

Visual Matching in the Orientation of Desert Ants (*Melophorus bagoti*): The Effect of Changing Skyline Height

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Abstract

Ants are known to use the terrestrial visual panorama in navigation. Recent evidence has accumulated for the use of the currently perceived visual panorama to determine a direction to head in. The pattern of the height of the terrestrial surround, the skyline, is one key cue for the Central Australian red honey ant *Melophorus bagoti* in determining a direction of travel. But ants might also possess some mechanism to match the skyline heights encountered during training, which functions to steer away from regions whose skyline is too high and towards regions whose skyline is too low. We made an initial test of this hypothesis by training ants to visit a feeder centred between two experimentally constructed walls of black cloth. Trained ants were then tested for their initial homing direction with the walls retaining their heights as encountered in training (controls), with one of the walls lowered or raised in height, or with one wall lowered and the opposite wall raised. Wall-height manipulations deflected the initial headings of ants towards the lower wall, with combined wall lowering and wall raising changing the initial headings by $\sim 30^\circ$ when compared with controls. The results suggest that the ants combined the dictates of the panorama in determining the best direction of travel (a heading towards the nest) with some attractor mechanism that functions to establish the skyline heights of training conditions (a heading towards the lower wall).

Introduction

Insects use three main systems in navigation: path integration (Collett & Collett 2000; Wehner 2003; Wehner & Srinivasan 2003), navigation based on terrestrial cues (Wehner 2003; Cheng et al. 2009) and systematic search (Wehner & Srinivasan 1981; Reynolds et al. 2007a,b; Schultheiss & Cheng 2011; Schultheiss et al. 2013). A fourth distinct system of backtracking, however, has just been reported (Wystrach et al. 2013b). In path integration, the insect keeps track of the distance and direction from the starting point as it travels and then runs or flies off the calculated vector when it is time to home (Collett & Collett 2000; Wehner 2003; Wehner & Srinivasan 2003). In using terrestrial cues, visual cues in the surrounding panorama play a prominent role (von Frisch & Lindauer 1954; Cartwright & Collett 1983; Graham & Cheng 2009a; Wystrach et al. 2011a), although cues in other sensory modalities are also used

(Steck et al. 2009; Buehlmann et al. 2012). Terrestrial visual cues are often used to chart stereotypical routes home (Wehner et al. 1996; Collett et al. 2001; Kohler & Wehner 2005; Wystrach et al. 2011b; Mangan & Webb 2012).

The thermophilic Australian red honey ant *Melophorus bagoti* lives in a visually cluttered habitat filled with tussocks, shrubs and trees (Muser et al. 2005; Schultheiss & Nooten 2013). It has been much used recently to investigate both search behaviour (Schultheiss & Cheng 2011, 2013; Schultheiss et al. 2013) and the use of the visual panorama (Wystrach et al. 2011a,b, 2012), the topic of the current account. *Melophorus bagoti* uses the skyline to orient (Graham & Cheng 2009a,b). The skyline is the distribution of the heights of terrestrial objects. When these skyline heights found at a feeder location were recreated approximately using a uniformly black surround, the ants followed the dictates of the artificial surround (Graham & Cheng 2009a), even when it conflicted with the compass direction home according to the sky compass (Wehner 1994), which indicates the compass direction from feeder to home. It is thought that a large part of the surrounding panorama is used, and not just isolated landmarks, even prominent ones (Wystrach et al. 2011a). Thus, the ants did not follow the dictates of a large beacon (3 m wide and 2 m high) usually found just behind their nest, when that beacon was displaced away from its original position. We call the use of skyline and quite likely other features of the distal terrestrial panorama to determine a direction of travel a terrestrial visual compass, the term 'terrestrial' differentiating it from the celestial compass based on cues emanating from the sky. What counts as 'distal' remains for the moment less than fully defined, but we mean to exclude behaviours by which an ant avoids or negotiates nearby landmarks along its route (Collett et al. 2001; Kohler & Wehner 2005; Wystrach et al. 2011b).

