Compensation of Escape Direction in Unilaterally Cercus-ablated Crickets, Gryllus bimaculatus, is Associated with the Distance Walked during Recovery Period

Authors: Kanou, Masamichi, and Kondoh, Yusuke

Source: Zoological Science, 21(9) : 933-939

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.21.933

ZOOLOGICAL SCIENCE **21**: 933–939 (2004)

Compensation of Escape Direction in Unilaterally Cercus-ablated Crickets, *Gryllus bimaculatus,* is Associated with the Distance Walked during Recovery Period

Masamichi Kanou* and Yusuke Kondoh

Department of Biology and Earth Sciences, Faculty of Science,
Ehime University, Matsuyama 790-8577, Japan

ABSTRACT—In response to an air puff stimulus, intact crickets, *Gryllus bimaculatus,* make an escape almost 180° opposite to the stimulus source. In order to verify our previous hypothesis that a self-stimulation of the wind-sensory system is necessary for a compensational recovery of the escape direction (behavioral compensation) in unilaterally cercus-ablated crickets, we investigated the relationship between the conditions of rearing after a unilateral cercal ablation and the degree of behavioral compensation. A unilaterally cercus-ablated cricket reared in a large cage to permit free locomotion showed a significantly higher degree of recovery of escape direction compared with those reared under restrained conditions in a small glass vial. However, the degree of behavioral compensation in a cricket reared alone in a large cage was smaller than that of crickets reared in a cage of the same size with 5–6 other cercus-ablated crickets. Mutual stimulation possibly increased the extent of locomotion of crickets reared in a group and improved the degree of compensational recovery of the escape direction. To ascertain this, the distance a cricket moved during the recovery period was associated with the degree of compensational change of the escape direction. The result suggests that the degree of compensation of the escape direction clearly depended on the distance walked by the crickets. The compensation seemed not to be caused by other factors such as chemical ones in the case of group rearing because forced locomotion induced by touch stimulation on the body surface was solely effective in improving the escape direction.

Key words: cricket, escape behavior, compensation, recovery, plasticity

INTRODUCTION

A cricket makes an escape in response to an air puff stimulus. A pair of appendages called cerci at the abdominal end and mechanosensitive filiform hairs on them are responsible for the wind-evoked escape behavior (Bentley, 1975). As giant interneurons (GIs) in the ventral nerve cord integrate the wind information and play a significant role in escape elicitation, the physiological properties of the cercus-to-GI system were investigated by many researchers (Murphey and Palka, 1974; Murphey *et al*., 1977; Tobias and Murphey, 1979; Kanou and Shimozawa, 1984; Shimozawa and Kanou, 1984a, b; Miller *et al*., 1991; Kanou, 1991, 1996; Matsuura and Kanou, 1998a, b). In spite of these large numbers of neurophysiological investigations, behavioral investigations of the wind-evoked escape of crickets were very limited (e.g., Gras and Hörner, 1992).

We previously observed some notable features of the wind-evoked escape behavior of the cricket*, Gryllus bimaculatus* (Kanou *et al*., 1999, 2001, 2002). The escape direction of an intact cricket is accurately oriented to the opposite direction of the stimulus source. However, the number of misoriented escapes increases after a unilateral cercal ablation. Such a misoriented escape of a unilaterally cercus-ablated cricket is corrected or recovered almost 14 days after the ablation. The behavioral compensation does not occur when the cricket is reared under restrained conditions in which free walking is inhibited.

As in crickets, cockroaches also have cerci and cercal filiform hairs, and show the wind-evoked escape behavior (Camhi and Tom, 1978; Camhi *et al*., 1978; Volman and Camhi, 1988). A similar result to that in crickets was reported regarding the compensational recovery of the wind-evoked escape system of the cockroach, *Periplaneta americana* (Vardi and Camhi, 1982a, b). The study showed that the housing of cockroach nymphs in small plastic cups prevented the compensational recovery of their escape turn after unilateral cercal ablation. Therefore, a common mech-

---

* Corresponding author: Tel. +81-89-927-9631;
FAX. +81-89-927-9631.
E-mail: kanou@mserv.sci.ehime-u.ac.jp

anism for the compensation of the escape direction likely exists in crickets and cockroaches.

