A new navigational mechanism mediated by ant ocelli

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Many animals rely on path integration for navigation and desert ants are the champions. On leaving the nest, ants continuously integrate their distance and direction of travel so that they always know their current distance and direction from the nest and can take a direct path to home. Distance information originates from a step-counter and directional information is based on a celestial compass. So far, it has been assumed that the directional information obtained from ocelli contribute to a single global path integrator, together with directional information from the dorsal rim area (DRA) of the compound eyes and distance information from the step-counter. Here, we show that ocelli mediate a distinct compass from that mediated by the compound eyes. After travelling a two-leg outbound route, untreated foragers headed towards the nest direction, showing that both legs of the route had been integrated. In contrast, foragers with covered compound eyes but uncovered ocelli steered in the direction opposite to the last leg of the outbound route. Our findings suggest that, unlike the DRA, ocelli cannot by themselves mediate path integration. Instead, ocelli mediate a distinct directional system, which buffers the most recent leg of a journey.

Keywords: ocelli; ants; navigation; path integration; compound eyes; Melophorus bagoti

1. INTRODUCTION

To navigate in the world, insects are guided visually by both celestial and terrestrial cues [1–3]. Both compound eyes and the less conspicuous ocelli encode visual information. Unlike compound eyes, ocelli do not encode detailed image information [4–6]. In flying insects, it has been shown that ocelli stabilize flight by quickly detecting changes of light intensities in the dorsal visual hemisphere owing to sudden deviations from a given flight attitude [4,5,7]. In ground-based ant species, it is only known that ocelli extract directional information from celestial compass cues (e.g., polarized skylight, sun’s position), whereas terrestrial compass information from surrounding landmarks are not computed [6,8]. So far, it has been assumed that such directional information obtained from ocelli contribute to a single global path integrator together with directional information from the compound eyes and distance information from the step-counter [1,9]. By manipulating the visual input of either the compound eyes or the ocelli of the ant Melophorus bagoti, we found that ocelli mediate a second navigational mechanism separate from the one mediated by the compound eyes.

2. MATERIAL AND METHODS

Data collection took place in Alice Springs, Northern Territory, Australia. To ensure that the ants had access to celestial compass cues [10], all experiments were conducted under clear or slightly cloudy sky.

Ants were free to collect food items at the end of a straight or two-leg training route. The two segments of the two-leg route were 5.8 m long and approximately 1.0 m wide and formed an angle of approximately 140°. White wooden planks, which were sunk into the ground and stuck out approximately 0.10 m, enclosed the nest and the outbound route, thus preventing the ants from foraging elsewhere. The ‘walls’ were low enough to allow a view of the sky and the surrounding landscape. Foraging ants that reached the feeder on the training field for the first time, and picked up a food item, were marked on the abdomen with a daily colour of enamel paint. All marked ants were able to dash between feeder and nest for at least one full day before being tested. A test consisted of releasing the ant on an unfamiliar test-field after one out of three painting treatments: either the eyes (Oc), the ocelli (Ey) or the back of the head (Ct) were covered with acrylic paint (figure 1a). The treatment itself had no noticeable effect on the homing behaviour of the tested ants (electronic supplementary material, figure S2). Treated ants that picked up a cookie crumb were transferred in the dark to the unfamiliar test-field approximately 60 m away from the training area. The unfamiliar surrounding of the test-field ensured that the ants relied only on celestial compass information for homing. A goniometer (diameter 1.2 m) with 24 sectors of 15° each was used to record the initial headings of the ants at 0.6 m from the release point. After travelling 0.6 m, the tested ants tended to stay with their initial headings and no switch in their homing direction appeared. The ants’ directional choices were analysed with circular statistics [11].

3. RESULTS

In previously published results [6], we caught M. bagoti foragers at a feeder after they had travelled a straight outbound route. These so-called full vector (FV) ants have information about distance and direction in order to integrate the shortest way home. We released the FV ants with untreated compound eyes but covered ocelli (figure 1a; Ey) onto an unfamiliar test-field that ruled out the possible use of panoramic cues. On the test-field, FV_Ey foragers headed straight towards the (fictive) nest direction [6]. In this study, we caught foragers after travelling a straight out- and inbound route just before they entered the nest. Such zero-vector (ZV) ants lack any distance and directional information from the global path integrator. Surprisingly, when released on the test-field with covered compound eyes and uncovered ocelli, these ants (ZV_Oc) did not orient randomly, as the ZV of the global path integration input would predict, but headed significantly in the direction opposite to the feeder-nest direction (figure 1b; V test: ZV_Oc11.53, n = 20, p < 0.001).

To examine the compass information obtained from ocelli, we tested ants after they had travelled a two-leg foraging route (figure 2). Foragers were caught at the feeder, treated and released on the unfamiliar test-field. Ants with covered ocelli (Ct; Ey) were significantly oriented towards the (fictive) nest direction on the test-field (figure 2a; V test: Ct15.9, n = 36, p < 0.001; Ey21.3, n = 30, p < 0.001; t-test: Ct1.6, p = 0.12;
Ants with covered compound eyes but functional ocelli (Oc), however, did not run towards the nest direction (t-test: Oc $t_{21.57} = 1.57, p < 0.001$). They chose the direction opposite to the second leg of the outbound route (figure 2a; V test: Oc $n = 41, t_{0.66} = 0.52, p = 0.001$; t-test against second leg direction: Oc $t_{0.66} = 0.52, p < 0.001$; Ey $t_{6.25} = 0.52, p < 0.001$). The headings of Oc foragers differed significantly from those of Ey (Watson-Williams test, $F = 21.4, p < 0.001$) and Ct ants (Watson-Williams test, $F = 17.0, p < 0.001$).

