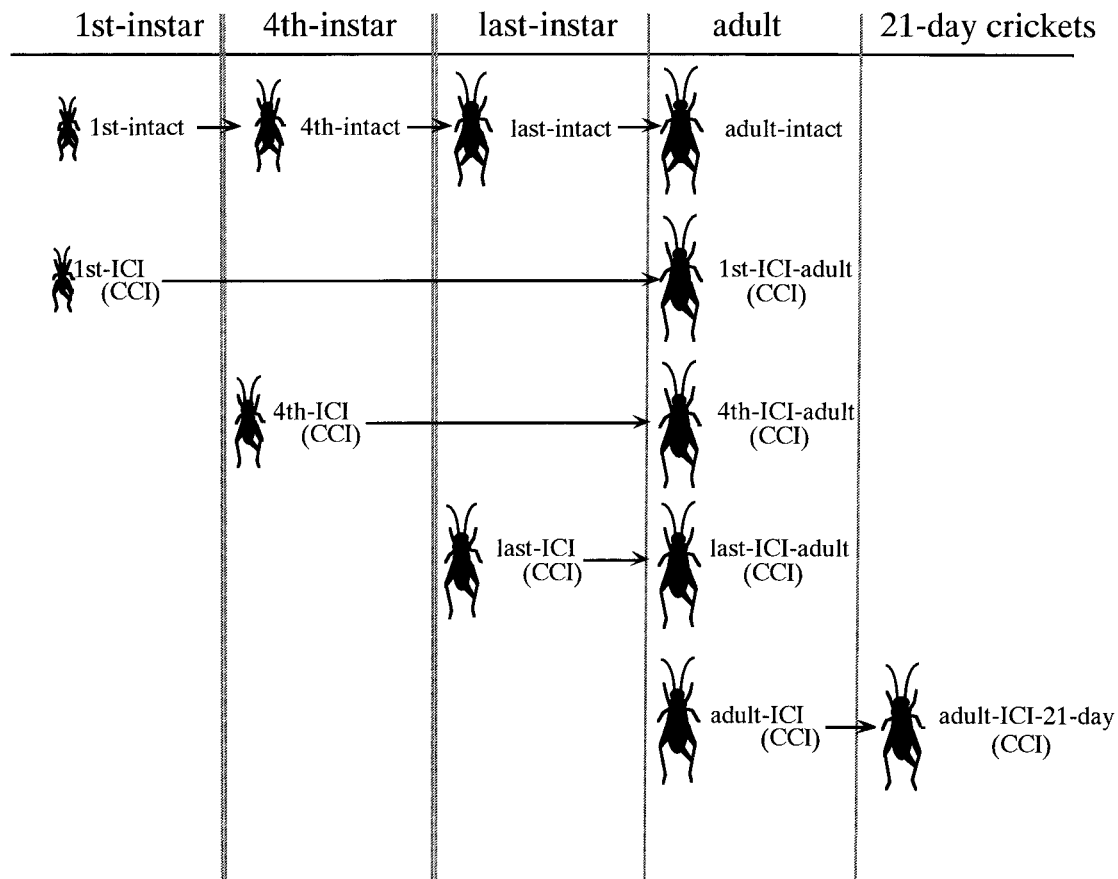
Both sexes of the first-, fourth- and last-instar crickets of *Gryllus bimaculatus* were used. The insects were collected from our culture room. The temperature of the culture room was 28–30°C and the light/dark cycle was 12/12 hr. Details of insect culture were the same as in our previous study (Kanou, 1996).

### Sensory deprivation

In cricket nymphs, one of a pair of cerci was ablated from its basal part with a sharp razor blade. Particular attention was paid to not leaving any mechanosensory filiform hairs. During the ablation, the insects were immobilized under low-temperature anesthesia when necessary. Five or six surgically ablated crickets were reared

together in a transparent polystyrene container (20cm×20cm×25cm). They were reared to maturity and the response properties of GIs were investigated after the final molt. A regenerating cercus that emerged at each molt was removed within 24 hr following the molt.