The skyline might be used in another way. Based on results from displacing ants in natural surrounds (without artificial landmarks added), Wystrach et al. (2012) proposed that when the ants were off their familiar route home, skyline-height comparisons might be used to help direct the ants back to their familiar route. Once on their familiar route, the ants run home readily (Kohler & Wehner 2005; Narendra 2007; Wystrach et al. 2011b), likely relying here on a terrestrial visual compass strategy (Collett 2010; Wystrach et al. 2012). In Wystrach et al.'s (2012) model, skyline-height comparisons consist of comparing the currently viewed skyline with the remembered skyline on the route. The skylines are pegged in compass direction, that is to say, skyline elevations are mapped onto directions as defined by the sky compass of the ants. If the perceived skyline is too low in a certain compass direction, it indicates that the ant has been displaced away from that direction, and ants should be attracted to that direction. If on the other hand the perceived skyline is too high, it indicates that the ant has been displaced towards that direction, and ants should be repelled from that region. Whatever the precise mechanism, some attractor mechanism might function to lead ants to locations at which skyline heights match what was found on their familiar route.

Past research on other ants provides evidence that ants sometimes use heights of terrestrial objects in navigation. Thus, in controlled laboratory situations, Pratt et al. (2001) manipulated the height of a wall along the route of the small ant *Leptothorax albipennis*. Changing the wall height along their route led the ants to veer towards a wall that was too low, and away from a wall that was too high. Similarly, wood ants *Formica rufa* in a laboratory also adjusted their routes parallel to an extended wall when the wall's height was changed (Graham & Collett 2002), again veering closer to a wall that was too low and away from a wall that was too high. Outdoors, in an artificial narrow channel, North African desert ants *Cataglyphis fortis* used the elevations projected by the walls to steer a course in the middle of the channel (Heusser & Wehner 2002).

Here we tested the importance of skyline heights by manipulating them directly. We created a sizeable part of the skyline for the ants artificially, using black cloth to define half the visual panorama (the left and right sides) at the starting point on the route from feeder to nest. Like Pratt et al. (2001) and Graham & Collett (2002), we then changed the height of the wall(s) on tests. Would changing skyline heights at the sides of the homebound route deflect the homing course of the ants?

Methods

Study Animals

The red honey ant *M. bagoti*, the most thermophilic ant on the Australian continent (Christian & Morton 1992), forages in the heat of the day in the summer season, when the ground temperature reaches 50°C (Muser et al. 2005; Schultheiss & Nooten 2013). They scavenge for dead arthropods and gather plant materials in a visually cluttered habitat filled with tussocks, shrubs and trees (Muser et al. 2005; Schultheiss & Nooten 2013). We studied one nest in their Central Australian habitat in the southern summer of 2012–2013, from mid-November to mid-March.

Study Site

We trained and tested ants at the grounds of the Centre for Appropriate Technology, located ~10 km south of Alice Springs town centre (23.7000°S, 133.8833°E, 608 m above sea level; Alice Springs Town Council: <http://www.alicesprings.nt.gov.au/alice-springs/location>). The landscape is dominated by the invasive buffel grass (*Cenchrus ciliaris*), which has largely replaced the native spinifex in the area. The nest was in an open area of the grounds, but trees can be seen in the surround (Fig. 1).

