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RESEARCH ARTICLE

Ants might use different view-matching strategies on and off the route

Antoine Wystrach[1,2,*], Guy Beugnon[2] and Ken Cheng[1]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109 Australia and [2]Centre de Recherches sur la Cognition Animale, CNRS, UMR 5169,Université Paul-Sabatier, Toulouse F-31062, France

*Author for correspondence (Wystrach@cict.fr)

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SUMMARY

Individual foraging ants are known to rely on views of their surroundings for route learning and for pinpointing goals. Different strategies have been proposed to explain how ants might process visual information for navigation, but little is known about the actual development and nature of the view-based strategies used by ants in complex natural environments. Here, we constrained the knowledge of *Melophorus bagoti* ants to either the nest vicinity or a curved route (length 10 m) and analysed their initial direction when released at both novel and familiar locations. In parallel, we used 360 deg pictures of the scene as a basis for modelling different navigational strategies. We propose here a new hypothesis based on skyline height comparison to explain how ants home from novel locations. Interestingly, this strategy succeeded well at novel locations but failed on familiar terrain. By contrast, the use of a visual compass strategy failed at novel locations but could explain the results on familiar routes. We suggest that ants might switch between skyline height comparison and a visual compass strategy, depending on whether they are on familiar terrain or not. How ants could switch between strategies and how their memories develop are discussed in turn.

Key words: insect navigation, skyline height comparison, visual compass, mismatch gradient descent, route learning, memory, *Melophorus bagoti*.

INTRODUCTION

Individual foraging ants show remarkable navigational abilities. Our current understanding is that such efficient navigation arises from the combined use of path integration and information learnt about the visual surroundings. The major strategy of path integration is well understood (Ronacher, 2008). Animals combine directional information from compass cues with distance information (e.g. from step-counting) to perform a continuous calculation of the direct path home (Müller and Wehner, 1988; Wehner and Srinivasan, 2003). However, much less is known about how insects acquire and use visual information, especially in complex natural environments.

In landmark-rich environments, the recognition of familiar surrounds completely overrides the information given by the path integrator (Andel and Wehner, 2004; Kohler and Wehner, 2005; Narendra, 2007; Wystrach et al., 2011a). The robustness of the strategies underpinning the use of visual information can be observed in the field by capturing homing ants just before they reach their nest (i.e. zero-vector ants) and displacing them to different locations (Wehner et al., 1996; Fukushi and Wehner, 2004; Kohler and Wehner, 2005; Collett et al., 2007; Narendra, 2007; Graham and Cheng, 2009a). By using information from the whole surrounding natural scene – and not only individual landmarks (Wystrach et al., 2011b) – such zero-vector ants can home robustly not only when released on their habitual route but also from novel locations after displacements sideways from their habitual route (Fukushi and Wehner, 2004; Kohler and Wehner, 2005; Narendra, 2007; Wystrach et al., 2011a) or to the opposite side of the nest from their habitual route (Wehner et al., 1996).

Several hypotheses have been suggested to explain how insects can process visual information to recapitulate a route or pinpoint a goal (Cartwright and Collett, 1983; Möller, 2001; Zeil et al., 2003; Möller and Vardy, 2006; Harris et al., 2007; Graham et al., 2010; Collett, 2010; Lent et al., 2010; Baddeley et al., 2011). However, little is known about the actual development and nature of the view-based strategies used by ants on and off familiar routes in complex natural environments.

In the present work, we trained *Melophorus bagoti* ants in the field to travel within predetermined areas and released them as zero-vector ants at familiar or novel locations (Fukushi, 2004; Narendra, 2007). In addition, we recorded panoramic pictures in the field that allowed us to develop, test and thus adjudicate between several navigational strategies. We focused mainly on three kinds of view-based strategies: mismatch gradient descent (Zeil et al., 2003); visual compass (Graham et al., 2010; Lent et al., 2010; Wystrach et al., 2011c); and a new hypothesis based on skyline height comparisons. Finally, we tested ants with different experiences (in duration and spatial extent), which provided us with insight into the development of their navigational memories.

MATERIALS AND METHODS

Study site and species

The study was conducted in the semi-arid desert of central Australia, 10 km south of Alice Springs, Northern Territory. The landscape is typically dotted by buffel grass (*Cenchrus ciliaris*) but also marked by larger trees (*Acacia estrophiolata*, *Hakea eyreana* and *Eucalyptus* species) providing distal landmarks for navigation. The thermophilic red honey ant *Melophorus bagoti* Lubbock 1883 forages during hot summer days, mainly on dead insects, seeds and sugary plant exudates (Muser et al., 2005; Schultheiss et al., 2010). Foragers navigate outdoors individually, relying heavily on vision and without the help of chemical trails (Cheng et al., 2009).

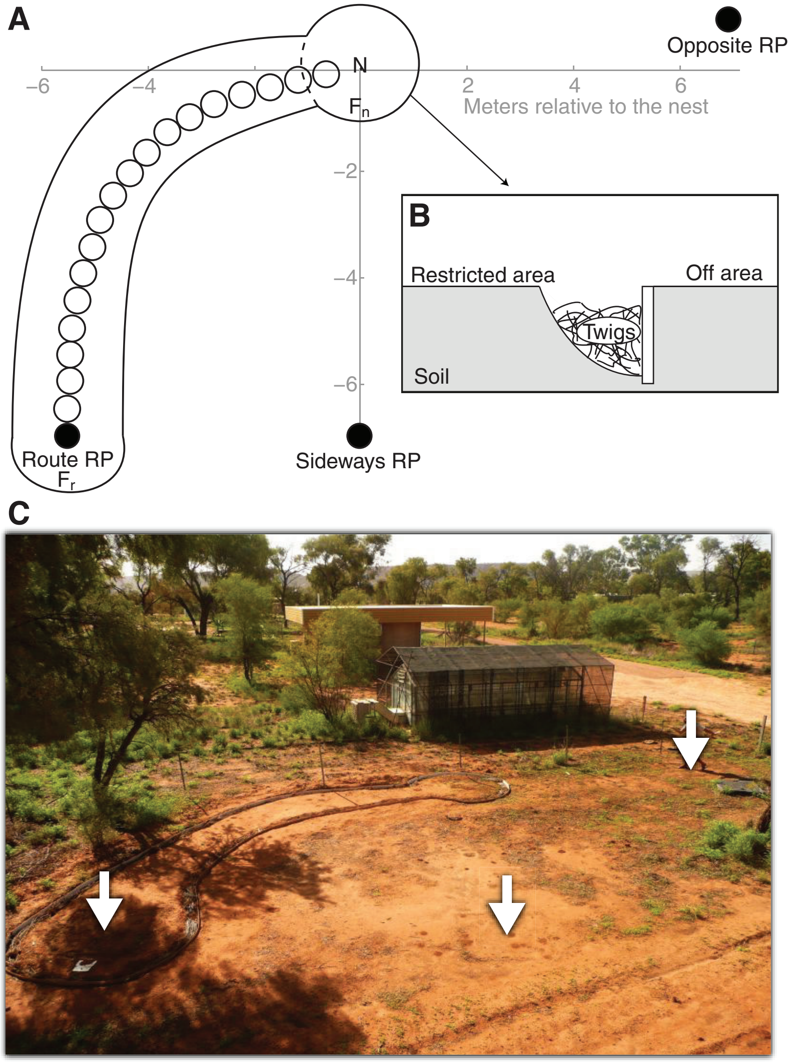

Fig. 1. (A) Scheme of the experimental setup. Continuous and broken lines represent the barrier that can constrain the foragers to a designated area without hindering their view of the scene. Naïve and Nexp ants were constrained to the immediate surroundings of the nest (N) (circle with broken arc line, feeder F_n), whereas Rexp ants could extend their knowledge to a curved route of length 10 m (unbroken line, feeder F_r). Black dots indicate the three release points (RPs). Open circles indicate the positions where the 360 deg pictures of the route were recorded for modelling. (B) Schematic cross-section of the barrier. A groove was dug in which long coated wooden planks (12 cm high; white rectangle) were placed to surround the area without sticking above the surface level. The slippery coated side faced inwards, preventing the ants from climbing out of the enclosed area. The groove was filled with twigs, making it hard for ants to walk there and thus inducing the foragers to keep away from the groove and stay at the surface level of the designated area, hence preserving their view of the surroundings. (C) Picture of the experimental setup. White arrows indicate the position of the RPs.

Experimental setup

We restricted the foraging area of the ants by erecting a barrier without occluding the 360 deg panoramic view (Fig. 1B). The barrier either restricted the ants to a radius of 1.1 m around the nest or to a 10 m curved route that ended at a feeder (Fig. 1). The width of the curved route was ~1.5 m.

The experiment was replicated on two different nests ~200 m apart from each other and with a 90 deg difference in the compass orientation of the route. The outbound route curved towards the right for nest 1 and towards the left for nest 2 (as in Fig. 1). All the data (the initial direction of the ants and panoramic pictures) from nest 1 were mirror reflected to enable comparison with the data from nest 2.

