RESEARCH ARTICLE

Ocelli contribute to the encoding of celestial compass information in the Australian desert ant *Melophorus bagoti*

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SUMMARY

Many animal species, including some social hymenoptera, use the visual system for navigation. Although the insect compound eyes have been well studied, less is known about the second visual system in some insects, the ocelli. Here we demonstrate navigational functions of the ocelli in the visually guided Australian desert ant *Melophorus bagoti*. These ants are known to rely on both visual landmark learning and path integration. We conducted experiments to reveal the role of ocelli in the perception and use of celestial compass information and landmark guidance. Ants with directional information from their path integration system were tested with covered compound eyes and open ocelli on an unfamiliar test field where only celestial compass cues were available for homing. These full-vector ants, using only their ocelli for visual information, oriented significantly towards the fictive nest on the test field, indicating the use of celestial compass information that is presumably based on polarised skylight, the sun's position or the colour gradient of the sky. Ants without any directional information from their path-integration system (zero-vector) were tested, also with covered compound eyes and open ocelli, on a familiar training field where they have to use the surrounding panorama to home. These ants failed to orient significantly in the homeward direction. Together, our results demonstrated that *M. bagoti* could perceive and process celestial compass information for directional orientation with their ocelli. In contrast, the ocelli do not seem to contribute to terrestrial landmark-based navigation in *M. bagoti*.

Key words: ocelli, compound eye, ant, navigation, celestial compass, compass orientation.

INTRODUCTION

Almost all animals, from humans to insects, encounter the problem of navigating through spatial environments. Visual orientation is often an important mode of animal navigation (Cheng, 2006; Gibson, 1998; Srinivasan, 1998). The visual system of many insects, for instance, is particularly sophisticated: in addition to their large multifaceted compound eyes they possess one, two or three less-conspicuous ocelli (reviewed by Taylor and Krapp, 2007). For over a hundred years, scientists have studied the function and evolution of compound eyes (Land and Fernald, 1992; Nilsson and Kelber, 2007). For instance, it has been shown that insect compound eyes are fundamental for orientation and colour vision, and that they are sensitive to UV-light and polarised skylight (von Frisch, 1914; Wehner, 1984; Wehner et al., 1996; Briscoe and Chittka, 2001). In contrast, little is known about the function of the ocelli. In locusts, it has been demonstrated that ocelli are light sensitive (Wilson, 1978) and can serve as a visual flight and gaze stabiliser and aid in detecting the horizon (Taylor, 1981) (for reviews, see Goodman, 1981; Taylor and Krapp, 2007). Ocelli are usually bigger in crepuscular and nocturnal flying insects and probably play a role in flight control (Warrant, 2008).

In central place foragers such as social hymenoptera, visual navigation is particularly important for finding a food source as well as returning to the safety of the colony. The Australian desert ant *Melophorus bagoti* is one of these central place foragers. The extreme heat of the ground prevents the ants from using chemical trails and every single forager has to learn her own routes

independently (Christian and Morton, 1992; Muser et al., 2005). To find food and their way back to the nest, *M. bagoti* rely mainly on two navigational strategies: landmark learning and path integration (reviewed by Wehner et al., 1996; Collett and Collett, 2002; Cheng et al., 2009). Landmark guidance is based on learning and memorising the positions of terrestrial landmarks, such as bushes and trees, as well as the panorama and the skyline along their route and enables the ants to relocate a precise earth-based absolute location (Graham and Cheng, 2009a; Graham and Cheng, 2009b; Wystrach et al., 2011). In contrast, path integration is based on egocentric information and enables foraging ants to return to the nest on the shortest direct track at any time and from any position without help of terrestrial cues such as landmarks or panoramic views (Graham and Cheng, 2009a; Kohler and Wehner, 2005; Narendra, 2007b; Narendra et al., 2008). To use path integration, the ants derive the directional (compass) information from the polarised skylight and the sun's position (reviewed by Wehner, 2003), while a special odometer, a step-counter (Wittlinger et al., 2006), provides them with information on the distance (Narendra et al., 2007a). Compass and odometric information are integrated to compute a vector home, which is, in turn, continuously updated according to the distance and direction of the nest relative to the insect.