On the basis of the results of behavioral investigations, we previously proposed a hypothesis that the stimulation of filiform hairs on the remaining cercus by a self-generated wind caused by walking was necessary for the compensation of the escape direction in unilaterally cercus-ablated crickets. As the insects can know the direction and velocity of only such type of wind, that is opposite to the walking direction and has the same velocity with the walking, the cricket CNS can estimate the responses of some wind-sensitive interneurons such as giant interneurons (GIs) during walking (Kanou *et al.*, 2002). In the hypothesis, we assumed that an efference copy signal (Holst and Mittelstaedt, 1950, 1973) of walking has an important role when the cricket CNS estimated the responses of some interneurons. By comparing the predicted response of a particular interneuron during walking with an actual response of it, the cricket CNS can recognize the defect of its sensory system because there must be some differences between them. An error signal derived from the difference between the predicted and the actual responses is likely used to modify the physiological properties of GIs (Kanou *et al.*, 2002). Such a modification is required to occur repeatedly because almost two weeks is necessary for the compensation of the escape direction (Kanou *et al.*, 1999). In order to verify the hypothesis, we are now carrying out a neurophysiological investigation to identify the neurons that carry the efference copy signal from the motor center to terminal abdominal ganglion (TAG).

In the present study, on the other hand, we attempted to obtain evidence that validates our hypothesis by behavioral investigations. If the hypothesis is true, that is, repeated self-stimulations are essential for the compensation of the escape direction, the degree of behavioral compensation must depend on the amount of locomotion during the recovery period. That is, a unilaterally cercus-ablated cricket with a larger amount of locomotion during the recovery period must show a larger degree of compensation in the escape direction. In order to explore this, we investigated the adequate conditions of rearing required for the better compensational recovery after unilateral cercal ablation. We also measured the total distance a cricket walked during the recovery period and related it to the degree of compensation. The results showed the validity of our hypothesis, that is the total distance walked significantly correlated with the degree of the compensation of the escape direction.

MATERIALS AND METHODS

Animals

Adult female crickets, *Gryllus bimaculatus*, 1–2 weeks after their imaginal molt, were used. They were collected from a breeding colony maintained in our laboratory. The temperature of the culture room was maintained at 29±1°C and the LD cycle was 12:12. Details were the same as those in previous studies (Kanou *et al.*, 2002; Matsuura and Kanou, 2003).

Cercal ablation and cricket rearing

Under a low-temperature anesthetization, the right cercus of a cricket was removed from a stump with a razor blade. Particular attention was paid to not leaving any wind-sensitive filiform hairs. Such cercus-ablated crickets were reared in a 280×210×230 (W×D×H, in mm) polystyrene cage for 14 days (Kanou *et al.*, 1999) under the following conditions. One cercus-ablated cricket was reared alone in a cage; that is, "1/cage-reared". Five or six cercus-ablated crickets were reared together in a cage; that is, "group/cage-reared". Other rearing conditions will be explained in the text when necessary.

Behavioral experiments

An air puff stimulus was delivered to a cricket from a nozzle made of aluminum tube (10 mm in inner diameter). The air puff was a jet of air produced by an air compressor (HITACHI, BEBICON 0.2OP-5S). The peak velocity of the air puff at the position of a cricket was 3.0 m/sec and the duration that a solenoid valve permitted the flow of the air was 70 msec (Kanou *et al.*, 1999).

The air puff-evoked escape was recorded on videotape with a video recorder (SONY, EVO-9500A). The stimulus and response angles were measured on a CRT screen using conventions shown in Fig. 1. These angles were plotted and the regression line and the correlation coefficient were calculated after a number of trials in order to express the averaged escape direction of a group of crickets (e.g., Fig. 3). Escape directions of two groups of crickets were compared as follows. First, the regression lines were compared by their error variance (F-test), slope of regression line (i.e. regression coefficient; t-test) and y-intercept (t-test). The regression lines of the two groups were assessed to be different when one of the three parameters showed a significant difference. Next, the significant difference between the correlation coefficients of the groups was investigated (z-test). The escape directions of the two groups were assessed to be identical when both the regression line and the correlation coefficient showed no significant difference.