Groups and procedure

Training

The ants were constrained by the barrier to the immediate vicinity of the nest (circle of radius 1.1 m). We marked ants over five consecutive days. These ants were excluded from the study. Unmarked ants that emerged from the nest after 5 days were considered naïve (Muser et al., 2005). We waited for these naïve ants to arrive at a feeder placed within the restricted area (F_n in Fig. 1A) and captured them either upon their immediate arrival (naïve group) or marked them with a distinctive colour and allowed them to forage for 2 days (nest-experienced group). While ants from the 'naïve group' experienced the nest surroundings a couple of times at most (on learning walks) before reaching the feeder for the first time and being captured, individuals from the 'nest-experienced group' did a mean of 27±11 trips over these 2 days (estimated from ants from the same nests after the experiments were completed). We also developed a third group of ants – the route-experienced ants. For this, we removed part of the barrier surrounding the nest, to open up the curved route (see Fig. 1). The feeder with cookie crumbs was removed from the vicinity of the nest and placed instead at the end of the foraging route, labelled F_r in Fig. 1. We scattered a few cookie crumbs along the route to induce the ants to forage along the route and discover the feeder. Unmarked ants that emerged from the nest were considered naïve. We waited for these naïve ants to arrive at the feeder placed at the end of the route, marked them with a distinctive colour and let them forage along the route for 2 days (route-experienced group). A good way of assessing the experience of the ants was to look at their homing paths along the route. Inexperienced ants that left the feeder followed the direction dictated by their path integrator and therefore aimed in the nest direction, crashed into the barrier and struggled among the twigs along the groove until they reached the end of the curve. By contrast, most of the 'route-experienced' ants proved able to suppress the direction dictated by their path integrator and ran efficiently along the route, following the curve and avoiding the groove. Only such experienced ants were tested and called here 'route-experienced' ants.

Overall, we implemented three training conditions for each of the two nests: (1) the 'naïve ants' that experienced the nest vicinity in a single excursion to the feeder (Naïve); (2) the 'nest-experienced' ants that experienced the nest vicinity during two consecutive days (Nexp); and (3) the 'route-experienced' ants that experienced the whole route during two consecutive days (Rexp).

Tests

Ants from all training conditions were tested in the same manner. A test consisted of capturing a zero-vector ant, releasing it and recording its headings after 60 cm of travel at the three different release points consecutively. Zero-vector ants are homing ants that have been captured just before reaching their nest. Thus, their path integrator is set to zero, but the captured ants can rely on terrestrial visual information to home from the release locations (e.g. Wehner et al., 1996; Fukushi, 2001; Kohler and Wehner, 2005; Narendra et al., 2007; Graham and Cheng, 2009b).

During a test, the ants were released, singly, at each of three different release points (RPs, with coordinates in metres along the *x*- and *y*-axes shown in Fig. 1), the 'route RP', the 'sideways RP' and the 'opposite RP'. At each RP, a wooden 360 deg goniometer (1.2×1.2 m) with 24 sectors of 15 deg each was placed onto the ground to enable the recording of the initial direction of travel of the ants at 60 cm.

In order to test each ant consecutively at all three RPs, the ants were recaptured just after leaving the goniometer of the first RP (e.g. opposite RP), then placed at a second RP (e.g. route RP) and finally at the last RP (e.g. sideways RP). The order of the RPs was counterbalanced across individuals and had no significant effect on the accuracy of the direction chosen (ANOVA: N=1178, F=0.82, P=0.441). Each ant was tested only once at each of the three release points.

Data analysis

We used circular statistics to analyse the distribution of directions taken by the ants at each RP (Batschelet, 1981).

Intra-group analysis

The intra-group analysis was conducted for each RP for the three groups of both nests (total of 18 circular distributions). We used a *V*-test to test whether the Naïve and Nexp ants were significantly oriented towards the nest at each of the RPs. As we did not want to assume any predicted direction for the route-experienced group (Rexp), we proceeded in three steps. First, we used a Rayleigh test to determine whether the directions were nonrandomly distributed. For the significantly oriented distributions, we then checked whether the nest direction was within the 95% confidence interval of the distribution. If not, we finally checked whether the mean vector of the distribution pointed instead towards the route.

Inter-group comparisons

The inter-group comparisons were conducted separately for the three RPs. We tested three potential effects: the experience effect, the knowledge effect and the nest effect. As dependent measures, we analysed both the direction taken (i.e. the mean orientation of the distribution) with a Watson–Williams test, and the group accuracy (i.e. the variance of the distribution) with a *K*-test (Batschelet, 1981).

The experience effect was tested by comparing Naïve *versus* Nexp for each nest separately. The knowledge effect was tested by comparing Nexp *versus* Rexp for each nest separately. The nest effect was tested by comparing nest 1 *versus* nest 2 in each of the group conditions. Such a nest effect might arise from differences in the scenery between the two nest locations.

This way of analysing the data led to multiple comparisons between groups. Nexp distributions were compared three times, and Naïve and Rexp distributions were compared twice. Hence, we used the Bonferroni correction, in which the *P*-values involving Nexp were multiplied by three and those involving Naïve and Rexp groups were multiplied by two.

Panoramic images and models

Recording

We recorded 360 deg panoramic pictures of the natural scene experienced by the ants. One picture was taken at each release point, one at the nest and 19 along the curved route (every 50 cm from the route RP to the nest) (Fig. 1) of each nest. These panoramic pictures were recorded with a Canon G10 camera mounted on a convex mirror (GoPano) placed on the ground. We took great care to keep the imaging system horizontal by using a thick wooden board and a spirit level. The field of view of the imaging system covers 360 deg horizontally and 120 deg vertically (70 deg above to 50 deg below the horizon). The pictures were unwarped with the software PhotoWarp (EyeSee Inc., Pittsburgh, PA, USA), trimmed in order to remove the floor (i.e. bottom 30 deg), converted into binary black and white to avoid any illumination artefacts and resized at 120×40 pixels (angular resolution=3 deg) in order to match approximately the visual acuity of *M. bagoti* (Schwarz et al., 2011).

The recorded panoramic pictures served as a basis to test different navigational models. The heading direction predicted by the models could thus be directly compared with the heading direction observed in the real ants.

Skyline height model

We tried to predict the direction chosen by the ants at each release point with a model based on the perceived skyline height. The skyline is the elevation of the tops of terrestrial objects, a cue these ants (Graham and Cheng, 2009a), like wood ants (Fukushi, 2001), are known to use. The model assumes that the ants have memorised how the skyline looks from the nest location. At an unknown release point, the ant will then be attracted by regions of the skyline that appear lower than in the memorised skyline. In other words, regions of skyline that are too high imply that the ant is too close to that part of the scene, whereas regions that are too low imply that the ant is too far away from those regions.

Before comparing the skyline heights, both memorised and perceived views need to be aligned correctly with respect to each other. We tried two possible ways of aligning the pictures. Either both pictures were aligned along the same absolute orientation, or one picture was rotated in order to produce the best possible pixel-by-pixel matching with the other.

The skyline heights were extracted from the picture as described previously (Philippides et al., 2011). We set the resolution of our model in order to match the resolution of the recorded data (i.e. 24 sectors of 15 deg each): the 360 deg images were divided into 24 sectors of 15 deg each. The average skyline height of each sector was then calculated, thus converting the skyline into 24 height values. Graham and Cheng (Graham and Cheng, 2009a) presented skylines at this resolution to the ants and found that it was sufficient for orientation. We used a two-value code for comparing the heights between the nest and release point skylines: the model assigned a value of +1 to the sectors for which the skyline appears lower at the release point than at the nest. The resulting predicted direction for the release point is calculated as the circular average of the +1 sectors.

Memory retrieval and image matching

The ants that experienced the curved route might have memorised several views along that route (Judd and Collett, 1998; Kohler and Wehner, 2005). Being released at a novel release point might trigger the retrieval of the memorised view that is the most similar to the view perceived at the location. Testing this hypothesis requires a quantification of the difference between the view at the release point and all the potential memorised views. We thus compared the images recorded at each RP with all the ones taken along the route. The difference between two pictures was calculated as the mean squared pixel difference (MSPD) over all corresponding pairs of pixels (Zeil et al., 2003). The MSPD between two pictures was calculated for all possible rotations of the images, and only the value of the best-matching rotation was kept.

Visual compass model

To enable homing from novel locations, the visual compass hypothesis assumes that ants stored several views around the nest while facing the nest (Graham et al., 2010; Müller and Wehner, 2010). We thus recorded 32 supplemental panoramic pictures within the constrained nest 1 area (eight pictures at each of the distances of 15, 30, 70 and 110 cm along eight radial directions centred on the nest). The pictures were transformed in the same way as the pictures taken on the route at the RPs (i.e. black and white, 3 deg angular resolution). When released at a RP, the ants are supposed to be able to retrieve the memorised view that best matches the current location. We thus calculated the best MSPD of the 32 nest pictures for each RP (route RP, sideways RP, opposite RP). The best-matching rotation of the current view, when compared with the best-matching retrieved view, can in theory lead the ants towards their nest (Graham et al., 2010). These calculations led to a model that can predict mean directions and whose performance can be evaluated and compared with the skyline models by using the Akaike Information Criterion (AIC) (Burnham and Anderson, 2002) (see footnote in Table 1).