Both landmark learning and path integration are dependent on the compound eyes of *M. bagoti*, but the role and function of the ocelli have yet to be revealed. It is assumed that the ocelli are connected to the celestial compass, which registers the pattern of

the polarised skylight and the position of the sun, as has been shown in the North African desert ant *Cataglyphis bicolor*, where foragers can perceive celestial compass information with their ocelli (Fent and Wehner, 1985). In the present study we analysed the role of the ocelli in spatial navigation in the desert ant *M. bagoti*. More precisely, we determined whether the ocelli could be used to determine direction according to celestial cues and/or terrestrial landmark information.

MATERIALS AND METHODS
Study area
From November 2009 to March 2010, ~10 km south of Alice Springs, Northern Territory, experiments on *Melophorus bagoti* Lubbock 1883 were carried out in the semidesert of central Australia. All tested ants were foragers of the same colony located in a cluttered habitat that consisted mainly of *Acacia* woodland, *Triodia* grassland and buffel grass (*Cenchrus ciliaris*) (Muser et al., 2005; Schultheiss et al., 2010). Throughout experimentation, the sky was either clear or only slightly cloudy. Therefore, the ants could in principle rely on celestial compass cues – primarily the polarised skylight but also the position of the sun and the colour gradient – for the determination of heading directions (Wehner and Müller, 2006). Experiments were usually carried out from 09:00 to 17:00 h with a break during noontime, a period during which foraging activity decreases.

Experimental set-up
A feeder with cookie crumbs and mealworm pieces was embedded in the ground 10 m away from the nest. The distance between nest and feeder lies within the usual foraging area of *M. bagoti* and the ants could be trained to scamper repeatedly between their colony and the feeder. The training field was surrounded with landmarks such as trees, rocks, bushes and tussocks. The test field was situated 60 m away from the training field in order to avoid any familiar landmarks, including the shape of the skyline. Thus, the foragers could rely only on the celestial compass information on the test field during their homebound runs.

To assess the directional choice of the ants in tests, a goniometer was used. It consisted of a wooden board (1.2 m diameter) divided into 24 sectors of 15 deg each. All sectors were numbered to simplify the recording of the ants' initial direction (0.6 m) from the centre of the goniometer. For an assessment of the path direction later in the journey, the position at which the foragers crossed a 3.0 m circle around the release point was noted (see Data analyses). The distance was sufficiently long, but a good deal shorter than the ~44% of outbound distance that *M. bagoti* runs off on average on an unfamiliar test field before initiating looping search movements (Narendra, 2007a; Narendra, 2007b). To trace the homebound path of the foragers, a grid was set up in both the test and training fields. The grids were divided into 100 (10×10) 1 m squares using pegs and string and were oriented in the same direction as the nest-feeder direction in the training field. A goniometer placed at the position of the feeder was used for tests on the training field.

Experimental procedure and treatment conditions
Forging 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. During training, the ants could gain familiarity with the vicinity. All marked ants were able to shuttle back and forth between the feeder and the nest for at least 2 days before they were subjected to one of the four treatment conditions and tested. Just before a test (and hence not during training), we covered either the eyes (Oc), the ocelli (Ey) or both compound eyes and ocelli (Bl) with acrylic paint (Fig. 1). In addition, a sham control group was included in which a small dot of paint was placed dorsal to the ocelli and between the compound eyes (Sh) (Fig. 1). We painted ants using household pins with the help of a magnifying glass. We placed the manipulated, painted ants back in the feeder and, after they grabbed a food item, we transferred them in the dark in small plastic tubes to the release point on the test or training field. To ensure a high homing motivation, only ants that held on to a food item were tested. The tested ants were always released at the centre of the goniometer. However, the exit direction from the plastic tube was chosen randomly to prevent any potential directional biases. The sector crossed on the goniometer at 0.6 m and the subsequent paths taken by the ant were recorded. Recording of the paths was conducted by following the route of the homing ant and drawing the route of each ant on a piece of paper that was printed with a similar grid as those found on the test and training fields. The recording of the path ended when the ant had left the grid or lost its food item. All paths were digitised and analysed (see Data analyses).