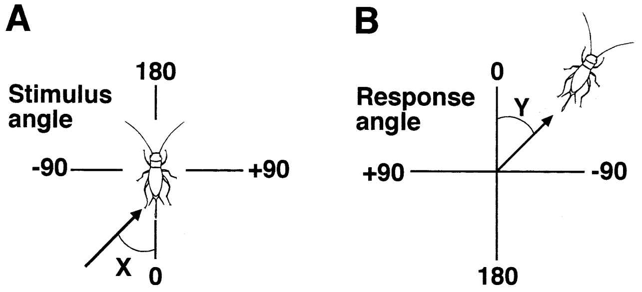

Fig. 1. Conventions for measuring stimulus (A) and response (B) angles.

In normal intact crickets, their escape direction was almost 180° opposite to the stimulus source. Therefore, the slope of regression line and the correlation coefficient were very close to one, and the y-intercept was very close to zero. After a unilateral cercal ablation, the slope of the regression line and the correlation coefficient became small, and the absolute value of the y-intercept became large (Kanou *et al.*, 1999). Details about the stimulating method and most of the procedures of the behavioral analysis were the same as those in our previous studies (Kanou *et al.*, 1999, 2002).

Measuring the amount of locomotion of a cricket

To estimate the amount of locomotion during the recovery period, the distance walked by a unilaterally cercus-ablated cricket

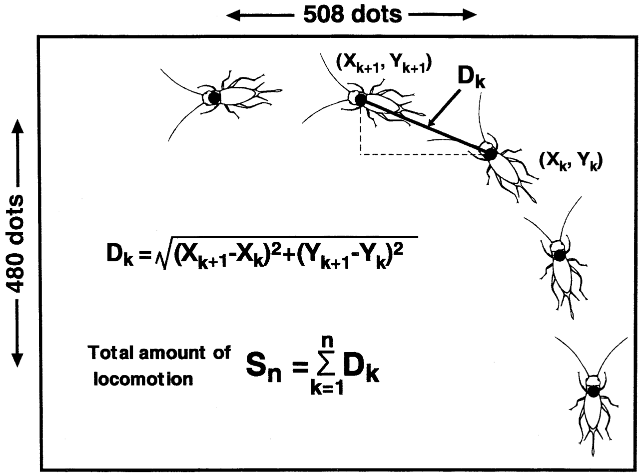

Fig. 2. Measurement of the amount of locomotion. The position of a cricket was recorded by an image sensor every 1.5 sec and the coordinates of their positions were stored in PC. The distance between successive two points was calculated using a trigonometric function and all the distances were summed in order to calculate the total distance that a cricket moved in one day (24 hours). The position of a cricket was recorded on a matrix of 508×480 dots of an image sensor. The resolution of the image sensor employed was between 0.3 and 1 mm.

was measured with an image sensor (KEYENCE, CV-700). In the measurement, the position of a cricket was recorded every 1.5 sec in one day (24 hours) and the coordinates of the position were stored in a personal computer (PC). The total distance walked in 24 hours was then obtained by sequentially calculating the distance from a position to the next position using a trigonometric function, and summing all the distances (Fig. 2). To reduce the effect of illumination (see below), this 24-hour measurement was carried out three times during the 14-day recovery period, i.e. on the second, seventh and twelfth day after unilateral cercal ablation. The average distance the cricket walked in one day was calculated from the 3-day data. The value obtained by multiplying 14 by the average distance (for 14 days of the recovery period) was denoted as the "total amount of locomotion" of the cricket.

The image sensor records the position of an object on the matrix of 508×480 coordinates (Fig. 2). Therefore, we could change the resolution of the sensor by changing the magnification or distance of camera from the object. We used the image sensor at a sufficient resolution of between 0.3 and 1 mm. The image sensor could trace eight objects simultaneously. Therefore, we could measure the locomotion of all crickets simultaneously even during the "group/cage-reared" experiment. However, the system could not record the position of a target in total darkness. Therefore, the insects were illuminated with the minimum necessary light, that was 60 lux, during the measurement of locomotion.

RESULTS

Behavioral compensation of 1/cage-reared crickets

Our previous study has revealed the following features of the compensation of a wind-evoked escape behavior of a cricket after unilateral cercal ablation (Kanou *et al.*, 2002). A unilaterally cercus-ablated cricket reared under restrained conditions in a small vial (hereafter 1/vial-reared crickets) showed no compensational recovery even after two weeks of rearing. Long time restriction in the vial itself did not affect the escape direction and ambient air motion from outside was not essential for the compensation. Therefore, it was evident that a space for walking was necessary for the compensation of the escape direction in the unilaterally cercus-ablated crickets.