As the ventral nerve cords that contain GIs' axons are on the contralateral side of their somata, we defined "ipsilateral" or "contralateral" with reference to the side of axons. As in our previous papers (Matsuura and Kanou, 1998a, b), we called contralateral cercus-ablated crickets as ICI (ipsilateral cercus intact) crickets, whereas ipsilateral cercus-ablated crickets were called CCI (contralateral cercus intact) crickets. In the present paper, for example, we called intact fourth-instar crickets as "fourth-intact" crickets and those that had a contralateral cercal ablation as "fourth-ICI" crickets. Furthermore, we called a cricket whose contralateral cercus was unilaterally ablated at the first-instar stage and reared until the final molt as a "first-ICI-adult" cricket, whereas a cricket whose ipsilateral cercus was ablated at the fourth-instar stage and reared to maturity was called a "fourth-CCI-adult" cricket. We previously reported the response properties of GIs in adult crickets measured 21-days after a unilateral cercal ablation (Matsuura and Kanou, 1998b), and in that paper, such crickets were called 21-day ICI or 21-day CCI



**Fig. 1.** A schematic summarizing the experimental schedules and the nomenclature of crickets used in the present study. For the first-instar cricket, a neural recording could not be conducted because of the small body size and only a unilateral cercal ablation was carried out. The unilaterally cercus-ablated first-instar crickets (first-ICI or first-CCI) were reared until the final molt, and then the response properties of GIs were measured (first-ICI-adult and first-CCI-adult). In the fourth-instar, last-instar and adult intact crickets, the response magnitudes of GIs were measured (fourth-intact, last-intact and adult-intact crickets; Matsuura and Kanou, 2003). After the contralateral cercal ablation (fourth-ICI, last-ICI and adult-ICI) or ipsilateral cercal ablation (fourth-CCI, last-CCI and adult-CCI), the response properties of GIs were also measured (Matsuura and Kanou, 2003). The unilaterally cercus-ablated crickets were reared until the final molt or 21 days after the ablation, and then the response properties of GIs were measured (fourth-ICI-adult, last-ICI-adult, adult-ICI-21-day, fourth-CCI-adult, last-CCI-adult and adult-CCI-21-day crickets).

crickets. In the present paper, however, we call such crickets as adult-ICI-21-day or adult-CCI-21-day crickets by applying the same nomenclatural procedure for other crickets. Details of the experimental schedules and the nomenclature of crickets used are summarized in Fig. 1.

#### Air current stimulus and neural recording from GlIs

An air current stimulus was applied to an insect in a wind tunnel consisting of a pair of push-pull-driven loud speakers (Kanou and Shimozawa, 1984; Kanou, 1991, 1996; Matsuura and Kanou, 1998a, b, 2003). The speakers were moved by an electric signal of one-half cycle of a 50Hz cosine wave so as to generate a unidirectional air current in the tunnel. The speakers were placed in the furthest position for 500 msec and then returned to the initial position. In the present study, an air current stimulus was applied parallel to the body axis of the insects, that is, from the anterior (0°) and/or from the posterior (180°). Each GI investigated in the present study shows a characteristic directional sensitivity (Kanou, 1996). Therefore, in the present study, we should have applied an air puff from the preferred direction of a GI. However, we could not determine the appropriate stimulus direction during the experiment because we could not identify the GI only from its physiological nature at the time of intracellular recording. Therefore, in the present study, we applied the air puff from 0° and 180° directions as the second-best method. The stimulus intensity (peak velocity of the air current) ranged from 0.095 to 300 mm/sec. Details of the stimulus equipment, including the calibration procedures, were the same as those in our previous papers (Kanou and Shimozawa, 1984; Kanou, 1991, 1996; Matsuura and Kanou, 1998a, b, 2003).

At each stimulus velocity (0.095, 0.3, 0.95, 3, 9.5, 30, 95 or 300 mm/sec), the response magnitude of a particular GI was intracellularly recorded from axons in the connective immediately anterior to the terminal abdominal ganglion (TAG), and I-R curves were obtained. GlIs investigated were GI 8-1 (medial giant interneuron; MGI), GI 9-1 (lateral giant interneuron; LGI), GI 9-2 and GI 9-3. Response magnitudes of the GlIs were measured by applying an air current stimulus only from an excitatory receptive field or fields in the wind tunnel, that is, GlIs 8-1, 9-1 and 9-2 were investigated only in ICI crickets exposed to 0° and 180° air current stimuli, whereas GI 9-3 was investigated in both ICI and CCI crickets exposed to a 0° air current stimulus (Matsuura and Kanou, 1998a). All of the differences in response magnitudes were statistically analyzed by a t-test. As the figures would be complicated if we add symbols or error bars suggesting significances for all the cases, such significances will be stated only in the text when necessary. Details of the neural recording, including the intracellular staining, are the same as those in our previous paper (Matsuura and Kanou, 2003).

## RESULTS

As shown in our previous study (Matsuura and Kanou, 2003), the response magnitudes of GlIs in intact crickets change during development to some extent. Therefore, the effects of unilateral cercal ablation carried out in nymphal periods were assessed by comparing the response magnitudes of a GI measured in the first-, fourth- or last-ICI (CCI)-adult crickets with those measured in adult-intact, adult-ICI and adult-CCI crickets. In some cases, the response magnitudes were also compared with those in adult-ICI (CCI)-21-day crickets in order to investigate the difference in the functional change between nymphs and adults.