Two experiments were conducted. First, to investigate whether the ocelli are used to encode celestial compass information, we tested the four treatment groups as full-vector (FV) ants on the distant test field. These ants were removed from the feeder, painted as one of the four treatments (i.e. Oc, Ey, Bl or Sh) and then taken to the test field after they grabbed a piece of food. FV ants are, in principle, able to gather both terrestrial (landmarks and skyline contour) and celestial cues (vector direction) to find the way back to their nest. The unfamiliar test field, however, excluded the use of familiar landmarks and panoramic information. Therefore, the FV ants were reduced to using information from the sky, the sun's position and the polarised skylight pattern for homing. Second, to assess whether the ocelli are used to encode familiar terrestrial landmarks or panoramic information, we tested the same four treatment groups as zero-vector (ZV) ants on the training field. Homing ants were captured just before they entered the nest entrance, manipulated and released on the training field goniometer. By capturing foraging ants just before entering the nest, the directional (vector) information was set to zero, thus excluding sky compass information based on path integration. Past research has shown that ZV *M. bagoti* do not use sky compass information and rely instead on the shape and contour of the panorama (Graham and Cheng, 2009a). We thus constrained the foragers to rely only on their visual memory of terrestrial landmarks and the panorama to find the way back to the
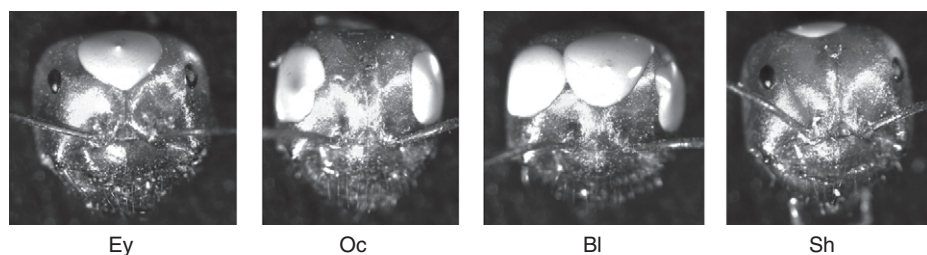

Fig. 1. *Melophorus bagoti* in different test conditions: Ey, open compound eyes and covered ocelli; Oc, open ocelli and covered compound eyes; Bl, covered compound eyes and ocelli; Sh, sham condition with small dot of paint between the compound eyes and dorsal of the ocelli.

Ey   Oc   Bl   Sh

nest. Otherwise, tests on the training field proceeded in the same manner as tests on the test field.

Data analyses

We used circular statistics to analyse the directions chosen by the tested ants at 0.6 and 3 m from the release point (Batschelet, 1981). The *V*-test for circular uniformity with a given direction was used to determine whether the distribution of the orientations of the ants from each group was significantly different from a random distribution and with the nest direction (or relative nest direction on the test field) within the 95% confidence intervals. The circular *K*-test was used to investigate whether two samples had significantly different concentrations. Because of multiple comparisons between the test groups, we lowered the alpha level in the *K*-test from 0.05 to 0.017. Furthermore, the individual paths of the tested ants were digitised and analysed at a fine scale in terms of their sinuosity. Two sinuosity measures were computed for each path: meander and straightness. To calculate both of these measures, we divided the path into 0.3 m line segments. A circle of 0.3 m radius was placed at the start of a route and a straight line segment was drawn to where the route crossed this circle; this defined segment 1. The circle was then centred at the end of segment 1, and the crossing between the

route and the circle defined the end of segment 2, etc. To calculate straightness, the direction of each segment (from start to end) was plotted on a circular plot, and the *r*-parameter in circular statistics of all the segments pooled was defined as straightness, with values ranging from 0 (no dominant orientation) to 1 (straight orientation). The meander index measures how much the path changes direction from segment to segment, or how much the path 'wiggles' along the way. The absolute angular deviation (rad) from one segment to the next was averaged over all segments. Thus, a deviation of 0 rad indicates that the two segments are collinear whereas a deviation of π rad means that the ant turned straight back.