To confirm the previous results, we reared a unilaterally cercus-ablated cricket in a large cage (1/cage-reared crickets) to permit free locomotion. In 1/cage-reared crickets, the slope of the regression line and the correlation coefficient measured 14 days after the ablation were y=0.66x+4.2 and 0.76, respectively (Fig. 3), whereas those in 1/vial-reared crickets reported in the previous study (Kanou *et al.*, 2002) were y=0.44x–10.5 and 0.71, respectively (Fig. 3 and Table 1). Therefore, as expected, the average escape direction in 1/cage-reared crickets was more similar to that in normal crickets than those reared under restraint in a vial (1/ vial-reared crickets). However, although a cage of the same size was used, the directionality was not as good as that obtained in the previous study in which 5 or 6 cercus-ablated crickets were reared together (group/cage-reared crickets), that is, the regression line and the correlation coefficient in group/cage-reared crickets measured 14 days after the ablation were y=0.94x–0.40 and 0.93, respectively (Kanou *et al.*, 1999; Fig. 3 and Table 1). In the present

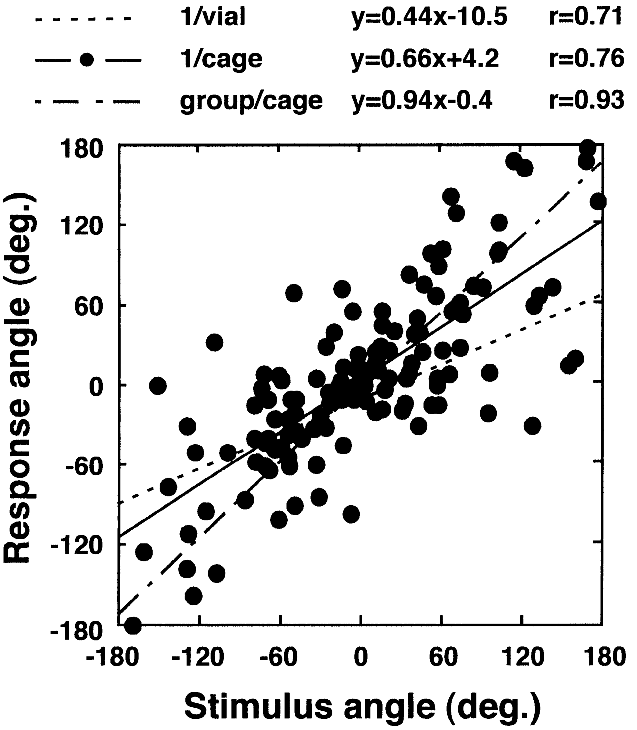

Fig. 3. Relationship between stimulus and response angles in 1/ cage-reared crickets. Their average response angle was similar to that in normal crickets (180° opposite to the stimulus source; Kanou *et al.*, 1999) compared with that in 1/vial-reared crickets (only a regression line is shown; data from Kanou *et al.*, 2002). However, their average response angle was not as good as that in group/ cage-reared crickets (only a regression line is shown; data from Kanou *et al.*, 1999). See text for details.

Table 1. Summary of the wind-evoked escape behavior 14 days after the unilateral cercal ablation and the total amount of locomotion during the period.

	Number of crickets used	Regression line		Correlation coefficient (r)	Total amount of locomotion during 14 days (m)	
1/vial	26	y=0.44x–10.5	*	0.71	–	Kanou *et al.*, 2002
group/cage	41	y=0.94x –0.4	****	0.93	–	Kanou *et al.*, 1999
1/cage	92	y=0.67x +0.5	**	0.77	$4102^{\dagger}$	present study
4/cage	90	y=0.81x –6.9	****	0.80	$10542^{\dagger\dagger\dagger}$	present study
8/cage	46	y=0.96x –9.0	****	0.97	$9450^{\dagger\dagger\dagger}$	present study
1/cage-enforced	40	y=0.75x –2.5	***	0.88	$5677^{\dagger\dagger}$	present study

1/vial; a unilaterally cercus-ablated cricket was reared in a small vial in order to limit their free walking. group/cage; 5–6 unilaterally cercus-ablated crickets were reared together. There were significant differences (P<0.05) in escape direction between values with asterisks. There were significant differences (P<0.05) in total amount of locomotion between values with daggers.

study, we again investigated the recovery of the escape direction in group/cage-reared crickets. The result was consistent with that in our previous study, that is, the escape direction in group/cage-reared crickets was largely improved compared with 1/cage-reared crickets (data not shown). Although 1/cage-reared crickets were provided a sufficient space for walking and occasionally moved spontaneously, they spent a long time at one corner of the cage without moving. Therefore, a mutual stimulation among crickets was considered to increase the amount of locomotion of individuals and seemed to cause a larger compensational change in their escape direction.