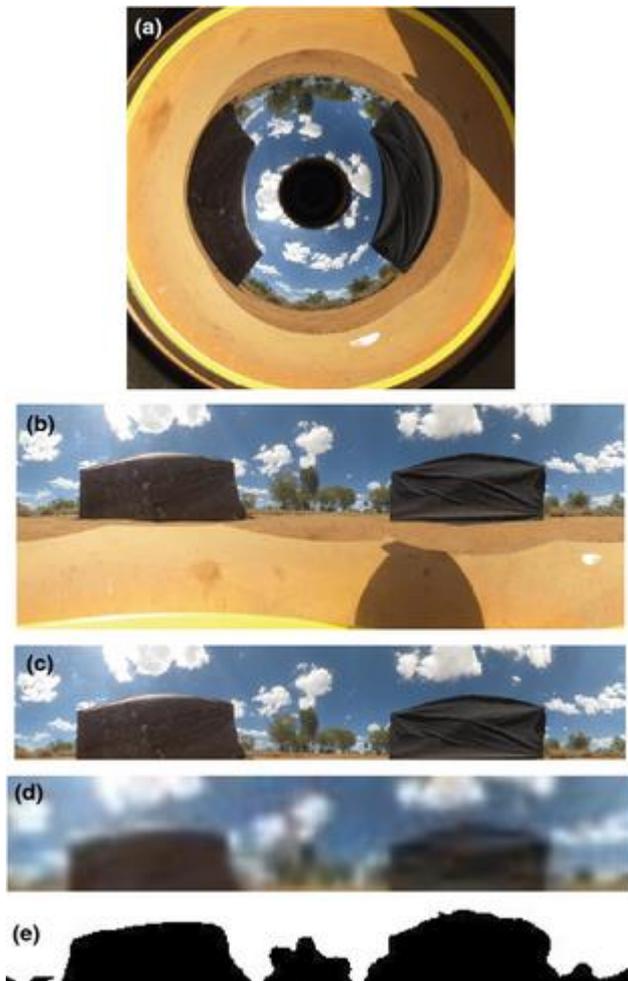


Figure 1

photograph was taken at the release point or feeder, the location at which the panoramic view was to be created. (b) The photograph was then 'unwarped' to a cylindrical view, in which the right and left edges coincide (at 180°). (c) The unwarped photograph was cropped $\sim 2^\circ$ below the horizon. (d) The photograph was blurred to 4° resolution, the approximate resolution of the ants' eyes. (e) The sky was rendered white while ground objects were rendered black.

Materials and Experimental Set-ups

To lure ants to a feeder, we sank a square plastic box ($\sim 15 \times 15 \times 9$ cm deep) into the ground and provisioned it with cookie crumbs (Arnott™ brand). The sides of the feeder were coated lightly with fluon, making it impossible for the ants to climb the walls. During training, wooden sticks were placed in the feeder box to allow easy entrance and exit. To encourage the ants to visit the feeder rather than forage elsewhere, we surrounded the area encompassing nest and feeder with thin, narrow (10 cm wide) and pliable wooden boards that were smooth on one side. This prevented most of the foragers from getting out of the enclosed area.

We set the feeder 5 m north of the nest entrance and placed artificial ‘walls’ on the two sides of the feeder, with an additional wall used in testing ants (Fig. 2). In the standard training set-up, the walls surrounding the feeder were 2 m wide, 80 cm high and 1 m from the feeder on both sides. Each wall thus projected an elevation of $\sim 38.5^\circ$ (from a height of 0.5 cm off the ground) and an azimuthal width of 90° at the feeder location. We clamped black cloth to metal stakes hammered into the ground in constructing walls. In one control condition, the wall was 80 cm high on the left and 53 cm high on the right (estimated elevation 27.7°), from the feeder-to-nest direction. The third wall was 2 m to the right of the right wall. We manipulated wall heights on tests.

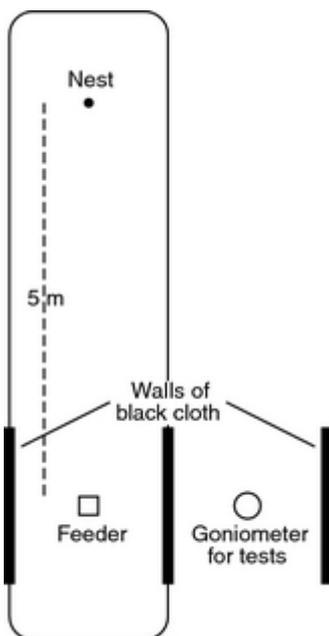


Figure 2

Schematic drawing of the set-up used for experimentation. The walls of black cloth were pegged to poles inserted into the ground, 80 cm high in training. The feeder, 5 m north of the nest, was a 15×15 cm plastic box sunk into the ground. The goniometer was a 60-cm-square board divided into 24 15° sectors. The enclosure around the nest and feeder consisted of 10-cm wide boards inserted into the ground to prevent ants from foraging elsewhere. Only the wall lengths and feeder–nest distance are drawn to scale; the rest is only schematic.

Experimental Procedures

After the experiment was set up, the ants were free to visit the feeder. We conducted experimentation during the latter part of the morning, after the ants became active ($\sim 10:00$ – $12:00$) and in the afternoon (from $\sim 14:30$ onwards). The ants were hardly active during the midday period, making it not worthwhile to conduct experiments. During January, an extreme heat wave came over the continent and especially in the Alice Springs area (Bureau of Meteorology, Australian Government 2013, www.bom.gov.au/climate/current/statements/scs43e.pdf), and perhaps due to that, the ants were barely

active in the morning; we limited experimentation to the afternoon period. On a training day, arriving ants were painted with a dot of colour (Tamiya™ brand enamel paint) signifying the day. Ants were left to shuttle between feeder and nest in training, with food provisioned in the feeder even when experimenters were absent. In a test period, the wooden sticks providing exits from the feeder were removed, trapping arriving ants. We tested only painted ants from the day before or earlier. Ants were tested individually and only tested once.

