Light compass in the provisioning navigation of the subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae)

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Abstract

The female of the subsocial shield bug, *Parastrachia japonensis*, provisions food to her nymphs using path integration, a type of navigational strategy that acquires information indicating the traveler’s direction and distance. In this study we investigated whether and how *P. japonensis* females use a light compass involved in orientation at a constant angle with respect to a light source. First, we let the female run toward its burrow in an experimental room when a lamp set on the floor was turned on. Then, we changed the direction of the light source 180° horizontally by switching off the lamp and turning on another lamp on the opposite side. In response to this change, the homing bug turned back immediately. Next, we examined the effects of the light source from two different elevations. It accomplished its path integration task when the light was placed at an azimuth of 45°. When the light was at the zenith (90°), however, the bug lost the correct home direction. These results suggest that in their path integration system *P. japonensis* use light sources as compass references and, further, that they can estimate their direction from a point located at mid-sky but not the zenith.

Key words: Homing; navigation; path integration; sun compass; subsocial shield bug

INTRODUCTION

Many animals use a light compass for long-distance navigation, which involves orientation at a constant angle with respect to a celestial light source, such as the sun, the moon, or the stars (von Buddenbrock, 1917). For insect navigators with sensory access to the sky, celestial cues undeniably offers angular information because they are effectively at infinity and thus not subject to the phenomenon of motion parallax. Therefore, the insect navigators can readily use the celestial light sources and/or celestial cues derived from the light sources as a means for defining direction (Rossel and Wehner, 1984; Wehner, 1984; Dacke et al., 2003; Homberg, 2004). Central-place foragers like social hymenopterans are semi long-distance navigators, have been observed to make the round trip between their nest and foraging sites regularly in their environment using the path integration (Wehner, 1992). Path integration, which refers to a method for computing one’s present location, requires external or internal information indicating the navigator’s instantaneous direction and distance of trip (Mittelstaedt and Mittelstaedt, 1982). Central-place foragers such as ants also use the sun as a means for defining direction in the path integration (Santschi, 1911, 1923).

In addition to the well-known navigators of Hymenoptera, the female of the subsocial shield bug, *Parastrachia japonensis*, which belongs to Heteroptera, is also a remarkable navigator. The female forages on the forest floor and provides food to her nymphs by walking. In mid-June, after the nymphs hatch, the female leaves its burrow to find drupes, fallen fruit with a hard stone-like endosperm, from the host tree, *Schoepfia jasminodora* (Olacaceae: Rosidae: Santalales) (Tachikawa and Schaefer, 1985; Tsukamoto and Tojo, 1992). The female searches for drupes far away from its...
burrow, which is located usually more than 5 m from the foraging area (Filippi-Tsukamoto et al., 1995; Filippi et al., 2001). After the bug leaves its burrow, it searches arduously until it encounters a drupe. When a drupe is discovered, the bug always takes the shortest route back to its burrow using path integration (Hironaka et al., 2007a, b).

It is possible that *P. japonensis* uses the visual information in its path integration because it has been observed that direct homing females become disoriented to their burrow direction when visual information is disturbed by the painting of the compound eyes and ocelli (Hironaka et al., 2003). The question of what kind of visual information the bug acquires, however, still remains to be answered.

In this study, we investigated whether *P. japonensis* females use a direct light source as a compass reference in their provisioning navigation.

**MATERIALS AND METHODS**

We carried out laboratory experiments from mid-June to mid-July 2000 and 2004 at Saga University in Japan. We collected *P. japonensis* females guarding their egg masses from the field site, Hinokuma-yama, a small forested hill in Saga Prefecture, Japan (33°16’N, 130°16’E), during June. We reared egg-guarding females individually in clear plastic cups (diameter 8 cm; height 4 cm) lined with substrate (soil and fallen leaves) for 1 week at 22°C on a 14:10 h light-dark regime and fed them on the ripe drupes of a single host tree, *S. jasminodora*. A plastic lid was used to cover the cups to keep the bugs from escaping. We turned the light source in the incubator on at 5:00 and off at 19:00 in order to imitate the appropriate seasonal outdoors conditions.

We conducted the experiments in a temperature-controlled room (8×5 m and 2.5 m high). To activate the provisioning behavior, the temperature in the experimental room was kept at 25±2°C. The floor was covered with soil and fallen leaves to simulate the natural forest floor. In addition, the whole area of the floor was transacted with yellow lines into a grid of 50 cm mesh to allow us to record the bugs’ paths on a reduced scale. All walls and the ceiling were covered with a blackout curtain. A compact fluorescent lamp (EFA25ED/22, Matsushita Electric Industrial Corp. Ltd., Tokyo, Japan) equivalent to a 100-watt incandescent bulb was used as the light source.