Degree of behavioral compensation vs. amount of locomotion

To explore the above-mentioned possibility, we reared a cricket or crickets under different conditions. In addition to 1/cage-reared crickets, four or eight unilaterally cercus-ablated crickets were also reared together in one cage; hereafter, they will be called as 4/cage- or 8/cage-reared crickets, respectively. The amount of locomotion of such crickets was measured by an image sensor during the recovery period and was compared with the degree of behavioral compensation.

The distances walked by a cricket were 293±14 m/day, 753±37 m/day and 675±57 m/day (mean ± SE) for 1/cage, 4/cage- and 8/cage-reared crickets, respectively. Therefore, the total distances during the 14-day were estimated to be 4102, 10542 and 9450 m for 1/cage-, 4/cage- and 8/cage-reared crickets, respectively (Table 1). The total amounts of locomotion were significantly different between 1/cage- and 4/cage-reared crickets, and between 1/cage- and 8/cage-reared crickets (p<0.05; Table 1). However, there was no significant difference between 4/cage- and 8/cage-reared crickets (p>0.05; Table 1). Similar to the amount of locomotion, the escape directions after the14-day recovery period also showed significant differences between 1/cage- (y=0.67x+6.9, r=0.77) and 4/cage-reared crickets (y=0.81x–6.9, r=0.80), and between 1/cage- and 8/cage-reared crickets (y=0.92x–9.0, r=0.91) (p<0.05; Fig. 4 and Table 1), whereas no significant difference was detected between 4/cage- and 8/cage-reared crickets (p>0.05; Fig. 4 and Table 1). These results suggest that the degree of compensation of the escape direction likely depends on the amount of locomotion of a cricket during the recovery period.

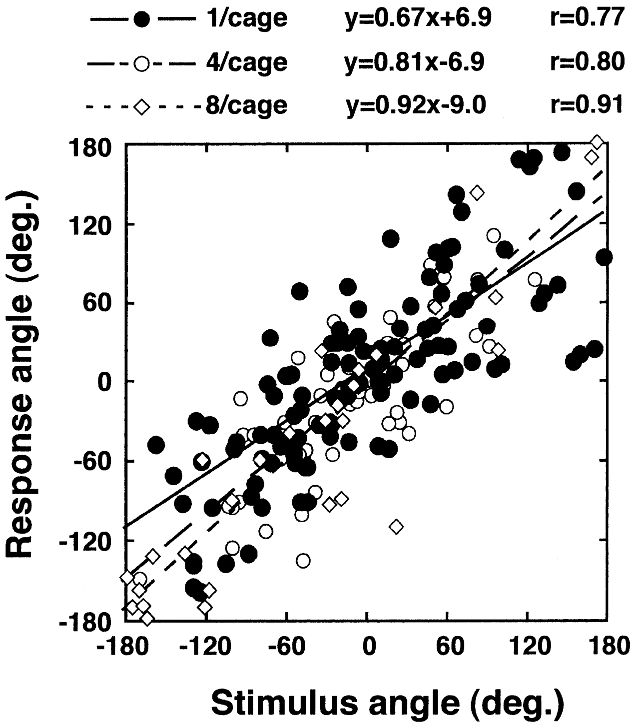

Fig. 4. Relationship between stimulus and response angles in 1/cage-, 4/cage- and 8/cage-reared crickets. There was a significant difference in escape direction between 1/cage- and 4/cage-reared crickets, and between 1/cage- and 8/cage-reared crickets (p<0.05; Table 1), whereas no significant difference was detected between 4/cage- and 8/cage-reared crickets (p>0.05; Table 1). The distances walked by these crickets were measured for 3 days during the 14-day recovery period under constant light conditions (60 lux). Note that the escape direction of such 1/cage-reared crickets was almost identical to that of crickets reared under LD=12:12 condition (Fig. 3).