The visual compass model can also be adapted to travel on a route. In that case, we assumed that the views memorised along the route are oriented along the familiar walking direction. At a given release point, the agent recalls the memorised view that best matches the current location and heads along the direction that matches best the recalled view.

RESULTS

When released on the goniometer at the different locations, the vast majority of the ants in all conditions did not meander on the board but paused, scanned the world by rotating on the spot and then dashed straight in the selected direction.

Intra-group data

Naïve ants

Remarkably, Naïve ants proved able to head towards the nest from both the sideways RP and opposite RP (nest 1: N=44; nest 2: N=55; V-test for nest direction: P<0.001) but showed less accuracy at the route RP (V-test for nest direction: nest 1 P=0.046; nest 2 P=0.105) (Fig. 2B). Naïve ants from nest 2 showed a bimodal distribution at the route RP: some ants aimed towards the nest, but others were attracted instead towards the east (towards the bottom on Fig. 2B), away from the nest. Interestingly, this alternative attraction is noticeable at the sideways RP as well (Fig. 2B).

Nest-experienced ants

The ants that experienced the nest surroundings for 2 days (Nexp) were significantly oriented towards the nest direction from all the tested release points (nest 1: N=70; nest 2: N=65; V-test for nest direction: P<0.001) (Fig. 2C). Interestingly, the Nexp ants from nest 2, as for the Naïve ants, showed also in addition an attraction towards the east at the sideways RP (i.e. towards the bottom, grey dots in the middle row of Fig. 2B,C).

Route-experienced ants

At the route RP, ants that had experienced the route (Rexp) presented a nonrandom distribution (nest 1: N=33; nest 2: N=45; Rayleigh test: P<0.001; Fig. 2D). They did not aim towards the nest but towards the route (the 95% confidence interval excludes the nest and includes the route; Fig. 2D). Similarly, at the sideways RP, these ants did not aim towards the nest but headed instead on average towards the half-way mark of the route (Rayleigh test: P<0.001; the 95% confidence interval excludes the nest and includes the route). The opposite RP led to clearly oriented choices for nest 2 (Rayleigh test: P<0.001; Fig. 2D) but not for nest 1 (Rayleigh test: P=0.119).

Inter-group comparisons

Experience effect

For both nests, experiencing the nest surroundings for two days (Nexp) rather than a couple of trials (Naïve) had no significant impact on the direction taken at the release points (Watson–Williams test: Naïve *versus* Nexp P>0.464) but had an effect on the group accuracy. Indeed, at all RPs, the distribution was more concentrated for Nexp ants than Naïve ants (Fig. 2, compare parts B and C), but this was significant only at the route and sideways RPs of nest 1 (K-test, route RP: P=0.001; sideways RP: P=0.044).

Table 1. The evaluation of different models

	Model	M error^2 (rad)	AIC
Nest knowledge (Naïve and Nexp)	Skyline height (absolute alignment)	0.24	–16.96
	Skyline height (best rotation alignment)	1.84	7.35
	Visual compass	2.77	6.10
Route experience (best matching memory recalled)	Skyline height (absolute alignment)	2.77	6.11
	Visual compass	2.90	6.38
	Mixed	0.36	–6.22

Akaike's information criterion (AIC) is based on the residual error [M (observation – model's prediction)] and provides a ranking of one model relative to another (the lower the value, the better). Model performance is based on the error relative to the number of free parameters (r) calibrated to fit the data. AIC=$n\times\ln(M\ \mathrm{error}^2/n)+r$, where n is the number of data points and r is the number of free parameters. The mixed model assumes that the agent relies on the 'visual compass' when on the familiar route, where the recalled memory and the current view are very similar (route RP in Fig. 3), and relies on 'skyline height' comparisons when released at novel locations, where the recalled memory and the current view mismatch (parallel and opposite RPs in Fig. 3).

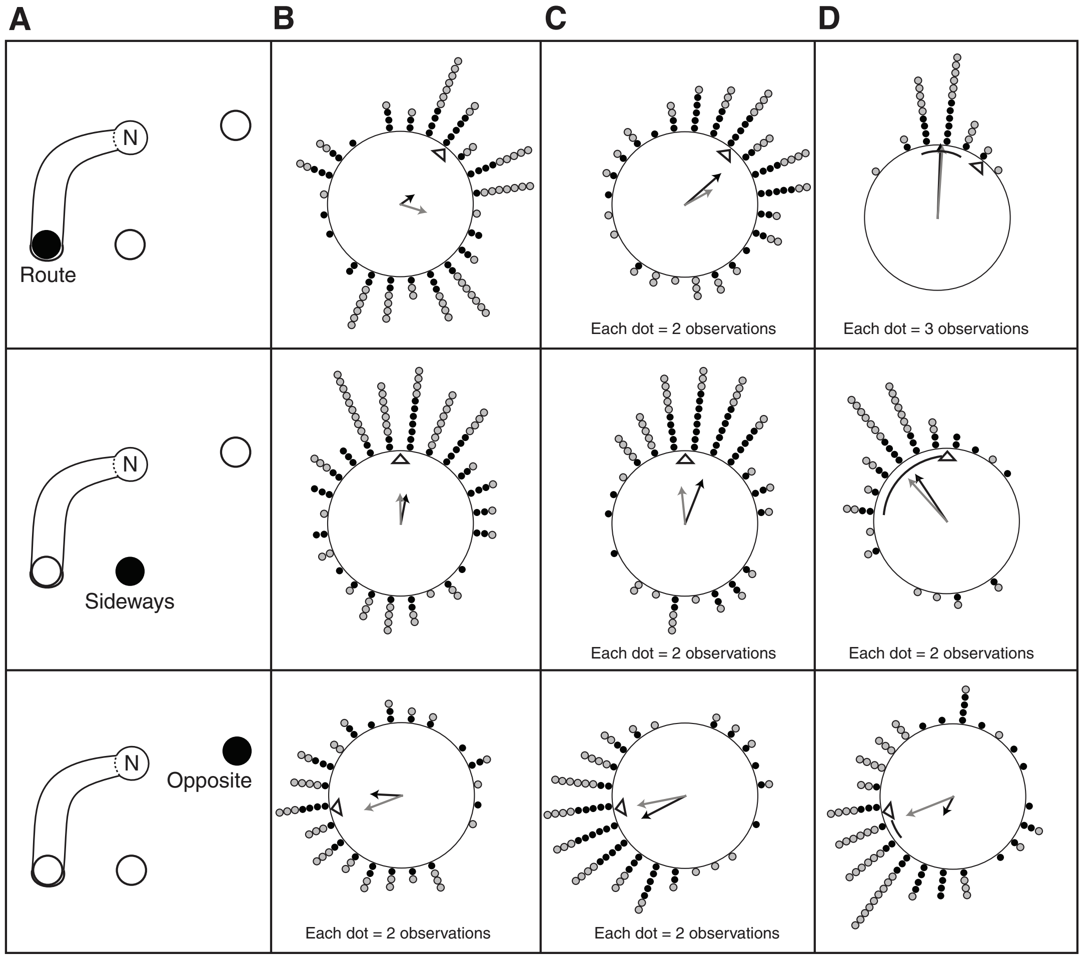

Fig. 2. Distribution of the initial directions (at 60 cm) taken by the ants at the three release points (RPs). (A) The black dots indicate the locations of the RPs in each experimental setup. (B) Naïve ants had experienced the nest surrounding for a couple of trials at most. (C) Nexp ants had experienced the nest surrounding for two consecutive days. (D) Rexp ants had experienced the whole curved route for two consecutive days. Black arcs represent the directions that point towards the route. In B–D, the arrows represent the circular average vectors of the distributions. Results are presented for both nest 1 (black dots and arrows) and nest 2 (grey dots and arrows). The open arrowheads indicate the nest direction. The number of ants tested for nest 1 and nest 2 was, respectively, 44 and 55 (Naïve), 70 and 65 (Nexp) and 33 and 45 (Rexp).

Knowledge effect

For both nests, experiencing the curved route rather than only the nest surroundings led to a significantly better accuracy at the route RP (*K*-test: $P<0.001$) and to a different heading direction at both the route RP (Watson–Williams test: $P<0.001$) and sideways RP (Watson–Williams test: nest 1 $P<0.001$, nest 2 $P=0.006$) (Fig. 2, compare parts C and D). Surprisingly, experiencing the curved route rather than only the nest surroundings resulted in a significantly lower accuracy at the opposite RP for nest 1 (*K*-test: $P=0.031$), but not for nest 2 (*K*-test: $P=0.794$) (Fig. 2, compare parts C and D).