On a test, we made sure that the ant carried a piece of food, thus ensuring homing motivation. We allowed the ant to run from the feeder to the vicinity of her nest, at which point we captured the ant again, using a plastic ring to impede the movement of the ant if necessary. We transported the recaptured ant, now having run off its vector based on path integration from feeder to home (zero-vector ants), in the dark back to the release site for the test. We released the ant at the centre of a goniometer. The goniometer consisted of a wooden board divided into 24 equal-sized numbered sectors of 15° each. We scored the sector at which the ant crossed circles 15 and 30 cm in radius, with sector 1 pointing to the nest.

Experimental Conditions

Seven different conditions were effected. In five conditions, the ants were trained for at least 2 d with both black walls at 80 cm height, while tests with zero-vector ants took place just to the right of the training location (viewing from feeder to nest), with the right wall used in training serving as the left wall on tests. In the control condition (N = 25), both walls were 80 cm high. In the 80-53 condition (N = 26), the left wall was 80 cm high (training height, elevation ~38.5°), while the right wall was 53 cm high (elevation ~27.7°). We chose this lowered height because it still managed to block any view of terrestrial objects above the wall. In the 80-160 condition (N = 25), the left wall was 80 cm high (training height, elevation ~38.5°), while the right wall was 160 cm high (elevation ~57.9°). Two other conditions both raised and lowered (different) walls. The 160-53 condition (N = 27) had the left wall 160 cm high and the right wall 53 cm high. The 53-160 condition (N = 25) had these wall heights reversed, with the left wall 53 cm high and the right wall 160 cm high.

Two other control conditions tested ants at the feeder, covered by the goniometer on a test. They differed in training conditions to test whether different unequal wall heights per se would lead to biases in homing. North African desert ants *C. fortis* show a spontaneous tendency to balance retinal elevations of walls in travelling between them (Heusser & Wehner 2002). Both conditions had tests that presented training conditions to the ants, after at least 1 d of training. The 80-80 control (N = 40) trained and tested ants with both walls 80 cm high (resembling the training condition for all groups described above), while the 80-53 control (N = 40) trained and tested ants with the left wall 80 cm high and the right wall 53 cm high. Both

groups were tested at the feeder as zero-vector ants, with the goniometer placed over the feeder on tests. Thus, these groups differed from the previously mentioned control condition, in that the latter ants were tested at a location 2 m to the right of the feeder, viewing from feeder to nest. These groups were tested at a later point in the field season than the other conditions were.

Image Analysis

Because the release point on tests was not at the feeder, but displaced slightly to the right from the viewpoint of the feeder–nest direction, it is pertinent to check that the best direction to head home based on a terrestrial visual compass used at the release point is still in the feeder–nest direction, on a parallel path. It is still unclear what characteristics of the surround the ant matches, so that our image analysis should be seen as providing only a proxy measure of mismatch. The way that we calculate image differences should not be taken to reflect what the ant actually does. We compared the images of the test panorama and the training panorama when the viewing direction on a test is rotated around 360°. The skyline contours were obtained by taking a panoramic photo at the feeder (training situation) or release point (Fig. 1a), using a panoramic lens (GoPano™ brand) attached to a digital camera (Canon™ G10). A spirit level and a thick wooden board were used to make sure that each photograph was taken on a level surface. The photos were ‘unwarped’ using PhotoWarp™ software (EyeSee Inc., Pittsburgh, USA; Fig. 1b) to a cylindrical format 360° in azimuth and 120° in elevation (70° above the horizon, and 50° below; Fig. 1b). We cropped the photo ~2° below the horizon (Fig. 1c) and then blurred the picture to 4° resolution, roughly matching the resolution of this ant's eyes (Schwarz et al. 2011; Fig. 1d), and transformed it to two tones (black and white; Fig. 1e). The picture thus had 90 pixels horizontally, one every 4°. Ground objects were transformed to black and the sky to white. The result is a picture with direction along the x-axis and skyline height on the y axis. The x-axis is circular, so that the left and right edges in Fig. 1b–e (denoted as +180° and –180°, respectively, in Fig. 3) both denote the nest–feeder direction, and the middle (0° in Fig. 3) denotes the feeder–nest direction.