When the amount of locomotion was measured, the regression line and the correlation coefficient measured for 1/cage-reared crickets were y=0.67x+6.9 and 0.77, respectively (Table 1). During the 14-day recovery period, those crickets were exposed under constant light conditions (60 lux) in three days. On the other hand, the regression line and the correlation coefficient obtained for 1/cage crickets reared under LD=12:12 conditions (amount of locomotion was not measured) were y=0.66x+4.2 and 0.76, respectively. There was no significant difference (p>0.05) between the escape directions of these two groups of crickets. Therefore, constant light conditions (60 lux) in the three days did not affect the compensation of the escape direction.

Effect of forced locomotion on compensation

The amount of locomotion of group/cage-reared crickets was increased by mutual stimulation and seemed to result in a larger degree of compensation of the escape direction. However, it was still possible that some other factors in the case of group rearing affected the compensation of the escape direction. To explore this, we increased the amount of locomotion of a cricket reared alone. During the recovery period, 1/cage-reared crickets were forced to move by touching their body surface with a metal rod. Hereafter, these crickets will be called "1/cage-enforced" crickets. One set of stimulations consisted of one-minute successive touching that was repeated 15 times with 3-minute intervals. Three sets of such stimulations were administered to a cricket every other day during the 14-day recovery period (i.e., 7 days in total) in order to reduce the excess stress and fatigue of the cricket. In these 7 days, the amount of locomotion including the stimulation period was measured with an image sensor for 24 hours. For these 7 days, the average distance walked was 518±24 m/day. As the average distance walked for the other 7 days (without stimulation) was 293 m/day (1/cage-reared crickets in Table 1), the total amount of locomotion during the 14 days was 5677 m (518 ×7+293×7). The distance was significantly larger than that of 1/cage-reared crickets (4102 m) but was significantly smaller than those of 4/cage- (10542 m) and 8/cage-reared (9450 m) crickets (Table 1). The regression line and the correlation coefficient of 1/cage-enforced crickets were y=0.75x–2.5 and 0.88, respectively (Fig. 5 and Table 1). The escape direction was significantly better than that in 1/cage-reared crickets but was significantly worse than that in 4/cage- or 8/cage-reared crickets (Table 1). Therefore, similar to the spontaneous locomotion, forced locomotion also affects the compensational recovery of the escape direction in unilaterally cercus-ablated crickets.

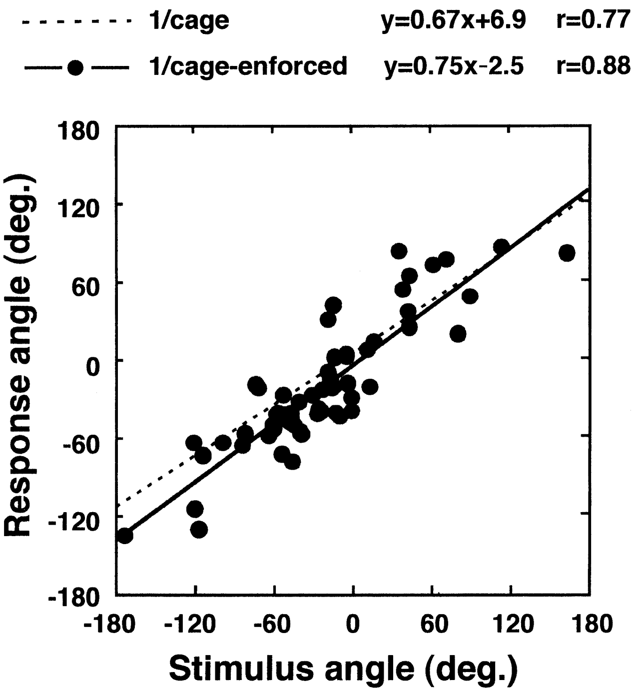

Fig. 5. Relationship between stimulus and response angles in 1/cage-reared and 1/cage-enforced crickets. Only a regression line is shown in the case of 1/cage-reared crickets (refer to Fig. 4). There was a significant difference (p<0.05; Table 1) in escape direction between the two groups. The escape direction of 1/cage-enforced crickets was also significantly different from that of 4/cage- and 8/cage-reared crickets shown in Fig. 4 and Table 1.