RESULTS
Full-vector ants on the test field

Except for the totally blinded foragers (FV–Bl), all treatment groups showed an unambiguous orientation towards the fictive nest at 0.6 m (*V*-test, *P*<0.001) and at 3.0 m distance (*V*-test, *P*<0.001) (Fig. 2). Foragers with covered eyes (FV–Oc), covered ocelli (FV–Ey) or a dot on the head (FV–Sh) were able to use the celestial compass information to run in the direction of their fictive nest. The absence of any significant orientation towards the fictive nest in the blind group (FV–Bl), both at 0.6 m (*V*-test, *P*=0.729) and at 3.0 m (*V*-test,
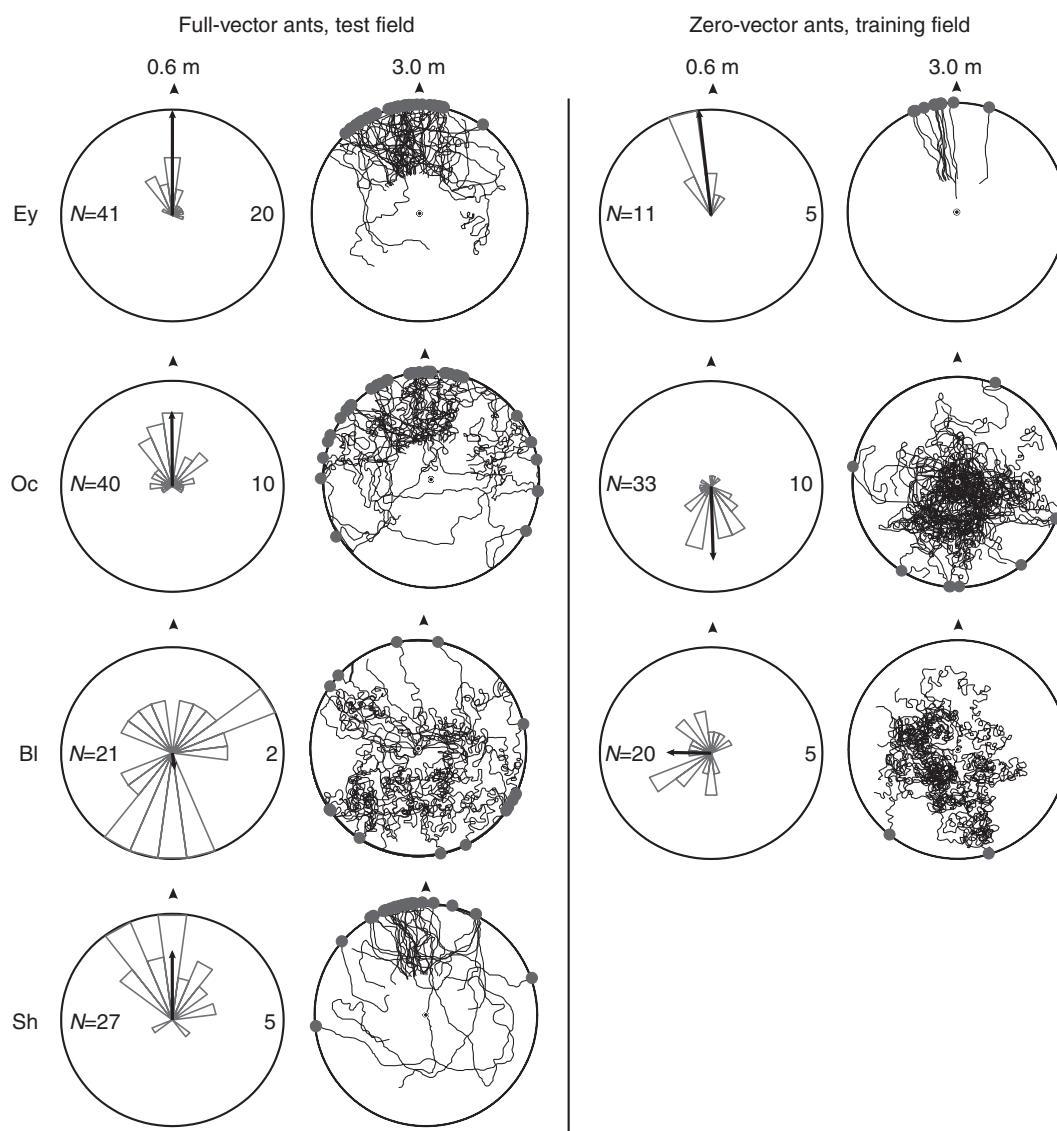