Nest effect

Two significant differences arose between the nests. First, the Nexp ants released on the route RP were significantly more accurate at nest 1 than at nest 2 (*K*-test: $P=0.033$). Second, Rexp ants released at the opposite point were significantly less accurate at nest 1 than at nest 2 (*K*-test: $P=0.029$). As the two replicates of the experiments occurred at different locations, such dissimilarities in the behaviour of the ants probably result from differences in the scene perceived at the two nest locations – innate differences between the two ant colonies seem less likely as an explanation.

Comparison of models for naïve and nest-experienced ants

According to the AIC values, the ‘skyline height with absolute alignment’ model explains the ant data much better than the visual compass or the ‘skyline height with best rotation alignment’ (Table 1, ‘nest knowledge’ section). The overall values of AICs, however, hide the pattern of successes and failures of the different models, which we clarify below.

Skyline height model

The predictions fit the ant data much better when memorised and perceived skylines are compared after being aligned along the same absolute orientation rather than aligned in order to produce the best match (Table 1). Indeed, aligning the two skylines along the same absolute orientation increases the chance of keeping the corresponding parts of the scene superimposed, which leads to a comparison of heights between corresponding parts of the scene. By contrast, rotating the pictures can produce spurious matches and result in comparing heights between unrelated parts of the scene.

The model predicts the results of the Naïve ants better than those of the Nexp ants (M error^2=0.16 and 0.32 rad, respectively). Indeed, the predicted directions of the model are sometimes ambiguous and reflect the uncertainty of the Naïve ants. Remarkably, the bimodal distributions observed in Naïve ants of the nest 2 at the route and sideways RPs are predicted by the model (see circular histograms in Fig. 3). It seems that Naïve ants released at those novel locations headed towards the region where the perceived skylines appeared lower than memorised at the nest, and therefore sometimes confounded the nest direction with other regions of the scene that also appeared too low.

Visual compass model

The visual compass hypothesis (Graham et al., 2010; Wystrach et al., 2011c) failed to predict the directions taken by the ants that had experienced only the nest surroundings (Table 1, 'nest knowledge'). This failure is not due to an ambiguous rotational image difference function (RIDF) but is due to the incapacity of our model to retrieve a correct memory from the nest-views collection. We next explain why.

This hypothesis assumes that ants stored several views around the nest while facing the nest, and, when released at a RP, are able to retrieve a view that has been stored at the same side of the nest as the current location. Finding the compass direction that best matches this retrieved view should indicate approximately the nest direction. The best-matching view from the memory collection should in theory be the one that has been stored at the closest location from the current position, and which is thus located on the same side of the nest as the current location. To retrieve the nest direction, it is crucial that views located on the correct side of the nest match the view at the current location better than do views on other sides of the nest. We

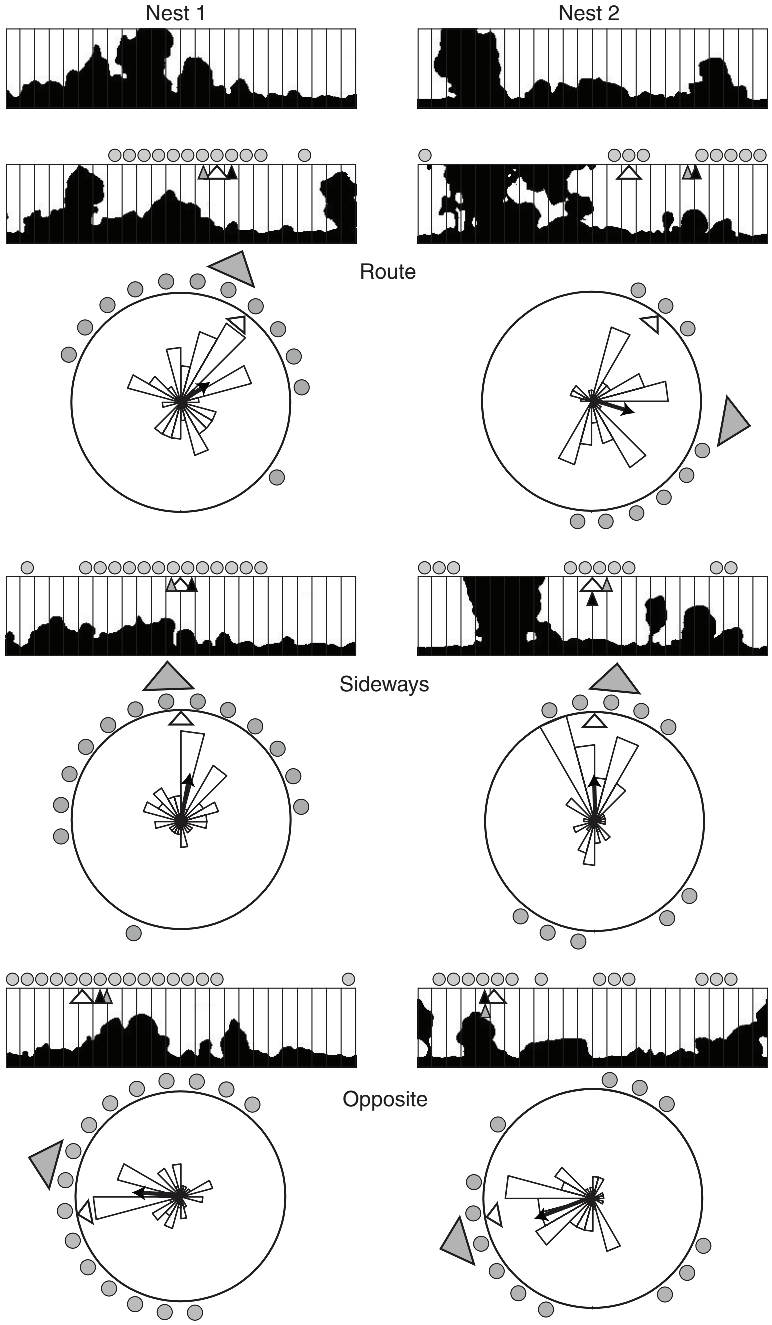

Fig. 3. Illustration of the skyline height comparisons. The black-and-white 360 deg pictures represent the views at the nest (top pictures) and at the different release points (RPs). The grey dots indicate the regions where the skyline appears lower than at the nest, and the grey arrowheads indicate the circular average of those regions. Circular histograms show the heading of the ants after 0.6 m in sectors of 15 deg. The black arrows and arrowheads indicate the circular average vector of the distributions of the ants. The open arrowheads indicate the nest position. The systematic errors displayed by Naïve ants at some RPs (nest 2 route and sideway RPs) seem to correspond to regions where the skyline appeared lower than at the nest.

tested whether the pictures taken at the correct side of the nest matched better than the pictures taken at the opposite side of the nest. This was true for the opposite RP (*t*=3.8, *P*=0.01) but not for the sideways RP (*t*=1.9, *P*=0.73). At the route RP, the matching was on average even better for the views located at the opposite side of the nest. These failures to retrieve the pictures located on the correct side of the nest are due to the very high similarity between the nest pictures (all taken within a circle of radius 1.1 m) and the very distinct views at the RPs (7 or 8.9 m away). At that distance, the relative difference in matching between the best and the worst nest pictures is very small (in percentage of matching pixels: route RP: worst=79.04%, best=82.31%; sideways RP: worst=82.10%, best=85.5%; opposite RP: worst=82.84%, best=86.96%). Basically, as compared with the scene at the distant RPs, the differences in matching due to the changes of the scene around the nest (the signal) are swamped by the differences in matching resulting from noise in our pictures (perhaps due to the uneven ground that, despite our care, might have led to small deviations from the vertical axis of the imaging system). As a result, to explain homing from distant novel release points, the visual compass hypothesis needs to assume that ants are able to cope with very small differences in levels of matching. Pixel-by-pixel picture comparisons could not usually detect such differences robustly.

Model comparison for route-experienced ants

Both skyline height and visual compass models can operate theoretically with route memories. The literature suggests that route memories can be constituted by a succession of individual views taken along the route (Judd and Collett, 1998; Harris et al., 2007). In that case, the agent needs to retrieve the appropriate memory from its memory collection. We thus attempted to explain the results obtained with Rexp ants as evidence shows that they memorised information along the route.