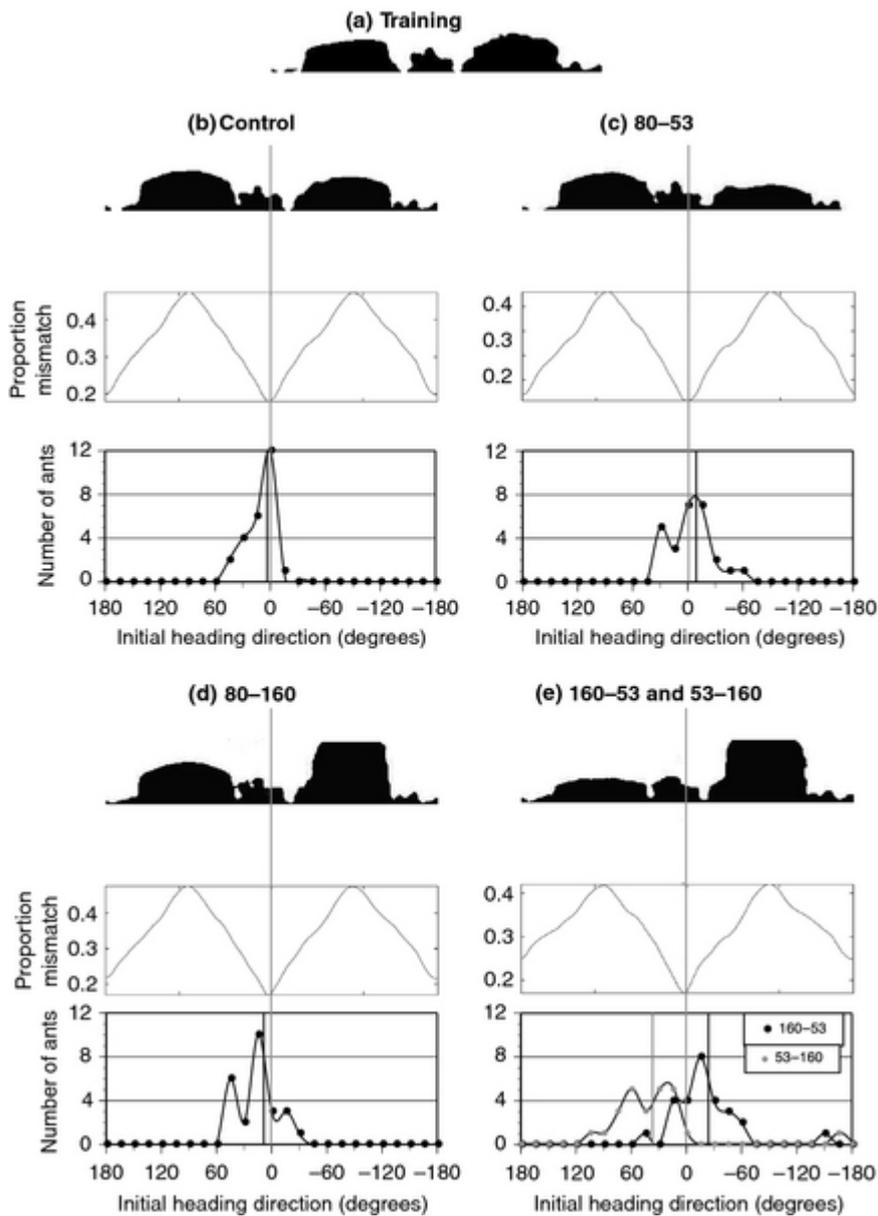


Figure 3

Skyline panoramas produced by the methods outlined in Fig. 2 (all panels), rotational mismatch with the training panorama (panels b–e, middle row), and distribution of initial headings at 15 cm in ants (panels b–e, bottom row) for (a) the training situation, (b) the control condition ($N = 25$), (c) the 80-53 condition ($N = 26$), (d) the 80-160 condition ($N = 25$) and (e) the 160-53 ($N = 27$) and 53-160 conditions ($N = 25$). The top and middle panels of (e) show the 53-160 condition, while the bottom panel shows data for both 160-53 and 53-160 conditions. The proportions of mismatch (middle row) were defined as the proportion of pixels that mismatched between the test panorama and the training panorama as an agent faced a particular direction (represented along the x-axis with the same scale as in the bottom row). The data points for heading distributions (bottom row) are joined by an atheoretical spline (using the graphics software DeltaGraph™) to facilitate visualisation of the data. The vertical lines in the bottom row represent the mean directions of each distribution, calculated using circular statistics. The long grey line running from top to bottom panel represents the feeder–nest direction. The rotational mismatch function for the 160-53 condition, which is not shown, also has its minimum near the feeder–nest direction.