Fig. 2. Ocelli functions were tested in *M. bagoti* under four different conditions: Ey, Oc, Bl and Sh. Each row presents one treatment out of the four tested groups. Circular histograms show the headings of the tested ants after travelling 0.6 m (with each sector of 15 deg). The number of ants per sector is relative to the number on the right side of the histogram circle. A plot of the paths of the different groups within a 3.0 m circle around the release point (the paths were not recorded during the initial 0.6 m on the goniometer) is also shown. Direction and length of the black arrows represent the direction and length of the mean vector for each distribution. Grey circles mark the positions on the homebound trips of each tested ant when she crossed a circle of 3.0 m radius centred at the release point. The correct nest direction is indicated by the small arrowhead on the top of each histogram. The central point in the histograms symbolises the release point.

P=0.892), showed, not surprisingly, that either the eyes or the ocelli were necessary for using celestial information and that no non-visual source of direction was available to the ants (Fig. 2).

We next compared the inter-individual scatter of the homing direction between pairs of treatment groups at the goniometer (0.6 m) and after travelling 3.0 m, excluding the disoriented blind ants. Ants with compound eyes only (FV–Ey) were more accurate than ants with ocelli only (FV–Oc) at 3.0 m (K-test, P<0.001). The initial headings on the goniometer showed no significant difference between groups (Fig. 2).

Both measures of sinuosity differed clearly across treatment groups, with the blind ants showing the highest meander and lowest straightness (Fig. 3). Both meander and straightness differed significantly between groups (one-way ANOVA, meander: $F_{6,186}$=71.83, P<0.001; straightness: $F_{6,186}$=24.33, P<0.001). Tukey's *post hoc* tests were then used to compare all pairs of groups (Fig. 3). The FV–Oc foragers displayed a similar sinuosity to the FV–Sh and FV–Ey foragers. However, FV–Oc foragers showed a significantly higher meander than FV–Sh (Tukey's *post hoc* test, P<0.001) or FV–Ey (Tukey's *post hoc* test, P<0.001) foragers (Fig. 3). No differences in straightness between FV–Sh, FV–Ey and FV–Oc foragers were found (Tukey's *post hoc* test, P>0.73).

Zero-vector ants on the training field

After being released on the training field, the blinded ants (ZV–Bl) appeared lost and displayed no significant orientation in the nest direction at either 0.6 m (V-test, P=0.426) or 3.0 m (V-test, P=0.960). Foragers with covered eyes and uncovered ocelli (FV–Oc) also displayed no significant orientation towards the nest direction,

neither after 0.6 m (V-test, P=0.999) nor after 3.0 m (V-test, P=0.978) (Fig. 2). Ants with covered ocelli but eyes open (ZV–Ey), however, showed a clear nestward orientation at both 0.6 m (V-test, P<0.001) and 3.0 m (V-test, P<0.001). Not surprisingly, sham ants with both ocelli and eyes functioning (ZV–Sh) were also significantly oriented towards the nest at both 0.6 m (V-test, P<0.001) and 3.0 m (V-test, P<0.001) (Fig. 2).

Because of the fact that only some tested ants from the ZV–Oc and ZV–Bl groups passed the 3.0 m circle around the release point on the training field, a comparison between the scatter of the homing directions became unnecessary.

The sinuosity of the tested ant paths on the training field showed significant differences between the test groups (one-way ANOVA, meander: $F_{6,186}$=71.83 P<0.001; straightness: $F_{6,186}$=24.33, P<0.001). In terms of meander (Tukey's *post hoc* test, P<0.001) and straightness (Tukey's *post hoc* test, P<0.001), ZV–Ey foragers had less sinuous homing paths than ZV–Oc or ZV–Bl foragers (Fig. 3). Accordingly, all ZV–Ey foragers passed the 3.0 m circle and ran back to the nest on the training field. In contrast, only 27% of the ZV–Oc foragers and 1% of the ZV–Bl foragers reached 3.0 m in any direction (Fig. 2).