Memory retrieval

We quantified the matching of the scenes along the route when compared with the scene at each RP. In general, the closer to the point of release a location on the route is, the better the matching of the route view from that location with that obtained at the RP. As expected, the scene at the beginning of the route (close to the feeder and the route RP) matches very well the route RP, and the scene becomes increasingly different as it progresses along the route towards the nest (Fig. 4A). The best memory recalled at the route RP would therefore be a view memorised at the beginning of the route (very close to the route RP itself) (Fig. 4A). At the sideways RP, the scene perceived is most similar to the scene found at both

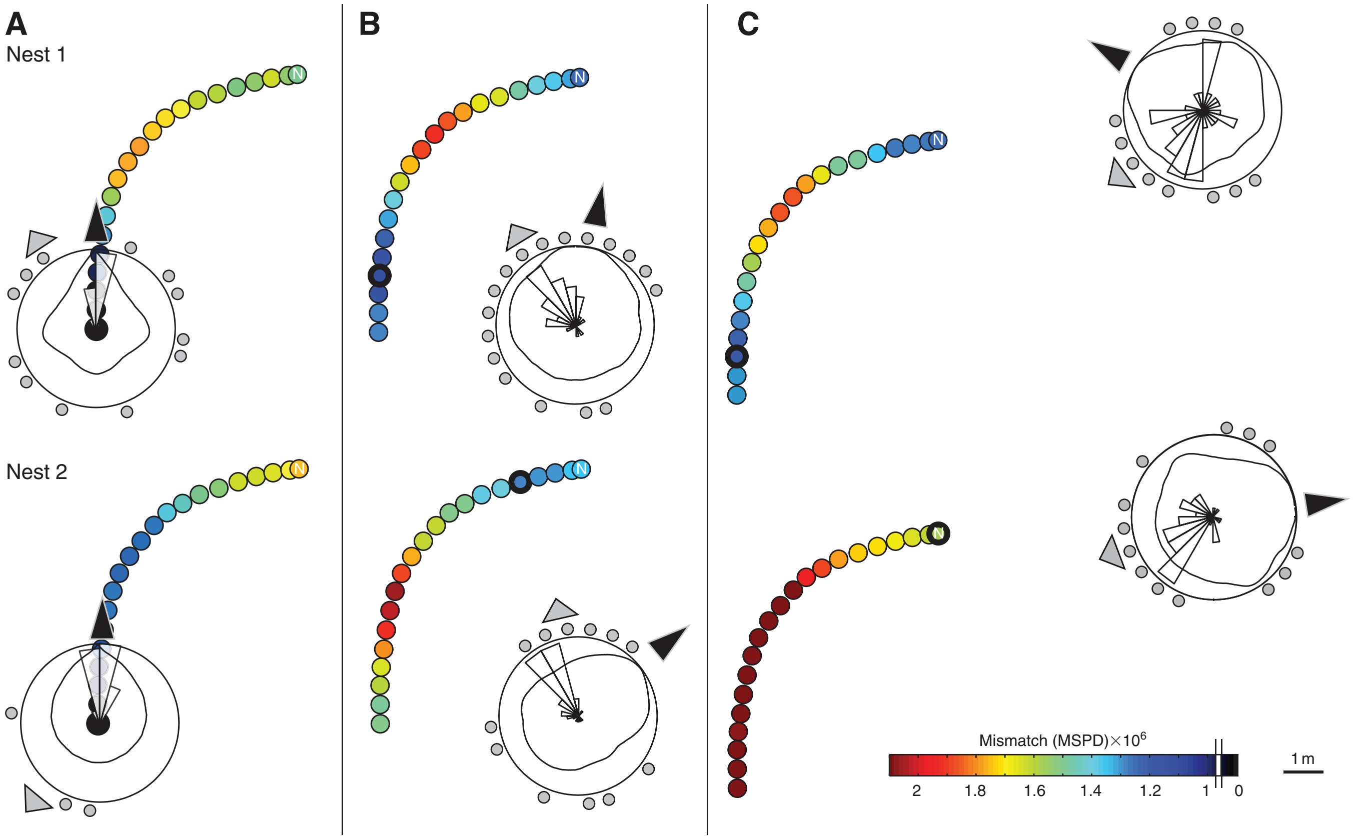

Fig. 4. Route-experienced ants and the results of models for the (A) route release point (RP), (B) sideways RP and (C) opposite RP. Circular histograms show the heading of Rexp ants after 0.6 m in sectors of 15 deg. Coloured dots indicate the mismatch of the different route pictures (route memories) when compared with the current RP. Bold circles indicate the best-matching route picture (memory), which is recalled and processed by the models at the different RPs. Skyline height comparison: the grey dots indicate the regions where the skyline appears lower than on the recalled memory, and the grey arrowheads indicate the circular average of those regions. Visual compass: the black circular plot corresponds to the inverted RIDF (degree of matching for each possible orientation) between the view at the RP and the recalled memory. The closer the line is to the exterior circle the better is the matching (relative for each plot). The black arrowheads indicate the best-matching orientation, which is the direction predicted by the visual compass model. Interestingly, the ant data are better explained by the skyline height comparison at novel locations (B,C), and by the visual compass at familiar locations (A). White 'N' label indicates the nest position.

the beginning (close to the feeder) and at the end (close to the nest) of the route, and most different from the scene around the middle of the route (Fig. 4B). The route picture that best matches the sideways RP happened to be at the beginning of the route for nest 1, and at the end for nest 2 (Fig. 4B, bold circles). For nest 2, at the opposite RP, the scene is most similar to the perceived view at the nest, and similarity decreases when comparing it with the scenes along the outbound route (Fig. 4C). The results for nest 1 are surprising. The scene is similar to the opposite RP at the nest location, then the match deteriorates as one progresses along the route and unexpectedly improves again as one approaches the feeder location (Fig. 4C). Such a good matching between the opposite RP and the beginning of the route must be due to coincidental similarities between the sceneries. As a result, views memorised at the nest and at the beginning of the route provide very similar matching values (MSPD: 1.25×10^6 and 1.17×10^6, respectively), and nest 1 ants released at the opposite RP might recall incorrectly a memory from the beginning of the route (Fig. 4C), which might explain their lower accuracy compared with ants from nest 2.

Skyline height model

Because the 'skyline height model with best rotation alignment' failed to explain homing in the nest knowledge conditions (i.e. Naïve and Nexp) (Table 1, 'nest knowledge'), we tested only the 'skyline height model with absolute alignment' for the route knowledge group. Overall, this model failed to explain the results observed in Rexp ants (Table 1). A closer look reveals that this failure is mostly due to incorrect predictions at the route RP (Fig. 4A, grey arrowheads). By contrast, the skyline model predicts well the heading of the ants at the sideways and opposite RPs (Fig. 4B,C, grey arrowheads). At those RPs, current and retrieved images were further apart and therefore produced more-reliable information on skyline height differences.

Visual compass

The visual compass model did not predict the behaviour of Rexp ants (Table 1). This model had difficulty explaining the homing observed in ants from the opposite RP (Fig. 4C, black arrowheads). At the route RP, however, the visual compass provides a neat minimum of matching and thus predicts well the remarkable accuracy of the ants for heading along the route (Fig. 4A, black line and arrowheads). Indeed, at the route RP, because current and memorised views are very close and similar, the visual compass retrieves very robustly the heading direction learned during training.

Mixed model

We created another model to capitalise on the different successes of the skyline height and visual compass models. The mixed model incorporates both skyline height and visual compass strategies. The model uses a visual compass strategy when the recalled (i.e. best matching) memory matches the current view extremely well (i.e. on familiar terrain, with the parameter of threshold set at $\text{MSPD}<0.5\times10^6$). When the best memorised view mismatches the current view above this tiny threshold (i.e. at novel locations), however, the mixed model uses the skyline height method. In the present case, this mixed model used the visual compass strategy only at the route RP (memory mismatch $\text{MSPD}<0.2\times10^6$ for both nests) and the skyline height strategy at both sideways and opposite RPs (memory mismatch $\text{MSPD}>1.1\times10^6$ for both RPs of both nests). These sizeable differences in mismatch levels, between the match at the route RP and the matches at the sideways and opposite RPs, mean that the threshold value can vary over quite a range. This mixed model resulted in a much better overall fit to the ant data (Table 1).

DISCUSSION

We investigated the mechanisms of navigational behaviour and the experience-dependent use of cues in a desert ant by devising a set-up that allowed us to control the experience and the information available to the ants during training. Some ants had access only to the immediate surroundings of their nest (circle of radius 1.1 m), whereas others could extend their knowledge to a curved route of length 10 m. Tests comprised releasing zero-vector ants (i.e. homing ants captured just before reaching their nest and therefore deprived of information from path integration) at three key locations: at the start of the homing route (route RP), beside the route (sideways RP) or opposite to it relative to the nest (opposite RP) (Fig. 1). The advantage of using a curved route is that route following can be distinguished from direct nest homing, allowing us to differentiate between different navigational strategies. Which navigational strategies the ants used and how their visual memories developed are discussed below in turn.

Different strategies for different purposes

Ants having experienced only the immediate surroundings of their nest proved able to extrapolate their knowledge and headed towards the nest from the three novel test locations (Fig. 1 and Fig. 2B,C). After 2 days of training along the curved route, the ants released at the same locations behaved differently from ants with nest knowledge only, revealing that they had memorised new information along the route. Both ants (Wehner et al., 1996) and bees (Becker, 1958; Capaldi and Dyer, 1999) have been shown to home successfully from novel release points at a much larger scale, although the information available to the insects was not quantified in these studies. Using panoramic pictures recorded on the field, we tested here different hypotheses to explain these performances.