DISCUSSION

Similar to the cockroach *Periplaneta americana* (Vardi and Camhi, 1982a, b), unilaterally cercus-ablated crickets reared under restriction in a small space did not show any recovery of the escape direction (Kanou *et al.*, 2002). On the basis of the results of some behavioral investigations, we previously proposed a hypothesis for the mechanism underlying the compensational recovery of a wind-evoked escape behavior in unilaterally cercus-ablated crickets (Kanou *et al.*, 2002). As has been stated in the introduction, the essential points in the hypothesis are, 1) an efference copy signal for walking must be necessary to estimate the responses of some wind-sensitive interneurons such as GIs caused by the walking-evoked self-stimulation of cercal filiform hairs on the remaining cercus, 2) the cricket CNS recognizes the defect of its sensory system by comparing the actual responses of each interneuron and those estimated from efference copy signal, 3) an error signal derived from the inconsistency between the actual and estimated responses of a particular interneuron compensates the physiological properties of the interneuron itself. Therefore, free walking during the recovery period was supposed to be essential to complete the compensation of the escape direction of a unilaterally cercus-ablated cricket.

In the present study, we confirmed that walking was essential for the compensation of the escape direction because 1/cage-reared crickets allowed to walk freely showed a significant recovery in the escape direction compared with 1/vial-reared crickets (Fig. 3 and Table 1). Moreover, it was also proved that the total amount of locomotion during the recovery period was closely related to the degree of compensation, that is, crickets with a greater distance walked showed a higher degree of compensational recovery of the escape direction (Fig. 4 and Table 1). As a working hypothesis, we previously assumed the presence of neural circuits that predict interneuron responses (Operator) and compare the actual and predicted interneuron responses (Comparator) in the TAG. An error signal from the Comparator is considered to change the physiological properties of some interneurons associated with escape elicitation (Kanou *et al*., 2002). In the previous study, we also predicted that the correction of the physiological properties of neural elements should occur repeatedly because almost two weeks was necessary for the behavioral compensation (Kanou *et al*., 1999). Therefore, the result obtained in the present study strongly supports our previous result because the number of the correction must be proportional to the amount of locomotion. However, the mechanism underlying the neural compensation is as yet unclarified. To obtain neural evidence, neurophysiological experiments on tethered-walking crickets are now in progress.

Mutual stimulation seemed to increase the amount of locomotion because group/cage-reared crickets showed a higher degree of recovery in the escape direction than 1/cage-reared crickets (Fig. 3; Table 1). Therefore, it was supposed that a cricket reared with a larger number of other crickets would show a higher degree of compensation. However, the amounts of locomotion of 4/cage- and 8/cage-reared crickets showed no significant difference and the degree of compensational recovery also showed no significant difference between the two groups (Fig. 4; Table 1). The reason is unknown but 8/cage-reared crickets generally stayed in a limited area in the cage as if keeping their own territory. Therefore, rearing too many crickets together did not necessarily increase the amount of locomotion of each cricket.

The amount of locomotion seems to correspond to the degree of compensation of the escape direction. However, we could not exclude other factors such as chemical ones of accompanying crickets. We, therefore, measured the degree of recovery of the escape direction in 1/cage-enforced crickets. To avoid too much stress and fatigue, the stimulation was presented to a cricket every other day. Probably due to this, we could not increase the total amount of locomotion of the 1/cage-enforced crickets to the same level with 4/cage- or 8/cage-reared crickets. Therefore, still we could not completely exclude the possibility of other factors. However, the amount of locomotion increased by touch stimulation was solely effective in improving the escape direction. Moreover, both the total amount of locomotion and the degree of compensation in 1/cage-enforced crickets are intermediate of 1/cage- and 4/cage- or 8/cage-reared crickets. Therefore, we suppose that other effects of accompanying crickets seemed nonexistence or very little if present.

Although the investigation of the neural mechanism underlying behavioral compensation is difficult, the results obtained in the present study is useful in designing such investigations. In the present study, it was revealed that the degree of behavioral compensation depends on the total amount of locomotion during the recovery period. Therefore, by controlling the amount of locomotion after unilateral cercal ablation, we can generate crickets that possess different neural systems regarding the elicitation of wind-evoked escape behavior. Comparing such differently recovered neural systems must be an efficient method of clarifying the basic neural mechanism underlying the behavioral compensation in animals.

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 to M. K.