#### GI 8-1 (MGI)

As mentioned above, the response magnitudes of GI

8-1 change during development, that is, GI 8-1 in younger nymphs shows larger response magnitudes. Namely, response magnitudes of GI 8-1 gradually decrease during the development (Fig. 2A, B, D, E; Matsuura and Kanou, 2003).

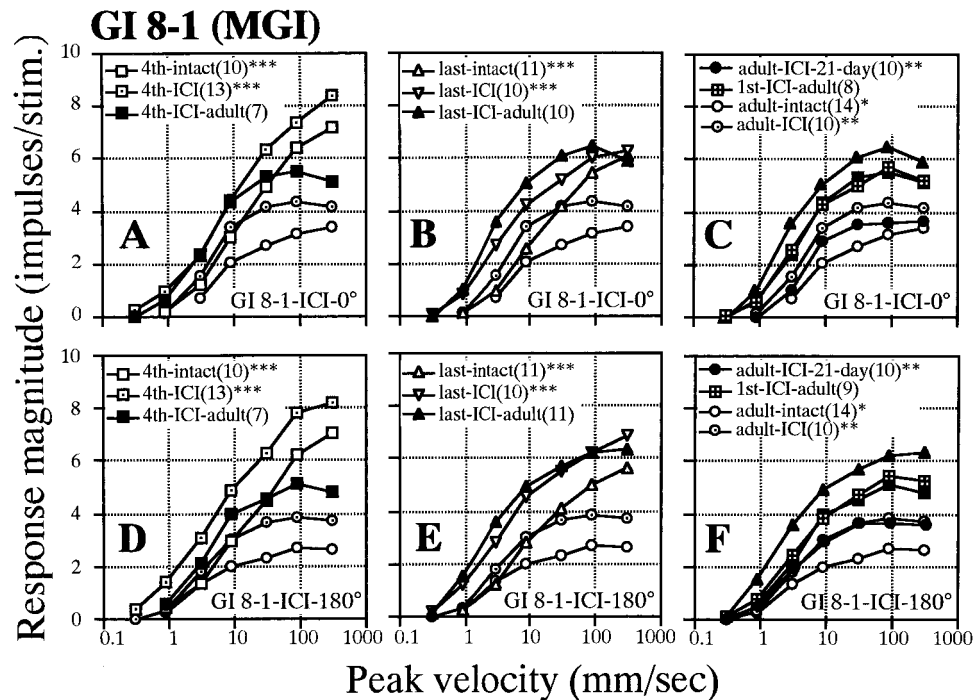
The response magnitudes of GI 8-1 in the first-, fourth- and last-ICI-adult crickets were larger than those in adult-ICI and adult-intact crickets in both stimulus directions (Fig. 2C, F). The response magnitudes of GI 8-1 in the last-ICI-adult crickets were significantly larger than those in the adult-ICI crickets ( $p < 0.05$ ). However, the response magnitudes of GI 8-1 in the first- and fourth-ICI-adult crickets were not significantly different from those in the adult-ICI crickets except for higher velocity air currents from the 180° direction in the first-ICI-adult crickets (Fig. 2C, F). Therefore, the degree of the compensational change in the response magnitude of GI 8-1 after the contralateral cercal ablation seems to depend on the duration of the ablation period to some extent.

All the response magnitudes of GI 8-1 in the first-, fourth- and last-ICI-adult crickets were also different from those in adult-ICI-21-day crickets. Although the response magnitudes in the adult-ICI-21-day crickets were similar to (0°) or smaller than (180°) those in adult-ICI crickets, those in the first-, fourth- and last-ICI-adult crickets were larger than those in adult-ICI crickets (Fig. 2C, F). Therefore, the pattern of the change in response magnitudes after contralateral cercal ablation was different between nymphs and adults.