Mismatch gradient descent

Under some conditions, a single stored view acquired at the goal location can allow an agent to return to where the view was acquired using a gradient-descent matching strategy (Zeil et al., 2003; Stürzl et al., 2008; Pahl et al., 2011). In gradient-descent matching, the agent moves in order to reduce the mismatch between the currently perceived view and the memorised goal-view. When the two views match perfectly, the agent has reached the goal. Although this strategy can explain homing from novel release points (Zeil et al., 2003), it cannot output a relevant initial direction of travel from a particular point. Mismatch gradient descent is a move-and-compare strategy, and any novel direction taken is chosen at random. To output a correct initial direction, the agent would need to assess first the matching quality of neighbouring locations or at least perform translatory movements (Möller and Vardy, 2006). This idea can explain remarkably well and parsimoniously how homing ants guide their tortuous search when they have arrived near the nest (Wehner and Räber, 1979; Narendra et al., 2007). However, such a homing strategy appears unlikely to explain the neat directional decisions taken after 'rotating on the spot', which we observed in ants released at more-distant novel locations. Another explanation is thus required.

Skyline height

An alternative, novel hypothesis is based on comparing the skyline heights between the memorised view at the goal and the current view at the novel location. Regions of the scene where the skyline appears lower than at the goal location might indicate that the agent is too far away from that region and therefore attract it. Conversely, regions of the scene where the skyline appears higher than at the goal location might indicate that the agent is too close to that area and therefore repel it. Our results show that such a model is robust only when the skylines are compared when aligned in the same absolute orientation. Insects can in principle achieve that by memorising views in association with a geomagnetic or a celestial compass reference (Dickinson, 1994; Collett and Baron, 1994; Åkesson and Wehner, 2002).

The skyline height model succeeded well at explaining the heading of an ant from novel locations (Fig. 3 and Fig. 4B,C). It would be valuable to test that hypothesis by experiments explicitly manipulating the heights of different parts of the skyline.

By contrast, the skyline height model failed badly in explaining the headings of the ants released on their familiar route (Fig. 4A). This is because, on familiar terrain, like at the route RP, the retrieved memory had been acquired at a location very close to the current position, and thus the current and memorised views present similar skylines. Obtaining navigational information from the small differences of similar skyline heights would require very accurate measurements of skyline heights that our way of recording pictures could not achieve. Skyline height comparison depends on large differences and therefore does not work if the views are similar. It seems therefore unlikely that the robust navigation displayed by ants on familiar routes involves such detailed and error-prone skyline height comparisons.

Visual compass

As two views taken in the same area match best when aligned parallel to each other (Zeil et al., 2003), views can serve as a visual compass (Graham et al., 2010; Wystrach et al., 2011c). Using views as visual compasses can in theory explain homing from novel locations (Graham et al., 2010). This requires the memorisation of several views taken around the nest, with each view memorised while facing the nest. When released further away at a novel location, the currently perceived view has to be compared with each of the memorised views in order to retrieve the best-matching one. The best-matching memorised view is hopefully the one taken at the closest position to the current location and therefore the one located between the nest and the current position. As this memorised view has been stored while facing the nest, the nest direction can be retrieved by aligning the current view along the best-matching direction. This hypothesis is supported by recent evidence that *Ocymyrmex* ants performed well-choreographed learning walks in order to memorise views while facing the nest (Müller and Wehner, 2010).

Aligning the body of an agent according to a reference view can operate successfully across large distances in the natural environment (Philippides et al., 2011). However, when it comes to homing from a novel location, the crucial point is to be able to retrieve the correct memory. Any retrieval error would lead the insect in a wrong direction, as our model frequently did (Table 1). In the present case, the memorised views were too close and similar to each other to allow robust retrieval of the correct memory from the distant RPs. Thus, it is doubtful that ants would use such an error-prone strategy to home from novel locations.

Although our visual compass model failed to explain homing from novel distant locations (Table 1 and Fig. 4B,C), it succeeded remarkably well when the release point was along the familiar route (Fig. 4A). The closer match between current and memorised views (because they are obtained at locations close to one another) facilitates the retrieval of the closest memory and guarantees a correct alignment. Moreover, the cost of retrieving a memory that is not the one taken at the closest location is minimal as all route memories would face roughly the same direction. Evidence shows that ants are able to align their body in order to match the retinal position of the features memorised along a familiar route (Lent et al., 2010; Collett, 2010). The extent of the rotation needed for aligning their body correctly is even calculated before the actual turn (Lent et al., 2010), revealing how ants excel in aligning views.

Whether the visual compass is helped by the use of celestial compass information cannot be disentangled here. It is probable that ants learn views in association with celestial compass information. An alternative is that the view is linked to a heading associated with the celestial compass, a local vector (Collett and Collett, 2009). The use of a visual compass *versus* a local vector on a familiar route cannot be disambiguated in the present work. Nonetheless, when released within an artificial reproduction of the skyline perceived at the feeder, *M. bagoti* head according to the skyline itself and not according to the celestial compass (Graham and Cheng, 2009b), favouring the visual compass hypothesis over the local vector hypothesis.

Switching between strategies

Homing from distant novel locations or recapitulating a well-known route are two very different tasks and therefore might require different strategies. The successes and failures of the two models we tested here complement one another. Comparing skyline heights is risky when locations of the current view and the retrieved memory are close to each other (i.e. on familiar terrain) but works well when homing from novel locations, more distant from familiar terrain. By contrast, the visual compass provides a parsimonious and robust strategy for heading along the familiar route but appears unreliable for homing from novel distant locations. Our results suggest that ants might use the visual compass on familiar terrain and skyline height comparisons at novel locations. Deciding which strategy to use could be achieved by assessing the mismatch between the current view and the best-matching memory. A very low mismatch indicates that the insect is very close to its familiar route (or on it) and would trigger the strategy of using the visual compass. Higher mismatch levels, however, indicate that the insect is on novel terrain and trigger the comparison of skyline heights. Our modelling revealed a sizeable gap in exactness of matching between locations, meaning that the threshold for switching between these strategies does not have to be very exact. We chose here arbitrarily a threshold of mismatch to make a difference between familiar (route RP) and novel terrain (sideways and opposite RPs). We do not know how ants might assess the level of unfamiliarity of a scene, but past work also suggests that they do possess such mismatch thresholds (Wystrach and Beugnon, 2009; Wystrach, 2009; Wystrach et al., 2011c; Wystrach et al., 2011b).

Examination of published paths of ants in the field also suggests the presence of two such strategies. Zero-vector ants released at novel locations several metres away from their route display indecisive headings, but usually roughly oriented in the correct direction [fig. 6 of Narendra (Narendra, 2007)]. Such uncertainty in their headings reflects the wide and sometimes ambiguous directions computed from skyline height comparison (see Figs 3 and 4, grey circles). By contrast, when the ants hit their route corridor, they display a dramatic switch of behaviour by suddenly heading unhesitantly straight along their route (Fig. 5) (see also Kohler and Wehner, 2005; Wehner et al., 2006; Narendra, 2007). Such resolute headings reflect the unique and unambiguous direction given by a visual compass strategy on familiar terrain.

In addition, a mismatch-gradient-descent strategy could well help homing from novel locations once a correct initial direction has been enabled by skyline height comparison. Also, the mismatch-gradient-