DISCUSSION

The purpose of the present study was to investigate the navigational functions of the ocelli in the Australian desert ant *M. bagoti*. This species uses vision in two interacting systems of navigation: landmark learning, which is based on terrestrial cues, and path integration, which relies on celestial cues and a step counter (reviewed by Cheng et al., 2009).

The first part of this study tested whether *M. bagoti* foragers use their ocelli to encode celestial compass cues in an unfamiliar test field. Because the totally blind ants (FV–Bl) were not able to find the nest direction on the test field, we can conclude that visual compass information, from either the compound eyes or the ocelli, is essential for determining directional headings in path integration. In contrast, ants with untouched eyes (FV–Sh) as well as ants with covered ocelli (FV–Ey) could readily orient towards the fictive nest on the test field. The crucial tested group with covered eyes but uncovered ocelli (FV–Oc) also oriented their homebound trips in the direction of the nest, revealing that ocelli contribute to the encoding of celestial compass information (Fig. 2).

The second part of the study focused on the ability of *M. bagoti* ocelli to detect terrestrial cues. In order to determine whether ocelli are sufficient for processing terrestrial visual cues, we tested ZV ants with no directional vector information from the path integrator in the familiar training field. ZV–Bl foragers ran disoriented over the training field with no peak in directional heading. ZV–Ey and ZV–Sh foragers showed good orientation towards the nest and were therefore able to use terrestrial cues for homing (Fig. 2). This replicates earlier findings in which ZV ants were shown to home successfully using terrestrial landmarks, and confirms that this ability is based on the compound eyes (Narendra, 2007b; Graham and Cheng, 2009a; Graham and Cheng, 2009b; Wystrach et al., 2011). Crucially, ants with only ocelli for acquiring visual information (ZV–Oc) failed to orient towards the nest (Fig. 2). These ants proved unable to rely on their ocelli for using any kind of terrestrial information. We can conclude, as the main outcome of this study, that the ocelli in *M. bagoti* can read the celestial compass, whose nature requires and deserves more investigation, but probably does not encode terrestrial landmark cues.

Surprisingly, the ZV–Oc foragers tended to head more in the direction opposite to the nest (Fig. 2). We plan to study this
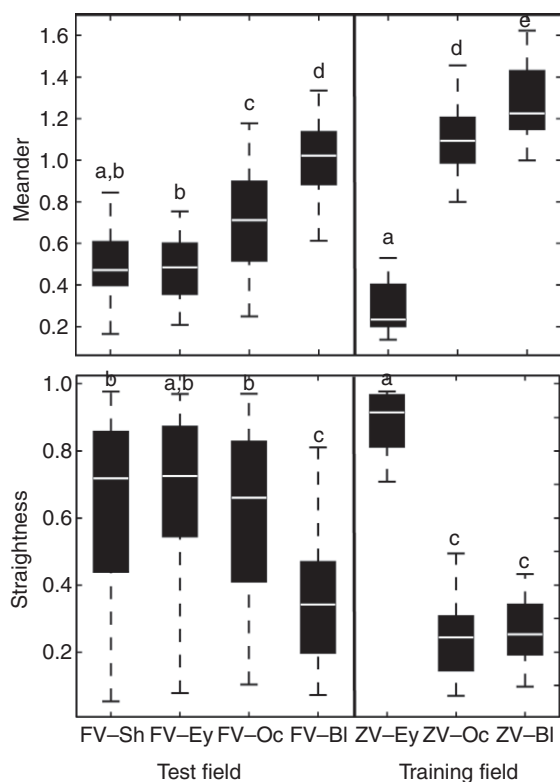

Fig. 3. Sinuosity of the paths. Meander and straightness in all tested *M. bagoti* groups from full-vector (FV) ants on the test field and zero-vector (ZV) ants on the training field. Whiskers correspond to the extreme values of each testing group. Test groups with identical letters are not significantly different by Tukey's *post hoc* test.

phenomenon in greater detail as it might illuminate the nature of the compass processing that is based on the ocelli. At this point we can only rule out certain explanations. The bias in the path directions was not due to the form or direction of shades and shadows on the training field or the sun's position because the tests were performed throughout the day. Possible odours from conspecifics or food were also unlikely as explanations. The same trend was found even when the release point was much farther away from the feeder (data not shown).