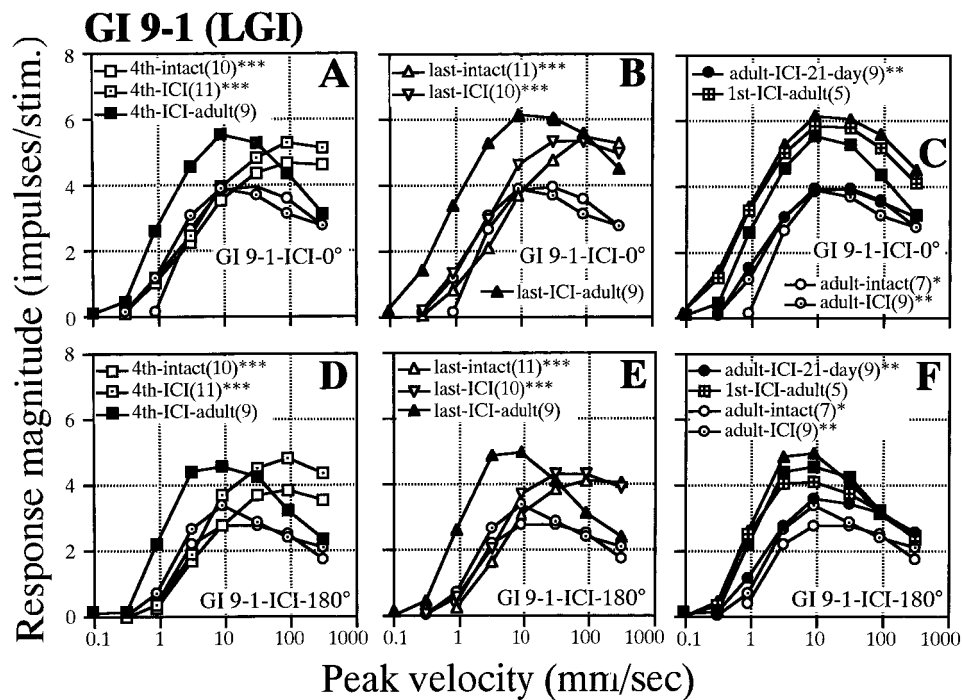
#### GI 9-1 (LGI)

In the fourth- and last-intact crickets, the response magnitudes of GI 9-1 were much larger than those in the adult-intact crickets when the stimulus velocities were higher than 95 mm/sec for the air current from the anterior (0°) and higher than 30 mm/sec for the air current from the posterior (180°). Thus, the response magnitudes of the GI in intact crickets change markedly at the final molt (Fig. 3A, B, D, E; Matsuura and Kanou, 2003). In both stimulus directions, the response magnitudes of GI 9-1 in the fourth-intact and the last-intact crickets showed no significant differences from those in the fourth-ICI and the last-ICI crickets, respectively (Fig. 3A, B, D, E; Matsuura and Kanou, 2003). Therefore, as in adult crickets (Matsuura and Kanou, 1998a), no functional connection exists between GI 9-1 in nymphs and filiform hairs, which are sensitive to the air currents coming from the 0° or 180° direction, on the contralateral cercus.

The response magnitudes of GI 9-1 in the fourth- and last-ICI-adult crickets were considerably larger than those in the adult-ICI or adult-intact crickets (Fig. 3A, B, D, E). Therefore, although there was no functional connection between GI 9-1 and some filiform hairs on the contralateral cercus as mentioned above, the absence of contralateral inputs affects the synaptic rearrangement between sensory afferents and the GI at the time of molt. However, the peaks of the response magnitudes of GI 9-1 in the fourth- and last-ICI-adult crickets were still at the same stimulus velocity as



**Fig. 2.** I-R curves for GI 8-1 measured in intact and ICI crickets with respect to the anterior (A, B, C) or the posterior (D, E, F) direction of air current stimulus. After a contralateral cercal ablation, the response magnitudes increased in all cases. The response magnitudes of this GI in the last-ICI-adult crickets were significantly different from those in adult-ICI crickets, whereas those in the first- and fourth-ICI-adult crickets were not. Numbers of crickets used for the measurements are in parentheses after the symbols. \*: data from Kanou, 1996. \*\*: data from Matsuura and Kanou, 1998b. \*\*\*: data from Matsuura and Kanou, 2003. Symbols are common to all figures. See text for details.



**Fig. 3.** I-R curves for GI 9-1 measured in intact and ICI crickets with respect to the anterior (A, B, C) or the posterior (D, E, F) direction of air current stimulus. In both adults and nymphs, a contralateral cercal ablation caused almost no change in the response magnitude. The response magnitudes of this GI in intact crickets showed a marked change at the final molt. However, those in the crickets that had a unilateral cercal ablation at the nymphal period showed a more marked change at the final molt. See legends of Fig. 2 for other explanations. See text for details.

those in adult-intact and adult-ICI crickets, that is, approximately 10 mm/sec. Therefore, the contralateral cercal ablation affects only the sensitivity but not the basic I-R characteristics of the GI. In the first-ICI-adult crickets, the response magnitudes of GI 9-1 were also larger than those in the adult-ICI crickets and were similar to those in the fourth- and last-ICI-adult crickets. There was no significant difference in the response magnitude of GI 9-1 among the first-, fourth- and last-ICI-adult crickets (Fig. 3C, F). Therefore, the duration of the contralateral cercal ablation during postembryonic development did not affect the response magnitude of GI 9-1 after the final molt.