Data Analysis

We measured goniometer crossings at 15 and 30 cm. Measurements at the two distances led to the same major conclusions, so that we will report only the 15-cm crossing as a measure of initial heading. The data at 30 cm are presented in a supplementary section. Using circular statistics (Batschelet 1981), we tested the significance of orientation towards the home direction using the V-test, with alpha set at $p = 0.05$. The groups 80-53, 80-160, 160-53 and 53-160 were each tested against the control group for difference in mean direction using the Watson–Williams test, and in directional scatter using the Var-test, a test that we created for the purpose. We used the Var-test because the conditions for using Batschelet's (1981) k-test for variances were not always met. In the Var-test, the absolute deviation of each heading from the mean heading was calculated. These distributions of deviations were compared between groups using non-parametric statistics, the Wilcoxon test. Alpha values were set at $p = 0.0125$ to correct for multiple testing.

For the other two control groups (80-80 control and 80-53 control), we also tested whether their headings were significantly oriented towards home using the V-test. We compared the two groups' mean initial headings with one another, using the Watson–Williams test, and their directional scatter, using the Var-test, with alpha set at $p = 0.05$.

Results

Ants released on the goniometer and suddenly facing a largely familiar but unexpected scene (because they had been displaced from near their nest) behaved as we had observed them to do in past studies (Wystrach et al. 2011a,b, 2012, 2014). They typically turned on the spot a number of times, often in a 'pirouetting' manner, before heading off at a run (Wystrach et al. 2014).

Figure 3 shows the distribution of headings for the control (panel b), 80-53 (panel c), 80-160 (panel d), and 160-53 and 53-160 groups (panel e) in cylindrical form (bottom row), along with the skyline contours (top row) and rotational image difference functions (rIDF, middle row) between the test set-up and the training set-up, whose skyline contour is shown in panel a. The mismatch was measured as the proportion of mismatching pixels (black pixels on white or white pixels on black) between the test and training pictures as the viewer in a test condition rotates to face different compass directions. The results were clear: in each case, the best match (minimum image difference) subtends the feeder–nest direction, including the case of 160-53 not shown, given the $\pm 2^\circ$ uncertainty due to the fact that each picture was blurred to 4° resolution. The segment of natural scenery between the walls was especially similar across conditions (see Lent et al. 2013 for some evidence for segmentation of scenes in ants). Hence, we take the best guess for the

theoretical heading according to a terrestrial visual compass (scene matching) to be in the feeder–nest direction in all conditions.

The initial headings at 15 cm were generally in the feeder–nest direction, but deflections are evident in some cases (Fig. 3, Table 1). The mean direction of control ants was slightly to the left of the nest (3.8°), while the mean directions of the 80-53 and 80-160 conditions, -10.2° and 8.8°, respectively, were to the right (by 14.0°) and left (by 5.0°) of the control condition, respectively. The 160-53 and the 53-160 conditions had mean directions further to the right (-24.4°) and left (38.5°), respectively.

Table 1

95% Confidence intervals in degrees to the left (positive) or right (negative) of the feeder–nest direction, mean vector direction in degrees, mean length of the vector and number of tested animals (N) for the distribution of headings at 15 cm distance for all experimental conditions. In the measure of direction, 0° represents the feeder–nest direction, positive is to the left and negative to the right

| Condition | 95% CI left | Mean direction | 95% CI right | Vector r | N |
|---------------|-------------|----------------|--------------|----------|----|
| Control | 9.9 | 3.8 | -2.4 | 0.97 | 25 |
| 80-53 | -0.6 | -10.2 | -19.7 | 0.92 | 26 |
| 80-160 | 17.6 | 8.8 | 0.0 | 0.94 | 25 |
| 160-53 | -9.7 | -24.4 | -39.0 | 0.85 | 27 |
| 53-160 | 54.6 | 38.5 | 22.4 | 0.83 | 25 |
| 80-53 Control | 28.6 | 3.9 | -20.8 | 0.50 | 40 |
| 80-80 Control | 34.1 | 18.8 | 3.4 | 0.72 | 40 |

Formal statistical tests confirm that the most extreme manipulations (in the 160-53 and 53-160 conditions) had the most effect. First, all conditions were significantly oriented in the feeder–nest direction by the V-test ($V_s > 17$, $p_s < 10^{-7}$). The smaller manipulations, effected in the 80-53 and 80-160 conditions, produced mean headings that did not differ significantly from the mean heading in the control group by the Watson–Williams test at the adjusted alpha level of 0.0125 (80-53 group: $F = 6.14$, $p = 0.017$; 80-160: $F < 1$, $p = 0.349$). The larger manipulations, effected in the 160-53 and 53-160 conditions, produced mean headings that differed significantly from the mean heading in the control group by the Watson–Williams test (160-53 group: $F = 15.4$, $p < 0.001$; 53-160 group: $F = 19.9$, $p < 0.001$).