Another interesting result is that ZV–Bl foragers walked less in any direction than FV–Bl foragers (Fig. 2, Bl). The ZV–Bl foragers just made several loops around the release point, a pattern characteristic of the behaviour of ants in searching for the nest (Narendra et al., 2007b). Only 10% of the ZV–Bl foragers (2/20) reached the edge of the 3.0 m radius circle whereas 76% of their FV counterparts (15/21) passed this threshold (Fisher's exact test, $P<0.001$). Although the travel was not oriented, it seems that the odometric information supplied by the path integrator induced the FV–Bl foragers to walk both farther and with less winding as compared to the ZV–Bl ants (Tukey's *post hoc* test, meander: $P<0.001$).

The analysis of the sinuosity of paths provides further information on the ocelli-based compass. Fent and Wehner (Fent and Wehner, 1985) found that homing FV–Oc *C. bicolor* ants performed a more winding path than ants with uncovered compound eyes, a finding that matches our quantitative results. In FV ants on the test field in the present study, the straightness measure did not differ significantly between groups of ants with visual input (FV–Oc, FV–Ey and FV–Sh). However, the meander of FV–Oc foragers was significantly higher than that of FV–Ey and FV–Sh foragers (Figs 3, 4). One hypothesis is that the FV–Oc foragers needed to perform a more winding homebound trip to obtain the required celestial compass information (Fig. 4). A second hypothesis is that ocelli may be less accurate than compound eyes for estimating the direction from the celestial compass, thus inducing more waggling (Fig. 4). Both hypotheses would explain why the group using only ocelli for navigation was more scattered in their homing directions at 3.0 m. A third hypothesis concerns the capacity to perceive terrestrial landmarks. In contrast to the ocelli system with its characteristically poor spatial resolution (reviewed by Taylor and Krapp, 2007), compound eyes are able to perceive terrestrial landmarks, a process that might help to reduce the sinuosity of the paths. Surrounding landmarks probably help the ant to steer in her heading direction. This would explain why ants with covered compound eyes display more winding paths. Perception of familiar landmarks (as opposed to unfamiliar landmarks) might especially help the ants to steer, perhaps explaining why the ZV–Ey foragers in the presence of the familiar terrestrial landmarks had a lower meander than FV–Ey foragers on the unfamiliar test field (Tukey's *post hoc* test, meander: $P=0.024$; Fig. 3).

Our results from FV ants replicate in general what was found in the North African desert ant *C. bicolor* (Fent and Wehner, 1985). Tested as FV ants on an unfamiliar test field, *C. bicolor* foragers with only ocelli (and their compound eyes covered) also travelled back in the general direction of the fictive nest. They showed larger directional scatter than ants with compound eyes open. Moreover, further manipulations implicated the pattern of polarised skylight as the source for the ocelli-based compass in *C. bicolor*. By moving a small trolley over the ant as she travelled, the view of the sun could be blocked, the spectral pattern of light gradients neutralised and the direction of the polarised sky pattern changed. When the pattern of polarised light was rotated, the ants followed the rotated home direction according to the polarised light. Indeed, in desert ants with normal vision, the role of the polarised light is far more important than that of the position of the sun (Wehner and Müller, 2006). In *M. bagoti*, the relative importance of spectral cues, the sun's position and the polarised skylight in the celestial compasses – both that based on the compound eyes and that derived from the ocelli – has yet to be determined. All these cues are used in insect celestial compass systems studied to date (Wehner, 1984; Wehner and Müller, 2006). The ocelli of desert ants are UV sensitive and this is a prerequisite for the detection of polarised light in bees and ants (Wehner, 1984). We strongly suspect that the polarised skylight provides essential navigational information for *M. bagoti* as well, both for their ocelli and for their compound eyes. The possible roles of spectral gradients and the position of the sun remain unknown.