REFERENCES

Bentley D (1975) Single gene cricket mutations: Effects on behavior, sensilla, sensory neurons, and identified interneurons. Science 187: 760–764

Camhi JM (1984) Neuroethology. Nerve Cells and the Natural Behavior of Animals. Sinauer Associates Inc, Sunder land, pp 342–345

Camhi JM, Tom W (1978) The escape behavior of the cockroach *Periplaneta americana*. I. Turning response to wind puffs. J Comp Physiol A 128: 193–201

Camhi JM, Tom W, Volman S (1978) The escape behavior of the cockroach *Periplaneta americana*. II. Detection of natural predators by air displacement. J Comp Physiol A 128: 203–212

Gras H, Hörner M (1992) Wind-evoked escape running of the cricket *Gryllus bimaculatus*. I. Behavioral analysis. J Exp Biol 171: 189–214

Kanou M (1991) Threshold and directional sensitivity of air-current sensitive giant interneuron of a cricket. Experientia 47: 447–448

Kanou M (1996) Directionality of cricket giant interneurons to escape eliciting unidirectional air-current. Zool Sci 13: 35–46

Kanou M, Ohshima M, Inoue J (1999) The air-puff evoked escape behavior of the cricket *Gryllus bimaculatus* and its compensational recovery after cercal ablations. Zool Sci 16: 71–79

Kanou M, Shimozawa T (1984) A threshold analysis of cricket cercal interneurons by an alternating air-current stimulus. J Comp Physiol A 154: 357–365

Kanou M, Teshima N, Nagami T (2002) Rearing conditions required for behavioral compensation after unilateral cercal ablation in the cricket *Gryllus bimaculatus*. Zool Sci 19: 403–409

Kanou M, Ureshi M, Suematsu Y, Hirao K (2001) Changes in the escape eliciting system of a cricket revealed by sensory deprivation during postembryonic development. Zool Sci 18: 791–796

Matsuura T, Kanou M (1998a) Organization of receptive fields of cricket giant interneurons revealed by cercal ablations. Zool Sci 15: 183–194

Matsuura T, Kanou M (1998b) Functional recovery of cricket giant interneurons after cercal ablations. Zool Sci 15: 195–204

Matsuura T, Kanou M (2003) Postembryonic changes in response properties of wind-sensitive giant interneurons in cricket. J Insect Physiol 49: 805–815

Miller JP, Jacobs GA, Theunissen FE (1991) Representation of sensory information in the cricket cercal sensory system. I. Response properties of the primary interneuron. J Neurophysiol 66: 1680–1689

Murphey RK, Palka J (1974) Efferent control of cricket giant fibres. Nature 248: 249–251

Murphey RK, Palka J, Hustert R (1977) The cercus-to-giant interneuron system of crickets. II. Response characteristics of two giant interneurons. J Comp Physiol A 119: 285–300

Shimozawa T, Kanou M (1984a) Varieties of filiform hairs: range fractionation by sensory afferents and cercal interneurons of a cricket. J Comp Physiol A 155: 485–493

Shimozawa T, Kanou M (1984b) The aerodynamics and sensory physiology of range fractionation in the cercal filiform sensilla of the cricket *Gryllus bimaculatus*. J Comp Physiol A 155: 495–505

Tobias M, Murphey RK (1979) The response of cercal receptors and identified interneurons in the cricket (*Acheta domesticus)* to airstreams. J Comp Physiol A 129: 51–59

Vardi N, Camhi JM (1982a) Functional recovery from lesions in the escape system of the cockroach. I. Behavioral recovery. J Comp Physiol A 146: 291–298

Vardi N, Camhi JM (1982b) Functional recovery from lesions in the escape system of the cockroach. II. Physiological recovery of the giant interneurons. J Comp Physiol A 146: 299–309

Volman SF, Camhi JM (1988) The role of afferent activity in behavioral and neuronal plasticity in an insect. J Comp Physiol A 162: 781–791

von Holst E, Mittelstaedt H (1950) Das Reafferenzprinzip (Wechselwirkungen zwischen Zentralnervensystem und Peripherie). Naturwiss 37: 464–476

von Holst E, Mittelstaedt H (1973) The reafference principle. In “The Behavioral Physiology of Animals and Man. Vol. I.” Ed by E von Holst, University Miami Press, Coral Gables, Florida

(Received June 4, 2004 / Accepted June 23, 2004)