The distributions in Fig. 3 all seem highly concentrated. We compared the scatter of each condition against the control group by the Var-test and found that none differed significantly from the distribution of initial headings in the control group ($F_s < 1.1$, $p_s > 0.39$).

80-80 and 80-53 Control Groups

These two groups were trained and tested at the feeder, one with equal wall heights and one with unequal wall heights, with the training panorama maintained on tests. We did not do a panoramic scene analysis for these groups, but given that the scene encountered in a test was identical to that found during training, both groups were assigned the feeder–nest direction as the theoretical homing direction. The results in Fig. 4 and Table 1 showed that both groups' headings were concentrated in the feeder–nest direction (V-test, $V_s > 19$; $p_s < 10^{-6}$), and although they showed more directional scatter than the control group, perhaps because they received less training, these differences were not significant by the Var-test ($p_s > 0.14$). The two groups did not differ significantly from each other in mean heading direction (Watson–Williams test, $F = 1.21$, $p = 0.273$). They also did not differ significantly from one another in directional scatter of initial headings by the Var-test ($F < 1$, $p = 0.388$). Like the control group, both the 80-80 control and the 80-53 control showed a mean heading slightly to the left of the feeder–nest direction. We have no evidence that encountering unequal wall heights during training *per se*, or during tests *per se*, affects initial heading direction. Any deviations depend on discrepancies between panoramas encountered in training and test conditions.

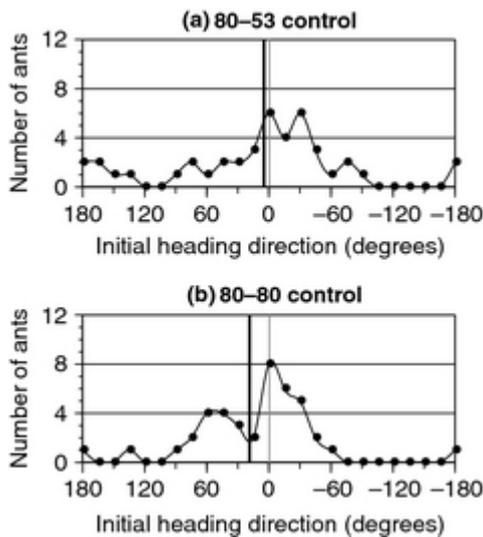


Figure 4

The initial headings at 15 cm for (a) the 80-53 control condition (N = 40) and (b) the 80-80 control condition (N = 40). The black line represents the mean direction of the distribution, calculated using circular statistics. The grey line represents the feeder–nest direction. The data points have been joined by an atheoretical spline (using the graphics software DeltaGraph™) to facilitate visualisation of the data.

Discussion

In our key experimental conditions, desert ants headed home with food with the skyline height on their left and right raised or lowered from that encountered in training. The results from initial headings (at 15 cm) showed that the ants' headings were deflected compared with the control condition that preserved the training skyline heights. Combining the effects of raising one wall and lowering the other wall (averaging the effects of the 160-53 and 53-160 conditions), ants deviated about 30° when compared to controls. These effects are 'dose dependent' in that only raising or lowering one wall led to smaller and non-significant deviations.

Two kinds of explanations may be entertained for explaining these results. The first is the simultaneous activation of two distinct mechanisms, some terrestrial visual compass and an attractor mechanism that works to recover remembered skyline heights. The second kind of model is a unitary mechanism, perhaps based on a modification of the terrestrial visual compass. We have not thought of such a model as yet, but would deem it at least possible. We next discuss these kinds of explanations in turn.

Running 'Modules' Simultaneously

One possible kind of explanation is that the ants were simultaneously using both a terrestrial visual compass and an attractor mechanism that is akin to comparing skyline heights, the two mechanisms active

in the brain at the same time. The terrestrial visual compass is a mechanism that uses the terrestrial panorama to deliver a currently best direction of travel to head home. The attractor mechanism, however it works in the brain, functions to recover the correct skyline heights at that part of the route. With one wall too high and the opposite wall too low at the start of the homing journey, this would be somewhere in the direction of the low wall. The final output for initial heading consists of a weighted sum of the outputs of these two separate computational streams or 'modules'. Both these kinds of mechanisms have been described before (Collett 2010; Wystrach et al. 2012). What is new in this explanation is that the two kinds of mechanisms need to run simultaneously rather than in series to account for the results.