To show that ocelli mediate a distinct compass mechanism, it is necessary to confirm that the directional information derived from the dorsal rim area (DRA) is not accessible via the ocelli. To test this, we captured ants at the feeder that had just run a straight outbound trip with covered ocelli (Ey) and tested them either with unchanged (Ey) or reversed (Oc) conditions (figure 2b). Ey ants showed no difficulties in heading home (V test: Ey $n = 20, p < 0.001$), but Oc foragers displayed random directional choices (figure 2b; V test: Oc $n = 47, p = 0.06$). The directional information encoded by the DRA is not transferred to the compass to which the ocelli contribute, supporting the hypothesis of two distinct compasses. The random directional choices of Oc ants could be also due to the unlikely possibility that ocelli might not be functional for several minutes after the removal of the paint.

4. DISCUSSION

After travelling a two-leg foraging route, ants on an unfamiliar test-field with covered compound eyes but open ocelli (figure 2a; Oc) did not compute direction

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Figure 1. (a) Different test conditions with sham painted control ants (Ct), ants with covered ocelli (Ey) and ants with covered compound eyes (Oc). Control ants were painted on a region of the head that covered neither ocelli nor compound eyes. (b) Directional choices of zero-vector (ZV) ants released on unfamiliar terrain with ocelli input only (Oc) after a straight outbound and inbound trip (route is not to scale). Circular histogram shows ants' headings after travelling 0.6 m in sectors of 15°. Black arrow, mean vector of the distribution. Black arc, 95% confidence intervals. Black arrowhead, nest compass direction.

Figure 2. Directional choices of treated ants released on unfamiliar terrain after a straight or two-leg outbound trip (routes are not to scale). Circular histograms show the ants' heading after travelling 0.6 m in sectors of 15°. Black arrow, mean vector of the distribution. Black arc, 95% confidence intervals. Black arrowhead, nest compass direction. Star, significant orientation (V test, $p < 0.001$). (a) Headings of ants released on unfamiliar terrain with both compound eyes and ocelli inputs (Ct), compound eye input only (Ey) or ocelli input only (Oc). Grey arrowhead, compass direction opposite to the second leg of the outbound route. (b) Headings of ants with covered ocelli during the straight outbound trip and released on unfamiliar terrain with compound eyes input only (Ey) or ocelli input only (Oc).
and distance towards the nest; instead these ants headed in a direction opposite to the last leg of travel. These results are consistent with the behaviour of the ZV ants with covered eyes but functional ocelli (figure 1b; ZV_Oc), heading opposite to the home direction that was the direction of the last leg of travel. The directional information mediated by the DRA of the compound eyes appears to be inaccessible to ocelli (figure 2b). This suggests the presence of two distinct mechanisms. The DRA provides directional information to the global path integrator—which keeps track of the nest position—whereas ocelli supply directional information to a distinct mechanism—which buffers the most recent leg of travel and overrides previous information (electronic supplementary material, figure S1b). Then what could be the function of the additional directional compass driven by the ocelli? Ant ocelli might act as a supporting system for the global path integrator mediated by the compound eyes. However, foragers with continuously covered ocelli during the two-leg outbound route, headed solidly in the direction of the fictive nest when released on the test-field (electronic supplementary material, figure S1a). Therefore, ocelli are not necessary for global path integration.

It could be assumed that the function of ant ocelli resembles that of flying insects in supplying a means of maintaining and controlling direction and body orientation through a variety of cues (e.g., horizon, image motion, sun). However, we know that the homing paths of ants with covered compound eyes and uncovered ocelli (Oc) are fairly tortuous and not as accurately oriented as those of ants with compound eyes only (Ey). In fact, Oc ants’ homing paths were almost as tortuous as paths of totally blinded ants [6]. Therefore, it seems that the maintenance and stabilization of the homing paths in walking ants are mediated by the compound eyes and not the ocelli. Another explanation is thus required.

Melophorus bagoti foragers follow visually guided idiosyncratic routes through a cluttered environment [12]. Sometimes, a newly appeared obstacle or the presence of aggressive conspecifics from other colonies may force the forager to leave her familiar route, ending up in unfamiliar surroundings. In such cases, the ocelli-driven compass could possibly allow the ant to return to her well-known route rather than homing towards the nest through unknown terrain. The discovery of this distinct navigational mechanism mediated by the ocelli also raises mechanistic and evolutionary questions. Ocelli are known for their fast neurological response [5] and it may be advantageous to process directional information independently. The directional information encoded by the ocelli appears indeed to be processed separately from that derived from the compound eyes, but what about the odometric information? Is the ocelli-mediated compass processed together with the step-counter that is also used for the global path integrator, or is it processed with another odometric cue such as optic flow or encoded only as a direction without odometric information? Interestingly, in many ant species ocelli are seldom found in workers but often present in winged alates [13] and other flying insects [7]. Therefore, the ocelli-driven compass might be just an exaptation derived from flying ancestors or flying reproductive alates. Conversely, the question of whether the ocelli of alates are used for some directional purpose, as they are by the foragers in this study, or merely for flight and gaze stabilization as in other flying insects [4,7], remains to be investigated.

In summary, our results demonstrated that ocelli could not by themselves mediate path integration in ground-based insects. Such a discovery, with its associated mechanistic, functional and evolutionary questions, reminds us how complex, flexible and well-adapted the structure underlying insect navigation is.

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