Although *M. bagoti* ocelli can process celestial compass information for orientation, they were incapable of encoding sufficient terrestrial visual cues to lead the ants back to their colony. It is already known that ocelli can support the compound eyes in phototaxis because of their high light sensitivity (Cornwell, 1955). The large and thick neurons in ocelli (L-neurons) enable a rapid transmission of information to the next processing stage and contribute to the functions of the ocelli as flight and gaze stabilisers (Taylor, 1981) (reviewed by Taylor and Krapp, 2007). The role of ocelli in navigating in dim light has also been reviewed (Warrant, 2008). None of these studies, however, mention any form of landmark perception mediated by the ocelli. Ocelli in flying insects do not provide detailed images on the retina, which implies that little or no spatial information from the visual scene is extracted (reviewed by Taylor and Krapp, 2007). Our negative results on the ocelli of zero-vector *M. bagoti* corroborate the implication raised by these studies that the ocelli are not used to perceive terrestrial
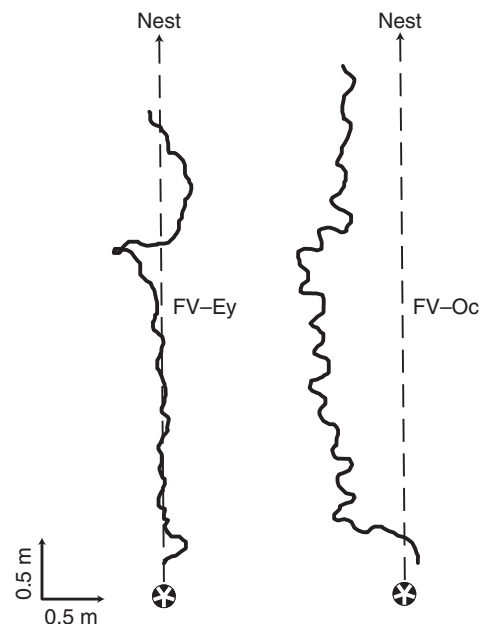

Fig. 4. Typical homing path of a full-vector (FV) ant on an unfamiliar test field where only celestial cues could be used to home to the fictive nest. The left path was performed by a *M. bagoti* forager with covered ocelli and uncovered compound eyes (FV–Ey); the right path shows the more winding homing path from a forager with covered compound eyes and uncovered ocelli (FV–Oc). The small goniometer represents the release point and the dashed line the direct connection between the release point and the fictive nest.

landmark cues. In general, it seems that the function of ocelli differs between walking insects such as ants and flying insects such as flies. So far it has been shown that ants use ocelli for navigational purposes whereas flying insects use them mainly for flight and gaze stabilisation.

How might the sky compass perception derived from the compound eyes and from the ocelli interact with each other? As mentioned before, the function of the ocelli is often characterised as a support for the compound eyes. Perhaps the ocelli supply a compass reading for the vector based on path integration that is combined with the compass reading derived from the compound eyes. The use of multiple sources of spatial information would increase accuracy (Cheng et al., 2007). If the ocelli add accuracy, homing ants with both compound eyes and ocelli (FV–Sh) should have performed better than ants with only compound eyes (FV–Ey) in the test field. But we found no significant differences in the homing performance of FV–Sh and FV–Ey foragers, neither in the scatter of directional headings nor in their straightness or meander (Figs 2, 3). It is possible, however, that the additional accuracy contributed by the ocelli is too little to be measurable by our methods. In blowflies, it has been shown that the neuronal pathways of visual input from compound eyes and ocelli are combined by common interneurons (Parsons et al., 2010). Thus, the speed of the ocelli and the accuracy of the compound eyes are both utilised to good advantage. In ants, however, the questions of whether one sensory system (ocelli) has access to the other (compound eyes) and whether the information from the path integrator is processed differently in each system remain unanswered. We would not rule out the hypothesis that the ocelli supply a different kind of compass information, and we are currently investigating this possibility.

In summary, we have demonstrated that in *M. bagoti*, as in *C. bicolor* (Fent and Wehner, 1985), the ocelli supply the ants with celestial compass information. In addition, we have demonstrated that the ocelli of *M. bagoti* could not utilise terrestrial landmark information for homing, at least under our conditions of testing. The function of the ocelli-based compass in *M. bagoti* may extend beyond or differ from supplying additional compass information based on celestial cues, a topic that we are currently investigating.

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