At low stimulus velocities, most response magnitudes of GI 9-1 in the first-, fourth- and last-ICI-adult crickets were larger than those in adult-ICI-21-day crickets in both stimulus directions. At high stimulus velocities, the response magnitudes were relatively similar to each other when the air currents were from the posterior (180°) and only the response magnitudes in the fourth-ICI-adult crickets were similar to those in adult-ICI-21-day crickets when the air currents were from the anterior (0°).

#### GI 9-2

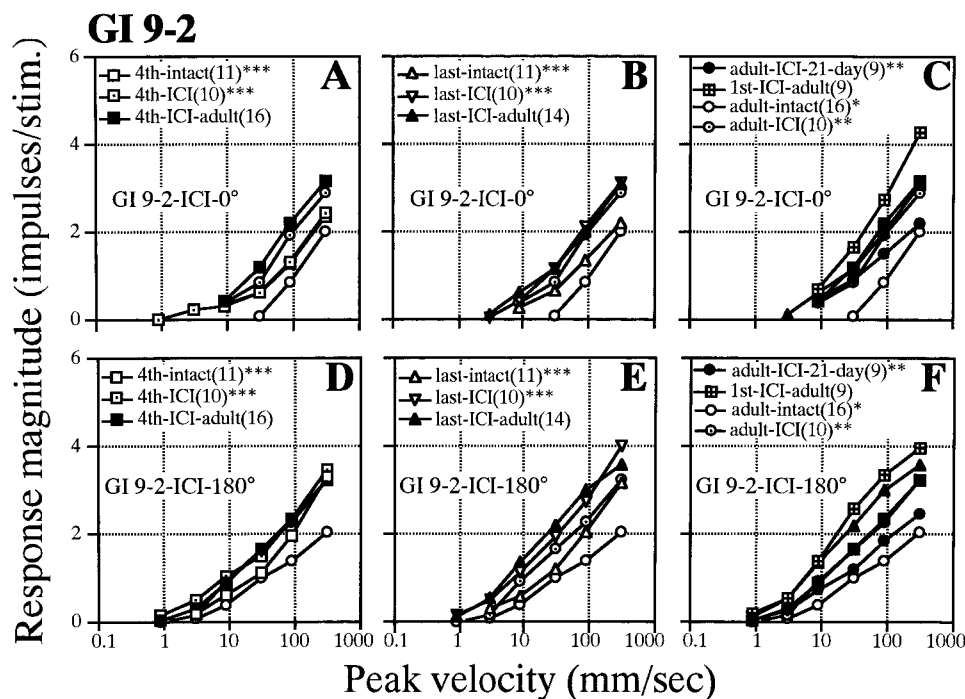
In the fourth- and last-intact crickets, the response magnitudes of GI 9-2 were slightly larger than those in adult-intact crickets in both stimulus directions (Fig. 4A, B, D, E). After the contralateral cercal ablation, the response magnitudes of this GI in the last-instar crickets, that is, in the last-ICI crickets, increased significantly in both stimulus direc-

tions ( $p < 0.05$ ; Fig. 4B, E), whereas almost no change was observed in the response magnitudes in the fourth-ICI crickets (Fig. 4A, D; Matsuura and Kanou, 2003; see discussion).