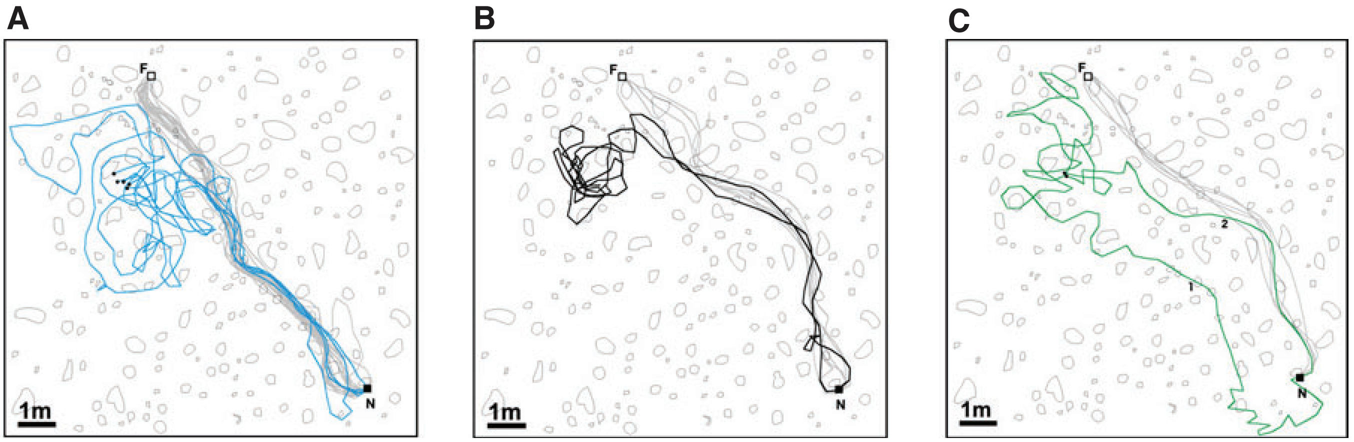

Fig. 5. Inbound runs of three zero-vector ants after displacement from the nest N to a location (black dot) sideways from the habitual routes of the ants (grey lines) and illustrating the switch between navigational strategies. Ants might use three distinct ways of processing views: (1) at novel locations that are not totally unfamiliar, skyline height comparison provides rough and sometimes ambiguous directional information; (2) on a familiar route, or close enough to it, a visual compass provides a robust and unambiguous direction parallel to it; (3) close to the nest (N), a mismatch-gradient-descent strategy drives a convoluted search for the nest entrance. (A) Ant H6: five runs shown in blue, (B) ant F7: two runs shown in black, (C) ant P8: two runs shown in green. In run '1', although the ant was still off its familiar route, it suddenly started to run parallel to it, following the turn-angles of the route, as if it had estimated the mismatch to be low enough to trigger a visual compass strategy. Once it arrived in the vicinity of the nest, however, its behaviour changed radically again to a more tortuous nest-search path, as would be predicted by the use of a mismatch-gradient-descent strategy. Reproduced, with permission, from Kohler and Wehner (Kohler and Wehner, 2005). F, feeder.

descent strategy seems to provide a parsimonious explanation for the tortuous search displayed by ants after they have arrived within the nest vicinity, although it has to be kept in mind that a visual compass might well be able to explain nest-pinpointing behaviour (Graham et al., 2010). Once again, the nest search strategy could be triggered when the perceived scene matches sufficiently well the view memorised at the nest. Remarkable examples of such switches in behaviour were published by Kohler and Wehner (Kohler and Wehner, 2005) (Fig. 5).

Finally, when *M. bagoti* ants are displaced to very distant locations where the view mismatch is extremely high, they perform a systematic search (Schultheiss and Cheng, 2011), apparently abandoning attempts at view matching altogether. The search patterns in *M. bagoti* on a test field distant from the training site share some characteristics with those found in the North African *Cataglyphis fortis* (Wehner and Srinivasan, 1981; Merkle et al., 2006), ants that live on open saltpans with little or nothing by way of views usable for matching. The size of the search distribution increases with increases in the feeder–nest distance, and searches proceed in loops that increase in size as the search duration increases [see also Beugnon et al. (Beugnon et al., 2005) for the rain forest ant *Gigantiops destructor*].

Development of navigational memories

Ants that have experienced the nest vicinity for a different number of times (a couple of trials *versus* two full days) or experienced different areas (i.e. nest vicinity or route) for the same amount of time showed distinct headings at the release points. This shows that the content of the memory of the ants is modified by both knowledge of a new area and repeated training.

Nest memory

Remarkably, Naïve ants having experienced the nest surroundings for a couple of trials at most were able to head towards the nest from novel distant locations (Fig. 2B). Nonetheless, some individuals displayed systematic errors indicated by headings away from the nest at some RPs (Fig. 3, 'nest 2, route and sideways RPs'). This alternative direction also points to regions where the perceived skyline appears lower than at the nest, suggesting that following a skyline height comparison strategy might have induced some Naïve ants to head in such a wrong direction (Fig. 3). Interestingly, the ants that have experienced the nest vicinity for two days were more accurate at finding the home direction (Fig. 2C) and avoided some of the mistakes observed in Naïve ants (Fig. 2B). Our model fits data from Naïve ants better and did not match the success achieved by nest-experienced ants. However, some nest-experienced ants were also attracted by those wrong alternative directions (Fig. 2C), and the skyline height comparison model was still by far the best we found to explain their behaviour. Thus, we suggest that the differences in behaviour observed between naïve and experienced ants stem from better memory in experienced ants, rather than different ways of processing views. It could be supposed that the experienced ants had time to memorise several views around the nest that enable better homing. This is unlikely. Using several goal-pictures from the nest vicinity did not improve the model because the pictures were highly similar and thus led to similar outputs. Another hypothesis would be that experienced ants had memorised and used more detailed views than naïve ants. However, increasing the resolution of the images added mostly noise to our model and did not improve its performance (data not shown). The present model, however, is based on black-and-white images, and it is possible that experienced ants have learned useful information from a potential light or colour gradient that improved their performance. A second viable hypothesis would be that the experienced ants had learned to filter relevant information from the scene, resulting in a more efficient processing of the views. For instance, relying on distal rather than proximal cues for retrieving a direction from a novel distant release point would be useful. Such 'proximal noise' could be detected and filtered out by relying on translational optic flow while experiencing the nest surroundings (Cartwright and Collett, 1987; Zeil, 1993a; Zeil, 1993b; Dittmar et al., 2010). Ants might have learned to filter the memory for the most informative cues.

Route memories

Experiencing the curved route rather than only the nest surroundings had a significant impact on the behaviour of the ants at the release points. Rexp ants headed towards the route and not towards the nest at both sideways and route RPs (Fig. 2D). This indicates that experiencing the curved route for two days led the ants to learn and recall information memorised along the route. The stored information could consist of a series of views taken along the route. If this is the case, an ant released at a RP would need to be able to retrieve the appropriate view from its memory collection. Ants can achieve this by storing and retrieving views sequentially (Chameron et al., 1998). But because zero-vector ants have already run the route and were about to reach the nest when captured, such a sequential retrieval of views would imply the recall of a nest view. This hypothesis is refuted by the attraction towards the route observed in our ants as well as the differences in the direction taken by nest-knowledge *versus* route-experienced ants. Another hypothesis is that the view at the RP triggers the recall of the memorised view that matches best the current location (Collett et al., 2006). Hence, zero-vector ants released on their familiar route normally resume their course to the nest (Kohler and Wehner, 2005). Such a hypothesis fits the present ant data well and also indicates how ants could choose between a visual compass strategy (when the best recalled memory matches the current scene very well, as at the route RP) or a skyline comparison strategy (when the best recalled memory presents a higher level of mismatch, as at sideways and opposite RPs) (see Fig. 4).

An alternative to the ‘multiple-views’ hypothesis is that the route might be learned more holistically, resulting in a single memory for homing along the whole route (Baddeley et al., 2011). Such a holistic memory could be built up by selecting and integrating the information from the scene that is relevant for the whole route or by memorising how the view changes rather than storing several different but similar views independently. A holistic memory would provide ants with a more compact way of storing the information required to recognise familiar views. A robot using this approach can successfully recapitulate a non-trivial S-shaped route through a real-world environment by using its holistic memory as a visual compass (Baddeley et al., 2011). In the present case, this model could explain the behaviour observed at the route RP (i.e. on familiar terrain) but failed badly at the other RPs (i.e. at novel locations) (B. Baddeley, personal communication), consistent with what we found with our visual compass model based on individual pictures. A holistic memory could also be combined with skyline height comparisons to explain most of the present results. The use of a holistic memory has proved useful for route navigation in robots. It would be valuable to develop such a model for ants, based realistically on their sensory processes, and test its predictions on ant navigation in their natural habitats.

Conclusions

The present work suggests that ants process memorised and perceived views differently according to the navigational task they need to achieve. If they are on their familiar route, using memorised views as visual compasses (Graham et al., 2010; Wystrach et al., 2011c) offers a remarkably simple solution to keeping a correct heading and recapitulating the route. However, if the ants have been displaced by several metres to novel locations – perhaps by gusts of wind (A.W., unpublished observations) – using a visual compass becomes very error-prone, but comparing skyline heights becomes robust enough for charting a heading, and such a model could explain the mistakes and successes of the ants. At the end of the route, when it comes to pinpoint the precise entrance of the nest, both a visual compass (Graham et al. 2010) and a mismatch-gradient-descent strategy (Zeil et al., 2003) could in theory be useful. Finally, being displaced to a very distant and totally unfamiliar area triggers systematic searches in zero-vector ants (Wehner and Srinivasan, 1981; Schultheiss and Cheng, 2011). Selecting the appropriate strategy can be simply achieved by assessing the accuracy of the matching between the memory and the current view.

This work also provides insight into the development of the navigational memories of ants. A couple of trials (i.e. potentially learning walks) are enough for ants to store relevant information that enables them to home from neighbouring novel locations. However, evidence shows that *M. bagoti* improves its memory of the nest surroundings after repeated experience. Our model probably fits the performance of naïve ants better because the memory of ants is closer to a raw image (like our model) at first, but then gets filtered to become more efficient with repeated training. When it comes to learning a route, the precise nature and development of the memories of insects are still unknown. Notably, the use of multiple stored views as well as a single holistic memory of the route can both potentially explain past and present results. Storing a single visual holistic memory, rather than multiple independent views at different stages of the route, appears more parsimonious but has never been shown in insects. A better understanding of the nature of the memories of insects should form a goal for future research on insect navigation.