After the females’ eggs hatched, we continued to rear the females with their nymphs on drupes until the nymphs reached the third stadium. Then we conducted the following two experiments during the daytime from 14:00 to 17:00. In all experimental trials, we tested those bugs that had never left the burrow before the start of the trial and used each individual bug only once.

**Experiment 1: Horizontal shift of light.** We carried out a horizontal shift experiment to investigate the possibility that the homing bug uses a light source for directional reference. We set an experimental plastic burrow and a square feeding site (one side 10 cm) containing several ripe drupes on the floor at a distance of 1 m. Two light bulbs (shown as ‘a’ and ‘b’ in Fig. 1) were placed on the floor (elevation of 0°) at a distance of 4 m. The axis between the two bulbs was perpendicular to the axis between the burrow and the feeding site. The light switching was controlled by the experimenter when the bug crossed the line between the two bulbs.

First, only lamp ‘a’ was switched on. When the lid of the cup was opened, the female spontaneously started the provisioning trip for its young, that is, the female left the burrow to search on the floor in a wandering path. When it reached the feeding site and found a drupe, the female started to return to its burrow showing a direct trajectory, so that it walked roughly toward the intersection.
point of the axis between the two bulbs and the axis between the burrow and feeding site. When the female crossed the line between the two bulbs, we immediately switched light ‘a’ off and turned light ‘b’ on. At the same time, we placed a metal marker where the bug was located precisely at the switching point. For the control experiment, we did not change the position of the light when the female reached the intersection point, that is, we kept lamp ‘a’ turned on for the duration of the experiment. We did, however, as with the experimental group, place a metal marker on the point where the bug crossed the line between the two bulbs. To measure the homing direction, we scratched a circle 50 cm in diameter with a compass centered on the metal marker. A small flag was placed at the point where the bug crossed the circle, and we then drew twine between the metal marker and the flag, and between the metal marker and the burrow, respectively. Next, using a protractor, we measured the interior angle between the two pieces of twine as the homing direction.

If the bug did not reach the feeding site within 15 min or take a wide detour around the direct outbound course, we ceased the trial and omitted it from the data. This criterion was also used in Experiment 2. In the Experiment 1, we analyzed 10 data of 28 and 22 females in the control and experimental conditions, respectively.

Experiment 2: Effect of the zenithal position of light. Only one light was used in Experiment 2, placed at an elevation of either 45° or 90° (zenith) from the intersection point (Fig. 1). The positional arrangement between the burrow and the feeding site was same as that of Experiment 1 except for the elevation of the light source. In these light settings, the angle at which the bug looked up at the lamp from the burrow or feeding site was ca. 76°. When the bug reached the feeding site and found a drupe, we placed a metal marker to designate the point of drupe discovery. To determine the homing direction, we scratched a circle of 50 cm in diameter with a compass centered on the point of drupe discovery in the feeding site. In addition, we placed a small flag at the point where the bug crossed the circle. We measured the angle between the two lines: the line from the burrow to the drupe discovery point and the line from the drupe discovery point to the crossing point of the circle. In this Experiment 2, we analyzed 14 data of 26 and 21 females in the 45° and 90°, respectively.

Statistics. Statistical analysis of the distributions of homing directions was performed according to the methods reported by Batschelet (1981). For the distribution, the mean resultant vector was calculated and a $V$ test was applied to determine whether the distribution differed from randomness.

RESULTS

Experiment 1: Horizontal shift of light

Each bug, once its burrow had been placed in the experimental room, foraged around on the experimental floor until it encountered a ripe drupe, which had been placed at the feeding site. In the homing trip, it walked back toward its burrow directly while dragging the drupe in its proboscis following the line between the feeding site and the burrow. The bugs under the control conditions homed with great precision. The homing directions of the control bugs were significantly clustered towards their burrows (Fig. 2A; $V$ test: $u=4.219$, $N=10$, $p<0.0001$) when measured at the crossing point of the line between the two bulbs. In the experimental condition, the light position was moved to the opposite side when the homing bug carrying a drupe crossed the line between the two bulbs. As soon as the position of the lamp was shifted, the bug stopped and turned or rotated several times. A few seconds later, the bug started to walk in the opposite direction, moving away from its own burrow. After walking to a place near the feeding site, the bug showed typical burrow-searching behavior (Fig. 2B). The homing directions of the experimental bugs were significantly clustered towards the feeding site (Fig. 2A; $V$ test: $u=3.566$, $N=10$, $p<0.0001$).