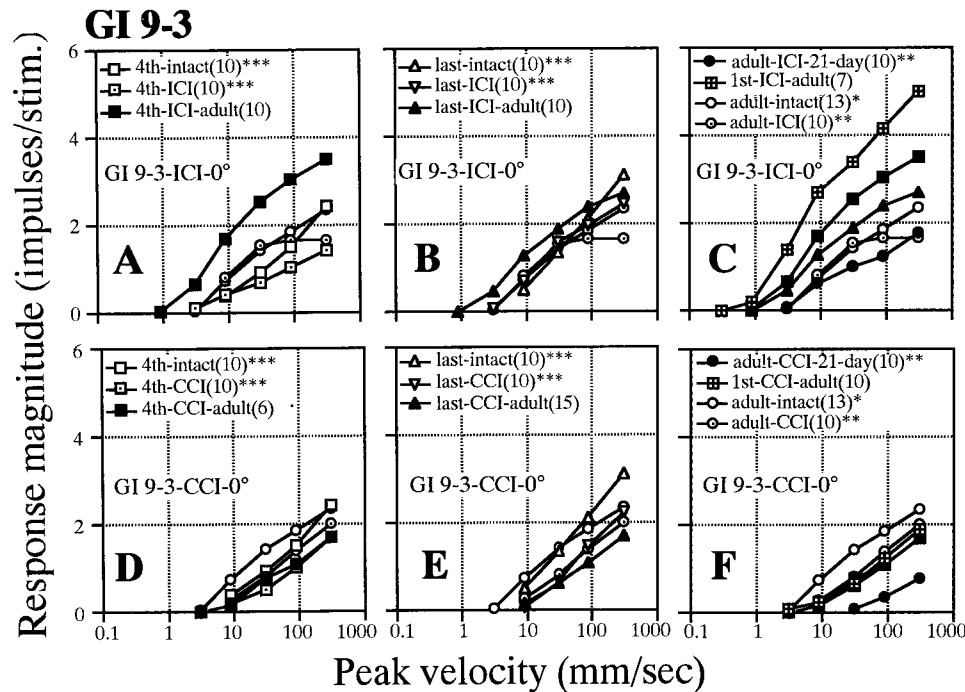
The response magnitudes of GI 9-2 in the fourth- and last-ICI-adult crickets were almost the same as those in the adult-ICI and adult-ICI-21-day crickets, and were slightly larger than those in adult-intact crickets (Fig. 4C, F). However, the response magnitudes of GI 9-2 in the first-ICI-adult crickets were significantly larger than those in adult-ICI crickets in both stimulus directions, particularly at high velocities (Fig. 4C, F). Therefore, the degree of change seems to depend on the duration after the contralateral cercal ablation as observed in GI 8-1. However, unlike GI 8-1, the response magnitudes of GI 9-2 in the first-ICI-adult crickets were larger than those in other crickets.

#### GI 9-3

The response magnitudes of GI 9-3 in the adult-ICI crickets were significantly smaller than those in the adult-intact crickets only at the highest air current velocity; 300 mm/sec (Matsuura and Kanou, 1998a). Similarly to this, only at high air current velocities that the response magnitudes of GI 9-3 in the last- and fourth-ICI crickets were significantly smaller ( $p < 0.05$ ) than those in the last- and fourth-intact crickets, respectively (Fig. 5A, B; Matsuura and Kanou, 2003). These results suggest that the sensory afferents from the contralateral cercus provide excitatory inputs to GI 9-3 and are connected to relatively short cercal filiform hairs (Shimozawa and Kanou, 1984a, b) throughout the development.



**Fig. 4.** I-R curves for GI 9-2 measured in intact and ICI crickets with respect to the anterior (A, B, C) or the posterior (D, E, F) direction of air current stimulus. The response magnitudes of this GI in the first-ICI-adult crickets were significantly larger than those in adult-ICI crickets in both stimulus directions. See legends of Fig. 2 for other explanations. See text for details.



**Fig. 5.** I-R curves for GI 9-3 measured in intact, ICI (A, B, C) and CCI (D, E, F) crickets with respect to the anterior direction of air current stimulus. The response magnitudes of this GI in the fourth-ICI-adult crickets were significantly larger than those in adult-ICI crickets, whereas those in the last-ICI-adult crickets were not. Note that the response magnitudes measured after the final molt depend on the duration of the ablation period in ICI crickets. The response magnitudes of this GI in the first-, fourth and last-CCI-adult crickets were almost the same as those in adult-CCI crickets. Therefore, the timing of the ipsilateral cercal ablation during development did not affect the response magnitude of this GI. See legends of Fig. 2 for other explanations. See text for details.

The response magnitudes of GI 9-3 in the last-ICI-adult crickets were significantly larger than those in the adult-ICI crickets only when the stimulus velocities were 3, 95 and 300 mm/sec ( $p < 0.05$ ) and no significant difference in response magnitude was ascertained at 9.5 and 30 mm/sec (Fig. 5B). However, in the fourth-ICI-adult crickets, the response magnitudes were significantly larger ( $p < 0.05$ ) than those in the adult-ICI crickets at all air current velocities tested (Fig. 5A). In the first-ICI-adult crickets, the response magnitudes of GI 9-3 were much larger than those in the last- and fourth-ICI-adult crickets (Fig. 5C). Therefore, the response magnitudes of GI 9-3 in contralateral-cercus-ablated crickets clearly depend on the duration of the ablation period, that is, the crickets that had the ablation for a longer period showed larger response magnitudes and vice versa (Fig. 5C).