LIST OF ABBREVIATIONS

Nexp	nest-experienced ants
Rexp	route-experienced ants
RIDF	rotational image difference function
RP	release point

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REFERENCES

Åkesson, S. and Wehner, R. (2002). Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial system of reference? *J. Exp. Biol.* **205**, 1971-1978.

Andel, D. and Wehner, R. (2004). Path integration in desert ants, *Cataglyphis*: how to make a homing ant run away from home. *Proc. R. Soc. Lond. B* **271**, 1485-1489.

Baddeley, B., Graham, P., Philippides, A. and Husbands, P. (2011). Holistic visual encoding of ant-like routes: Navigation without waypoints. *Adatp. Behav.* **19**, 3-15.

Batschelet, E. (1981). *Circular Statistics in Biology.* New York, NY: Academic Press.

Becker, L. (1958). Untersuchungen über das Heimfindevermögen der Bienen. *Z. Vergl. Physiol.* **41**, 1-25.

Beugnon, G., Lachaud, J. P. and Chagné, P. (2005). Use of long-term stored vector information in the neotropical ant *Gigantiops destructor*. *J. Insect Behav.* **18**, 415-432.

Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach.* New York: Springer-Verlag.

Capaldi, E. A. and Dyer, F. C. (1999). The role of orientation flights on homing performance in honeybees. *J. Exp. Biol.* **202**, 1655-1666.

Cartwright, B. A. and Collett, T. S. (1983). Landmark learning in bees – experiments and models. *J. Comp. Physiol. A* **151**, 521-543.

Cartwright, B. A. and Collett, T. (1987). Landmark maps or honeybees. *Biol. Cybern.* **57**, 85-93.

Chameron, S., Schatz, B., Pastergue-Ruiz, I., Beugnon, G. and Collett, T. S. (1998). The learning of a sequence of visual patterns by the ant *Cataglyphis cursor*. *Proc. R. Soc. Lond. B* **265**, 2309-2313.

Cheng, K., Narendra, A., Sommera, S. and Wehner, R. (2009). Traveling in clutter: navigation in the central australian desert ant *Melophorus bagoti*. *Behav. Processes* **80**, 261-268.

Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proc. Natl. Acad. Sci. USA* **107**, 11638-11643.

Collett, M. and Collett, T. S. (2009). The learning and maintenance of local vectors in desert ant navigation. *J. Exp. Biol.* **212**, 895-900.

Collett, T. S. and Baron, J. (1994). Biological compassses and the coordinate frame of landmark memories in honeybees. *Nature* **368**, 137-140.

Collett, T. S., Graham, P., Harris, R. A. and Hempel-De-Ibarra, N. (2006). Navigational memories in ants and bees: memory retrieval when selecting and following routes. *Adv. Study Behav.* **36**, 123-172.

Collett, T. S., Graham, P. and Harris, R. A. (2007). Novel landmark-guided routes in ants. *J. Exp. Biol.* **210**, 2025-2032.

Dickinson, J. A. (1994). Bees link local landmarks with celestial compass cues. *Naturwissenschaften* **81**, 465-467.

Dittmar, L., Stürzl, W., Baird, E., Boeddeker, N. and Egelhaaf, M. (2010). Goal seeking in honeybees: matching of optic flow snapshots? *J. Exp. Biol.* **213**, 2913-2923.

Fukushi, T. (2001). Homing in wood ants, *Formica japonica*: use of the skyline panorama. *J. Exp. Biol.* **204**, 2063-2072.

Fukushi, T. and Wehner, R. (2004). Navigation in wood ants *Formica japonica*: context dependent use of landmarks. *J. Exp. Biol.* **207**, 3431-3439.

Graham, P. and Cheng, K. (2009a). Which portion of the natural panorama is used for view-based navigation in the Australian desert ant? *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **195**, 681-689.

Graham, P. and Cheng, K. (2009b). Ants use the panoramic skyline as a visual cue during navigation. *Curr. Biol.* **19**, R935-R937.

Graham, P., Philippides, A. and Baddeley, B. (2010). Animal cognition: multi-modal interactions in ant learning. *Curr. Biol.* **20**, R639-R640.

Harris, R. A., Graham, P. and Collett, T. S. (2007). Visual cues for the retrieval of landmark memories by navigating wood ants. *Curr. Biol.* **17**, 93-102.

Judd, S. P. D. and Collett, T. S. (1998). Multiple stored views and landmark guidance in ants. *Nature* **392**, 710-714.

Kohler, M. and Wehner, R. (2005). Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: how do they interact with path-integration vectors? *Neurobiol. Learn. Mem.* **83**, 1-12.

Lent, D. D., Graham, P. and Collett, T. S. (2010). Image-matching during ant navigation occurs through saccade-like body turns controlled by learned visual features. *Proc. Natl. Acad. Sci. USA* **107**, 16348-16353.

Merkle, T., Knaden, M. and Wehner, R. (2006). Uncertainty about nest position influences systematic search strategies in desert ants. *J. Exp. Biol.* **209**, 3545-3549.

Möller, R. (2001). Do insects use templates or parameters for landmark navigation? *J. Theor. Biol.* **210**, 33-45.

Möller, R. and Vardy, A. (2006). Local visual homing by matched-filter descent in image distances. *Biol. Cybern.* **95**, 413-430.

Müller, M. and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.

Müller, M. and Wehner, R. (2010). Path integration provides a scaffold for landmark learning in desert ants. *Curr. Biol.* **20**, 1368-1371.

Muser, B., Sommer, S., Wolf, H. and Wehner, R. (2005). Foraging ecology of the thermophilic Australian desert ant, *Melophorus bagoti*. *Aust. J. Zool.* **53**, 301-311.

Narendra, A. (2007). Homing strategies of the Australian desert ant *Melophorus bagoti* – II. Interaction of the path integrator with visual cue information. *J. Exp. Biol.* **210**, 1804-1812.

Narendra, A., Si, A., Sulikowski, D. and Cheng, K. (2007). Learning, retention and coding of nest-associated visual cues by the Australian desert ant, *Melophorus bagoti*. *Behav. Ecol. Sociobiol.* **61**, 1543-1553.

Pahl, M., Zhu, H., Tautz, J. and Zhang, S. (2011). Large scale homing in honeybees. *PLoS ONE* **6**, e19669.

Philippides, A., Baddeley, B., Cheng, K. and Graham, P. (2011). How might ants use panoramic views for route navigation? *J. Exp. Biol.* **214**, 445-451.

Ronacher, B. (2008). Path integration as the basic navigation mechanism of the desert ant *Cataglyphis fortis* (Forel, 1902) (Hymenoptera: Formicidae). *Myrmecological News* **11**, 53-62.

Schultheiss, P. and Cheng, K. (2011). Finding the nest: inbound searching behaviour in the Australian desert ant, *Melophorus bagoti*. *Anim. Behav.* **81**, 1031-1038.

Schultheiss, P., Schwarz, S. and Wystrach, A. (2010). Nest relocation and colony founding in the Australian desert ant, *Melophorus bagoti* Lubbock (Hymenoptera: Formicidae). *Psyche* **2010**, 1-4.

Schwarz, S., Narendra, A. and Zeil, J. (2011). The properties of the visual system in the Australian desert ant *Melophorus bagoti*. *Arthropod Struct. Dev.* **40**, 128-134.

Stürzl, W., Cheung, A., Cheng, K. and Zeil, J. (2008). The information content of panoramic images I: the rotational errors and the similarity of views in rectangular experimental arenas. *J. Exp. Psychol. Anim. Behav. Process.* **34**, 1-14.

Wehner, R. and Räber, F. (1979). Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia* **35**, 1569-1571.

Wehner, R. and Srinivasan, M. V. (1981). Searching behavior of desert ants, genus *Cataglyhis* (Formicidae, Hymenoptera). *J. Comp. Physiol. A* **142**, 315-338.

Wehner, R. and Srinivasan, M. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour* (ed. K. J. Jeffrey), pp. 9-30. Oxford: Oxford University Press.

Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.

Wehner, R., Boyer, M., Loertscher, F., Sommer, S. and Menzi, U. (2006). Ant navigation: one-way routes rather than maps. *Curr. Biol.* **16**, 75-79.

Wystrach, A. (2009). Ants in rectangular arenas: a support for the global matching theory. *Commun. Integr. Biol.* **2**, 388-390.

Wystrach, A. and Beugnon, G. (2009). Ants learn geometry and features. *Curr. Biol.* **19**, 61-66.

Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G. and Cheng, K. (2011a). Views, landmarks, and routes: how do desert ants negotiate an obstacle course? *J. Comp. Physiol. A* **197**, 167-179.

Wystrach, A., Beugnon, G. and Cheng, K. (2011b). Landmarks or panoramas: what do navigating ants attend to for guidance? *Front. Zool.* **8**, 21.

Wystrach, A., Cheng, K., Sosa, S. and Beugnon, G. (2011c). Geometry, features and panoramic views: ants in rectangular arenas. *J. