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Authors: Okada, Jiro, and Toh, Yoshihiro

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Shade Response in the Escape Behavior of the Cockroach, *Periplaneta americana*

Jiro Okada* and Yoshihiro Toh

Department of Biology, Faculty of Science, Kyushu University,
Fukuoka 812-8581, Japan

ABSTRACT—The termination of the escape behavior in the cockroach *Periplaneta americana* was investigated. Escape behavior was effectively terminated when cockroaches were allowed to select a dark shelter and hide beneath it. This shade-induced pause in escape running (a shade response) was observed even in very low-light levels (less than 0.01 lux). Contributions of the ocelli and the compound eyes to the shade response were examined. Removal of both compound eyes resulted in complete disappearance of the shade response. Animals with just the ocelli removed were less likely to shelter in the shadowed area, especially under a low-light condition. Input from compound eyes seems to be essential to the shade response. The ocellus may enhance the function of compound eye, and its modulatory function is effective in low-light conditions.

INTRODUCTION

Escape behavior in the cockroach has been extensively studied as a neurophysiological model for simple behavior (reviews: Camhi, 1980; Ritzmann, 1993; Comer and Dowd, 1993). Cockroaches are sensitive to external stimuli such as air displacement and antennal touch, and escape in the direction opposite to stimulus presentation. Escape behavior is composed of following sequence: 1) perception of an external stimulus, 2) orientation of the body, 3) initiation of running, 4) running accompanied with course control, 5) cessation of running. Of these components, the neural mechanisms of processes (1)-(4) have been studied at the cellular level (Roeder, 1948; Westin *et al*., 1977, 1988; Westin, 1979; Ritzmann, 1981; Ritzmann and Pollack, 1981, 1988; Ritzmann *et al*., 1991). By contrast, the cessation mechanism (5) is still obscure, although hiding from view of a potential predator is also an important process in cockroach escape behavior.

The only report concerning termination of the cockroach escape behavior is that of Meyer *et al*. (1981), who showed that casting a shadow on the cockroach can terminate escape. Ritzmann *et al*. (1991) also reported that some thoracic multimodal interneurons implicated in the escape response fired impulses at light-off. Visual stimuli, therefore, appear to be involved in the cessation of the escape.

In this study we have reexamined the visually induced pause of escape behavior by using an environmental shade made from an opaque shelter. Under various light conditions, the roles of both the compound eyes and the ocelli were evaluated in the shade response. A preliminary report appeared in abstract form (Okada and Toh, 1997).

MATERIALS AND METHODS

Adult male cockroaches (*Periplaneta americana*) were used, raised in a laboratory culture maintained at 27°C.

To examine the roles of compound eyes and ocelli in the shade response, animals deprived of one or both were prepared. After immobilization of animals on ice for 15 min, the retina of the compound eyes was removed bilaterally, including the cornea. A similar surgical method was applied to remove the ocellar retina. Sham-operated animals were prepared by cutting around the cuticle of the compound eyes and ocelli, bilaterally, with a fine razor blade. Operations were followed by a recovery period of 2 days or more.

All experiments were performed in a white-painted cylindrical arena of 45 cm in diameter, with 12 cm high wall (Fig. 1). The base was made from plywood and the wall from steel sheet. To prevent animals from climbing up the wall, liquid paraffin was spread on it. A halogen light projector was positioned 2 m above the arena. In the experiments involving changing light conditions, the unit light intensity was 100 lux, and test light intensity was varied using neutral filters. The behavior of individual cockroaches was observed, recorded and analyzed with a video camera and a VHS video recorder.

To induce an escape response, an air puff or a light touch to the body surface was applied manually to an animal by using either a photographic duster or a thin brush, respectively.

A dark zone was made inside the arena from a black acrylic shelter (8 cm square, and 2.5 cm or 5 cm high), placed against the wall (Figs. 1 and 2). If the height was lower than 2 cm, cockroaches often climbed up on the shelter roof instead of going under it. The ratio of light intensity inside the shelter to that outside was independent of test light intensity, and was about 5% and 8%, respectively, for the low and high shelters.

A criterion was needed to quantify when an escaping cockroach had terminated its escape under each of the three tested shelters. A "stop" was judged to have occurred when an animal ran into the shel-

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* Corresponding author: Tel. +81-92-642-2315;
FAX. +81-92-642-2645.

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ter without hesitating, and then remained there for more than 3 sec. Temperature in the experimental room was kept at 27°C.

RESULTS

Termination of the escape response

When cockroaches were released into the arena, they usually ran straight to the wall, and ran around the perimeter of the arena for a while, and then stopped at the wall. This behavior was also observed when an external stimulus was applied to the quiescent animals.

The shelter of 2.5 cm height reliably induced termination of the escape running (mean stop rate ± SD, 80.0 ± 15.0%, N = 5) (Fig. 2). To examine the participation of the mechanical sense on passing the shelter, a high shelter (5 cm height) and a transparent shelter (2.5 cm height) were prepared. In the high shelter mean stop rate appeared to decrease slightly (relative difference to the low shelter 14%), but a statistical analysis (t-test) showed that there was no significant difference between the high and low conditions ($P > 0.05$). On the other hand, a transparent acrylic shelter (transmittance 90%) did not have any significant effect in stopping escape running. These results suggest that the termination of the escape run-

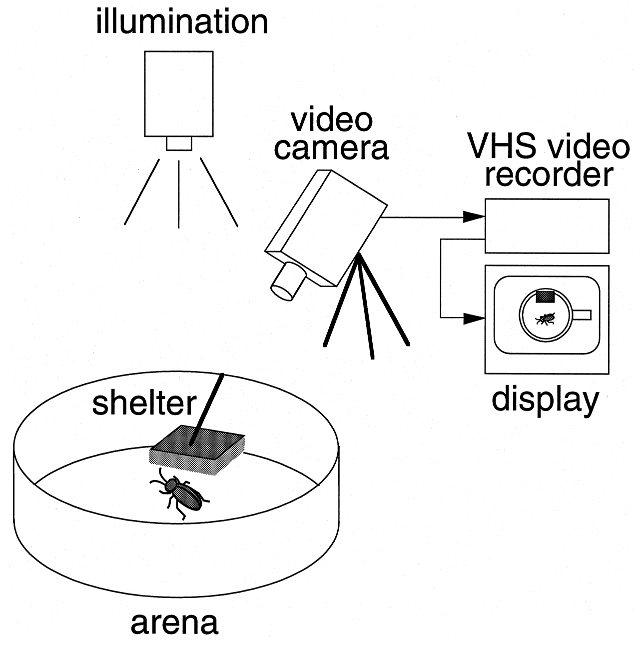

Fig. 1. Schematic drawing of the experiment. Behavior of animals was recorded and replayed by video camera and recorder system.

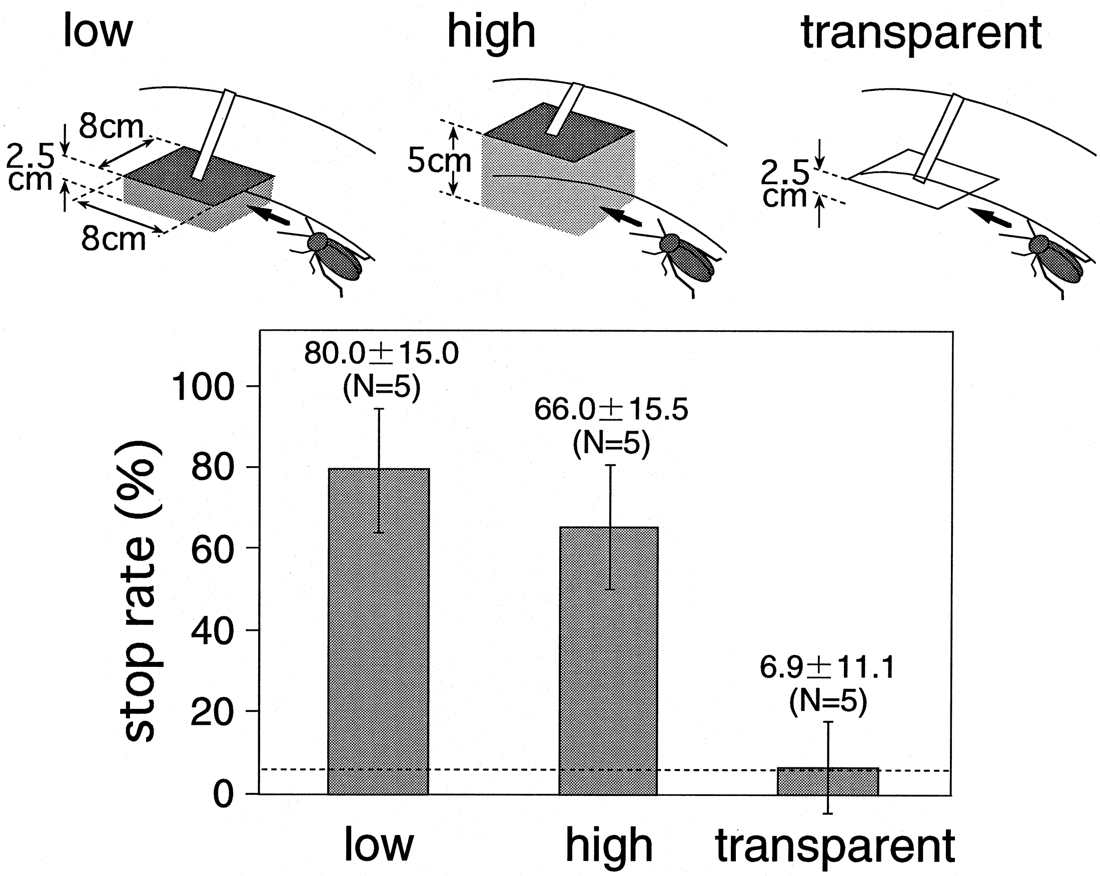

Fig. 2. Effects of three kinds of shelters on the escape running. The experiments were performed under a light intensity of 50 lux. The stop rate in each condition was calculated as an average (± SD) taken from stop rates of 5 animals (trials in each animal 5-13, total trials in each test 40-49). Escaping animals reliably stopped at the shade of low and high shelters. The transparent shelter had no significant effect on the escape behavior. Broken line at 5.7% shows the ratio of length of tested tools (8 cm) to the circumference of arena (141 cm).

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ning is induced mainly by shade of the conditions employed.

Shade response in various light conditions

Relationship between stop rate of escape running and light intensity was examined (Fig. 3). Test light intensities ranged from 0.01 to 100 lux. The height of the shelter in this and the following experiments was fixed at 5 cm. Mean stop rates were calculated from the data of 7 animals in each light condition (Table 1A). Cockroaches responded reliably to the presence of the shaded zone by stopping, even in the lowest light condition (0.01 lux). Mean stop rates in tested light intensities ranged from 70.7 to 80.6%. Statistical analysis (t-test) showed no significant difference between any pair of these groups ($P > 0.05$).

Roles of compound eye and ocellus in the shade response

To evaluate the contributions of compound eyes and ocelli to the shade response, four kinds of operations were applied to animals: removal of both compound eyes; removal of both ocelli; bilateral removal of both of compound eyes and ocelli; or a sham operation. Using these four kinds of treated animals, stop rates were examined in various light conditions (Fig. 3; Table 1B-E).

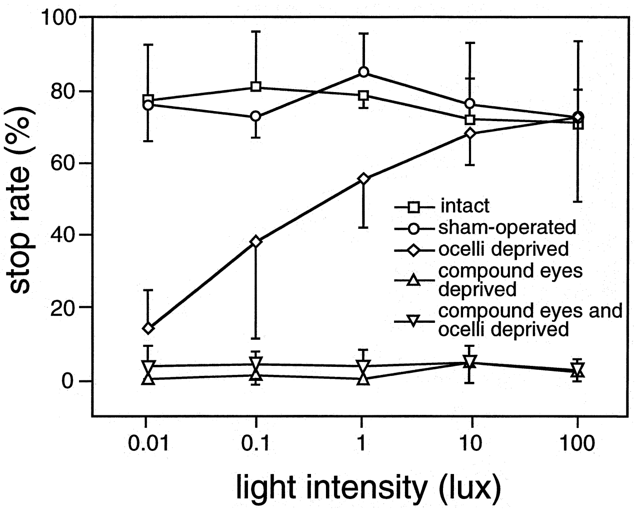

Fig. 3. Relationship between stop rate and light intensity in intact and treated animals (mean ± SD, SD bars omitted when the values were smaller than the size of symbols). The shade response was observed even in the lowest light condition (0.01 lux) at similar frequencies in intact and sham-operated animals. Bilateral removal of compound eyes resulted in drastic decrease in the stop rate. The effect of bilateral removal of ocelli appeared at low light intensity (< 1 lux). For detailed data, see Table 1.

Sham-operated animals still showed high stop rates over all light conditions tested. There was no significant difference in the stop rate between intact and sham-operated animals through all the light conditions ($P > 0.05$). The removal of the compound eyes resulted in complete disappearance of the shade response in all tested light conditions, and the stop rates were almost zero in animals in which both the compound eyes and ocelli were destroyed. Ocelli-deprived animals responded the same as the intact animals in bright light (intensities 100 and 10 lux), and the responses were not significantly different

Table 1. Relationship between stop rate (%) and light intensity (lux) in intact (A) and treated (B-E) animals

A. intact

LI	mean	SD	N	T	t
0.01	77.0	15.0	7	120	14-21
0.1	80.6	15.0	7	117	16-20
1	78.4	3.4	7	111	15-17
10	71.6	11.5	7	112	15-17
100	70.7	9.3	7	112	15-17

B. sham-operated

LI	mean	SD	N	T	t
0.01	75.8	10.2	5	81	13-21
0.1	72.5	5.8	5	79	12-18
1	84.7	10.6	5	88	17-18
10	75.9	16.8	5	80	14-17
100	72.5	23.5	5	85	15-18

C. compound eyes deprived

LI	mean	SD	N	T	t
0.01	0	0	5	59	8-16
0.1	1.1	2.5	5	67	11-18
1	0	0	5	65	7-21
10	4.3	5.2	5	77	8-28
100	2.0	2.8	5	85	8-22

D. ocelli deprived

LI	mean	SD	N	T	t
0.01	13.9	10.4	5	52	11-19
0.1	37.4	26.1	5	56	8-18
1	55.1	13.2	5	65	7-21
10	67.9	8.9	5	89	9-31
100	72.5	20.8	5	95	9-31

E. compound eyes and ocelli deprived

LI	mean	SD	N	T	t
0.01	3.8	5.2	5	58	5-19
0.1	3.9	3.7	5	70	9-20
1	3.3	4.7	5	64	6-20
10	4.5	4.7	5	69	9-20
100	2.4	3.3	5	61	8-19

LI: light intensity (lux)
mean: mean of stop rate (%)
SD: standard deviation
N: number of animals used in each experiment
T: total number of trials
t: number of trials in each animal

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from those of the sham-operated and intact animals (P > 0.05). However, the lower the light level, the lower was the stop rate. Finally, at 0.01 lux, there was no significant difference in the stop rate from animals in which both the compound eyes and ocelli were removed (P > 0.05).

DISCUSSION

Shade-induced termination of the escape response

Visual control was involved in the escape response as the termination of running. Meyer *et al.* (1981) reported that the termination of escape could be induced by the manual casting of shadows to the escaping cockroaches in a high probability, 87% (N = 112). This value is not only similar to the mean stop rates in this study (70.7% to 80.6%), but also slightly larger. If cockroaches utilize a visual cue for locating a safe place, stationary black shelters may be more recognizable as visual goals than manually cast shadows. Cockroaches may not have an intended visual goal in their escape behavior, but simply stop at the first dark place encountered.

The relationship between the startle (escape) response and visual input has been studied in some insects. The jumping responses in the locust (Pearson *et al.*, 1980) and the fruit fly (reviewed by Wyman, 1984) are elicited by visual stimulation. In the early experiments of this study, the effects of light-on (or removal of shadow) and light-off (or shadow casting) were examined in either quiescent and escaping animals. However, only light-off or shadow casting reliably terminated the escape, while other stimuli did not have this effect.

The experiment using three kinds of shelters showed that the stop rate only in the transparent shelter was very low compared to those in the low and high black shelters. This indicates that the shade response may be inducible simply by the decrease of light, and that the proximity of the roofs to the floor had only a minor effect, at most.

Light condition in the shade response

Cockroaches stopped reliably beneath a shaded region of the arena over 4 orders of magnitude below 100 lux. Although the test light intensities were narrow-ranged, mean stop rates in intact animals (70.7% to 80.6%) showed no significant difference among this range. The cockroach has a pair of large ocelli lenses (about 0.7 mm in diameter), and consequently has a very large number of ocellar photoreceptors (> 10,000) among insects (Weber and Renner, 1976). Outputs from the photoreceptors converge onto only 4 ocellar second-order neurons (Weber and Renner, 1976). These morphological characteristics reflect that the ocellus of the cockroach is highly adapted to the low-light environment. Our present study clearly showed that cockroaches have the ability to hide away from nocturnal predators' sight during night, if there would be very weak light such as moon light (full moon, 1 lux; Caelli, 1981).

Function of compound eye and ocellus in the shade response

Removal of compound eyes and/or ocelli gives information about their function in the shade response. Although it is always possible that the removal operation itself impairs mobility, most operated animals survived for more than 10 days without notable abnormality in mobility in this study. On the other hand, cauterization outside the eyes often resulted in serious impairment of mobility. Occlusion with opaque paints might be a less severe method to remove the function of compound eyes and ocelli. We also tried this method using some paints, but this was incomplete occlusion because of the following results in the animals whose compound eyes and ocelli were double-painted: 1) apparent shade response occurred at more than 10 lux of light intensity, 2) the descending spike discharge in the ventral nerve cord was observed by light-off stimulation at more than 10 lux. The painting method may be doubtful even if the occlusion was complete at the painted area, because the head capsule of *P. americana* is semitransparent. Thus, we used surgical operations, and sham operations as a control, in the present study.

The lesion experiments in this study show that compound eyes are essential for the shade response in the cockroach escape behavior. The ocellus may modulate the function of the compound eye, although its effectiveness is masked by the sufficient response of compound eyes to the decrease of light under the bright condition. In the bee, measurements of the latencies of visual signals from ocelli and compound eyes to descending neurons showed that the information from the former always reached those neurons more rapidly than that from the latter (Guy *et al.*, 1979). In the cockroach, some of ocellar interneurons in the brain extend their processes to the medulla and lobula (Mizunami and Tateda, 1986). Ohyama and Toh identified small multimodal ocellar interneurons (1990a) and descending ocellar interneurons (1990b) in the brain of the cockroach, and demonstrated that both of these interneurons receive inputs from various sensory organs including both the compound eyes and ocelli. It may be possible that the preceding signal from ocelli modulate the slow compound eye signal in the optic lobe, brain and/or segmental ganglia through these identified ocellar interneurons. Compound eyes of insects are responsible for the spatial vision, such as pattern recognition and movement detection (reviews: Laughlin, 1980; Hardie, 1985; Goldsmith, 1989). The primary function of ocelli is thought to be light detection and modulation of inputs from compound eyes (reviews: Goodman, 1981; Toh and Tateda, 1991; Mizunami, 1994). This study adds a new example to the behavioral repertoire of insect compound eyes and ocelli.

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