In the two-model approach, some kinds of models seem less reasonable to us. For example, it is unlikely that ants found the higher one of the two walls more aversive in some way, thus veering away from it. We tested this by training ants with one wall 80 cm high and the other 53 cm high. Their performance could not be distinguished from a cohort trained and tested with both walls 80 cm high.

It is of course possible that the brain of the ant actually compares skyline heights at different azimuths, much as in Wystrach et al.'s (2012) model. That is, the brain encodes that in direction θ , the skyline should be x , but perceives that it is currently $x + \Delta$. As a result, it generates a signal to turn in the direction opposite θ , with similar computations across the span of the visible azimuth. But we actually think it unlikely that such a seemingly complex explicit process is at play. Another possibility is that the navigator can predict what the view would be like were it to move in various directions (Möller 2012), and arrives at the outcome that moving away from a wall that is too high produces a better match. No doubt other kinds of mechanisms that have this effect are possible. All that we can conclude is that the pattern of results provides some support for the operation of some mechanism that works to recover the pattern of skyline height experienced at the start of the return journey (the feeder).

It is possible that the dictates of different navigational modules or systems can be averaged in a weighted fashion because they converge on a common summator. This kind of process has been proposed in a number of recent models of insect navigation (Cruse & Wehner 2011; Collett 2012; Wystrach et al. 2013b).

Multiple Modules Turning into One

On the other hand, we should be cautious about accepting a two-model account of our data, because sometimes what was thought to indicate the operation of multiple modules may have a unitary account. We have not tested all currently proposed models, let alone adjust them to try to account for the data. And new models might yet be devised. The study of insect behaviour has often come up with simpler, more ingenious models to replace complex ones (Wystrach & Graham 2012). For example, results that have been accounted for by the matching of multiple views (Judd & Collett 1998) have recently been explained by an

alternative single holistic representation system (Wystrach et al. 2013a) based on Baddeley et al.'s (2012) holistic model.

Lent et al. (2013) reported some visual matching mechanisms in testing wood ants (*Formica rufa*) in the laboratory, but the mechanisms that they identified would not account for the current results without modifications. One mechanism is to encode and use the visual mass of the skyline to the ant's left and right. In navigation, the ant would try to match the proportions of the skyline to its left and right that it encountered during training when it headed in the feeder–nest direction. Such a mechanism would attract the ant to the higher wall, which adds visual mass to that side. Another mechanism is to segment the scene and match segmented parts of it. If the ants segmented the artificial walls from the natural scenery in front, which we think likely given Lent et al.'s (2013) findings, the scenery in front should dictate a direction of travel in the feeder–nest direction, contributing perhaps to the precision of the terrestrial visual compass. But this mechanism would not predict any systematic differences in heading between the control ants and ants encountering altered wall heights.

Finally, our 80-53 control condition, in which ants were trained and tested with walls of unequal heights, found no evidence for centring by matching retinal elevations on the two sides, unlike *C. fortis* (Heusser & Wehner 2002). The *M. bagoti* ants went more or less down the middle, where retinal elevations were unequal. Besides the fact that different species were tested, however, it must be pointed out that training conditions differed in the two studies. Heusser and Wehner's (2002) walls were closer together (1.5 m apart vs. 2 m in our case), and the channel was longer (4 m vs. 2 m in our case). The landscape for *C. fortis* also lacked the ample vegetation available to *M. bagoti*, the former being mostly bare. Perhaps most importantly, the *C. fortis* ants were not trained with walls; the walls only appeared on tests. They were thus trained with equal 0-cm 'walls' on either side. A conclusion of differences between species in this behaviour is thus not justified without further experimentation, although differences between these two species in other behaviours have been noted (Cheng et al. 2014).

Conclusions

When ants faced situations in which the skyline heights found at the feeder had been changed, without directional input from path integration (i.e., as zero-vector ants that have already run off their vector), their initial headings were deflected towards the wall that was too low. Current models, by themselves and unmodified, cannot account for such deflections. It is possible that the ants might have used two strategies simultaneously, compromising between the directional dictates of some attractor mechanism that is akin to comparing skyline heights and those of a visual terrestrial compass. The stronger the skyline-height mismatch, the more the ants followed the dictates of the skyline-height attractor mechanism. This suggests

the possibility that inputs from multiple modules converge on a summator and are averaged in a weighted fashion, a feature common to recent models of insect navigation (Cruse & Wehner 2011; Collett 2012; Wystrach et al. 2013b), although it remains to be seen whether a unitary view-matching model may be devised or modified to account for the data.

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