The response magnitudes of GI 9-3 in the last-CCI crickets were significantly smaller ( $p < 0.01$ ) than those in the last-intact crickets at all air current velocities (Fig. 5E) and those in the fourth-CCI crickets were significantly smaller than those in the fourth-intact crickets at the 300 mm/sec air current (Fig. 5D). These results suggest that, as in adults (Matsuura and Kanou, 1998a), the sensory inputs from filiform hairs on the ipsilateral cercus are also excitatory in nymphal periods (Matsuura and Kanou, 2003). In the first-, fourth- and last-CCI-adult crickets, the response magnitudes of GI 9-3 were not significantly different ( $p > 0.05$ ) from those

in the adult-CCI crickets (Fig. 5F). Thus, different from the ablation of contralateral cercus, the timing of the ipsilateral cercal ablation during development did not affect at all the response magnitude of GI 9-3 after the final molt. Therefore, the attenuation of the excitability of GI 9-3 in CCI crickets was obvious only in the adult-CCI-21-day crickets (Matsuura and Kanou, 1998b).

## DISCUSSION

Each GI showed a characteristic functional change after a long-term unilateral cercal ablation during postembryonic development. Their I-R curves measured after the final molt were generally different from those for crickets who had the same unilateral cercal ablation after the final molt (adult-ICI or adult-CCI crickets). This suggests that the absence of contralateral or ipsilateral cercal inputs during development affects the synaptic rearrangement between the remaining sensory neurons of cercal filiform hairs and GIs in most cases. Furthermore, the response magnitudes of GIs in the first-, fourth- and last-ICI (CCI)-adult crickets were also different from those in adult-ICI (CCI)-21-day crickets. Therefore, the pattern of functional change occurring after the unilateral cercal ablation was completely different between nymphs and adults. The major factor underlying this difference between nymphs and adults is whether they will still undergo further molting or not. In insects, some modifica-

tions of the sensory system such as the regeneration of lost sensilla and reinnervation of sensory neurons to postsynaptic neurons generally occur at the time of molt. Therefore, it is likely that the pattern of change differs according to the number of remaining molts.

Even under similar experimental conditions, the pattern of functional change after the unilateral cercal ablation was different from GI to GI. For example, GIs 8-1 and 9-2 receive inhibitory inputs from filiform hairs on the contralateral cercus throughout the development, that is, the ablation of a contralateral cercus resulted in an increase in response magnitude in both adults and nymphs (Matsuura and Kanou, 1998b, 2003). However, the pattern of change in the response magnitude after the contralateral cercal ablation was completely different from each other. In GI 8-1, the response magnitudes of the first- and fourth-ICI-adult crickets were not significantly different from those in adult-ICI crickets, but those in the last-ICI-adult crickets were much larger than those in adult-ICI crickets. Probably, it is due to the shortest time before the final molt in the last-instar crickets or a slow change at a late stage of development (Murphey, 1986). Therefore, the functional change of GI 8-1 seems compensational and the degree of compensation depends to some extent on the duration of the contralateral cercal ablation. In GI 9-2, on the other hand, the change in the response magnitude was not compensational, that is, the response magnitudes of the first-ICI-adult crickets were the largest compared with those in other crickets. Such a difference might partially be caused by the difference in the pattern of change in the efficacies of ipsilateral excitatory and contralateral inhibitory inputs in these GIs (Matsuura and Kanou, 2003). In GI 8-1, the efficacy of ipsilateral excitatory inputs substantially decreases but that of the contralateral inhibitory inputs slightly decreases during development. On the other hand, in GI 9-2, the efficacy of ipsilateral excitatory inputs is almost constant and that of the contralateral inhibitory inputs gradually increases, that is, the efficacy of the inhibition is weak in early-stage nymphs. This is the reason that inhibitory inputs from the contralateral cercus are weak in the fourth-instar nymphs and the ablation of the contralateral cercus had almost no effect on the response magnitude of GI 9-2 (Fig. 4A, D).

As in adult crickets (Matsuura and Kanou, 1998a), the unilateral ablation of a contralateral cercus in nymphs did not cause any change in the I-R curves for GI 9-1 (Fig. 3A, B, D, E). However, the response magnitudes of GI 9-1 in the cercus-ablated crickets showed a marked change after the final molt (fourth- and last-ICI-adult crickets; Fig. 3A, B, D, E). This seems contradictory because, as in adult crickets, the ineffectiveness of the contralateral cercal ablation against the response properties of GI 9-1 must be due to the absence of excitatory or inhibitory connections with filiform hairs, which are sensitive to air currents from the anterior ( $0^\circ$ ) or the posterior ( $180^\circ$ ) directions on the contralateral cercus (Matsuura and Kanou, 1998a). Therefore, the results obtained in the present study suggest that the ablation of the