Experiment 2: Effect of the zenithal position of light

In this experiment, each bug foraged around and returned to its burrow under a lamp set at two different elevations, but not horizontally on the floor as in Experiment 1 (Fig. 1). A comparison of the two conditions, i.e., 45° or 90°, with respect to the elevation from the intersection to the lamp, the behaviors as reflected in the outbound trajectories of the homing bugs were indistinguishable (not shown), both being similar to the case of the control bugs described in Experiment 1. However,
there was an apparent difference in the inbound trajectories. When the light bulb was placed at the 45° elevation, the bugs left the feeding site and rather directly returned to their burrows (Fig. 3A). The homing directions in this case were significantly clustered towards their burrows (Fig. 3B; \( \chi^2 \) test: \( u = 4.820, N = 14, p < 0.0001 \)), similar to those observed in the control bugs in Experiment 1. On the other hand, when the bulb was placed at the 90° (zenith) elevation, the homing bugs lost their way and showed wandering behaviour mainly around the feeding site; moreover, the homing directions were randomly distributed (Fig. 3C and D; \( \chi^2 \) test: \( u = 1.495, N = 14, p > 0.05 \)).

**DISCUSSION**

Behavioral studies in honeybees, ants, and several other species have shown that insects largely navigate by a vector-based mechanism of orientation called path integration (Wehner, 1992; Collett and Collett, 2000). In the path integration system, an insect updates an accumulator that keeps a running tally of its current direction and distance upon leaving a starting point, such as a nest, so that it can always take a direct path back to the starting point. Hence, the insect in effect utilizes a compass by which it can measure the angular components of its movement (Collett and Collett, 2000). Generally, insects continually monitor their direction of travel using celestial light sources (Wehner, 1984). Santschi (1911) first demonstrated in mirror experiments that ants use the angle subtended by the sun and the nest to guide their return trip to the nest.
using path integration. For nocturnal foraging ants, a moon compass response is equally feasible, and has, in fact, been demonstrated by Santschi (1923) and Jander (1957). It has been reported that honeybees also use the sun compass in their path integration (von Frisch, 1965). Our results in Experiment 1 confirmed that *P. japonensis* use a similar light compass to monitor their angular movement as a part of their path integration system. This is the first report in the heteropterans to demonstrate the utilization of the light compass for path integration.

Some insects are known to use stars as a light compass reference for their navigation in addition to the sun and moon (Sothibandhu and Baker, 1979; Baker and Mather, 1982), but such utilization of stars as a reference was doubted by Wehner (1984). In addition, environmental structures such as canopy gaps may also function as references. In fact, *P. japonensis* females have been observed to provision for entire days using visual cues in the forest during the busiest provisioning period (Hironaka et al., 2003, 2007b). Thus, they seem to be able to use different cues as light compass references depending on the current celestial conditions and structural surroundings in the field.

For angle measurement in the sun compass, insects refer only to the azimuth of the sun and not to its elevation (Wehner, 1984). Therefore, if the sun is directly in the zenith at noon, or its zenithal angle is indistinguishable from 0°, then the sun compass is useless around midday (Wehner, 1984). For example, the homing orientation in *Cataglyphis* ants has been found to not be influenced even when the altitude of the sun was increased by 30° using a mirror (Dueli and Wehner, 1973). Moreover, Lindauer (1957) confirmed, from observations in Ceylon (Sri Lanka), which is located near the equator, that honeybee dances become disoriented when the sun passes within 2.5° of the zenith. Coinciding with the results of these studies, our present study demonstrated that the homing *P. japonensis* bugs became disoriented to their burrows by several degrees when the light was set to the zenith (Fig. 3C and D). This result suggests that *P. japonensis* also measures the angle from the azimuth in their light compass system. We estimate that the *P. japonensis* females in our observatory, located at 33° N, are typically exposed to the sun at its highest altitude of 80° at noon in their provisioning season of late June, which approximately coincides with the angle (ca. 76°) at which they looked up at the lamp from their burrow or feeding site in Experiment 2. Given this observation, we can suspect that *P. japonensis* females are either able to perceive the sun’s position relative to the zenith accurately to within only a few degrees, similar to honeybees (New and New, 1962), or that they use different cues to recognize direction, as has been observed in equatorial sandhoppers (Ugolini, 2002). Further investigation is needed to clarify this point.

Numerous ecological and agricultural studies have demonstrated that attraction to artificial lights generally occurs in heteropteran (e.g. Ito et al., 1993; Kato et al., 1995; Schuh and Slater, 1995). Therefore, it is reasonable to suppose that the light compass is a basic and widely shared trait in Heteroptera. However, among heteropteran, thus far only one study has demonstrated the existence of the light compass (Birukow, 1956). The study showed that a water bug, *Velia currens*, uses the direction of the sun when determining its escape response. When an artificial light source in a room was moved to another position, *V. currens* adjusted its escape direction in accordance with the new azimuth. Further, when the light source was changed to be exposed to the bug from an angle between 85° and 90°, the bug became completely disoriented and tried to escape to an indefinite direction. Thus, as the present results show that a similar light compass mechanism also functions in *P. japonensis*, we can conclude that the mechanism is more general, or even universal, in heteropteran.

With respect to the foraging behavior of *P. japonensis*, the effects of several cues on the light compass have been confidently proven, and further studies of the light compass and its biological background in this species will provide new insights into ecological and agricultural management in heteropteran.

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