contralateral cercus affects the synaptic rearrangement between ipsilateral filiform sensory neurons and GI 9-1, and causes the changes in the response magnitude of GI 9-1, although the contralateral inputs themselves did not directly affect the response magnitude of this GI. Although a marked change in the response magnitude of GI 9-1 at the final molt was also observed in intact crickets, that is, the response magnitudes at high stimulus velocities decreased significantly (Fig. 3A, B, D, E), the change must be caused by the weakening of excitatory connection with relatively short filiform hairs (Shimozawa and Kanou, 1984a, b) on the ipsilateral cercus. The change could not be caused by the formation of new inhibitory connections because no inhibitory connection between GI 9-1 and filiform hairs sensitive to  $0^\circ$  and  $180^\circ$  air currents was ascertained (Matsuura and Kanou, 1998a). In the case of ICI crickets, however, another change likely occurs in addition to the weakening because the response magnitudes of GI 9-1 in the first-, fourth- and last-ICI-adult crickets were much larger than those in adult-ICI and adult-intact crickets. In GI 9-1, weak excitatory or inhibitory connections with filiform hairs on the contralateral cercus, which were sensitive to the air currents other than those from the  $0^\circ$  or  $180^\circ$  directions, were ascertained (Matsuura and Kanou, 1998a). We, therefore, suppose that the contralateral cercal ablation resulted in a degeneration of such contralateral sensory neurons and formation of a space on the dendrites of GI 9-1 for ipsilateral excitatory sensory neurons to form new synaptic connections. Such a synaptic competition (Wiesel and Hubel, 1963; Hubel *et al.*, 1977) was ascertained also in the cricket cercal system, that is, when some neurons are destroyed and degenerated, remaining neurons extend their axonal arbors to deafferented regions and form contacts with postsynaptic neurons (Murphey, 1986; Shepherd and Murphey, 1986).

In both ICI and CCI cricket nymphs, the response magnitudes of GI 9-3 to the anterior air current ( $0^\circ$ ) were slightly smaller than those before the ablation (Fig. 5A, B, D, E). This suggests that GI 9-3 in nymphs also has excitatory connections with filiform hairs on both ipsilateral and contralateral cerci as in adult crickets (Matsuura and Kanou, 1998a). In ICI crickets, such a decrease in response magnitude was obvious particularly at high stimulus velocities. Therefore, the filiform hairs on the contralateral cercus those have a connection with GI 9-3 are supposed to be relatively short ones (Shimozawa and Kanou, 1984a, b). In ICI crickets, the effect of unilateral cercal ablation depended on the duration of the ablation period, that is, GI 9-3 of a cricket that had a longer period of ablation showed larger response magnitudes (Fig. 5C). In CCI crickets, on the other hand, the pattern of change in response magnitude was completely different from that in ICI crickets. The response magnitudes of GI 9-3 in the first-, fourth- and last-CCI-adult crickets were almost the same as those in adult-CCI crickets (Fig. 5F). Therefore, in contrast to the contralateral cercal inputs, the absence of ipsilateral cercal inputs during development did not affect the response magnitudes of this GI. These results



suggest that, although the ipsilateral and contralateral inputs are excitatorily connected to GI 9-3, both are completely different in physiological nature. Moreover, the pattern of change in response magnitude of GI 9-3 observed in 21-day adults was also different between ICI and CCI crickets. In contrast to the nymphal period, the response magnitudes of this GI 9-3 in the adult-ICI-21-day crickets were almost the same as those in adult-ICI crickets. In CCI crickets, on the other hand, the change, that is, the weakening of the response magnitudes, was obvious only when the ablation of ipsilateral cercus was carried out after the final molt; adult-CCI-21-day crickets (Fig. 5F; Matsuura and Kanou, 1998b). Thus, the pattern of change in response magnitude of this GI after the unilateral cercal ablation showed differences between nymphs and adults, and between ipsilateral and contralateral cercal inputs.

Behavioral investigations in our previous study revealed that some important characteristics of a wind-evoked escape behavior such as relative occurrence and escape direction in unilaterally cercus-ablated crickets showed marked recovery when a cricket experienced a long period of ablation during postembryonic development (Kanou *et al.*, 2001). For example, both the occurrence and the escape direction of a cricket that had a unilateral cercal ablation from the first-instar stage were very similar to those of adult-intact crickets (Kanou *et al.*, 2001). However, in all of the GIs investigated in the present study, the response magnitudes in the first-ICI-adult and first-CCI-adult crickets were different from those in adult-intact crickets. These results suggest that in order to maintain identical properties of the wind-evoked escape behavior, functional changes occur not only in GIs but also in many other neural elements in the escape-eliciting system of a cricket.

## ACKNOWLEDGEMENTS

This work was partially supported by grants from the Japan Society for the Promotion of Science and the Japanese Ministry of Education, Culture, Sports, Science and Technology.

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(Received June 18, 2003 / Accepted October 3, 2003)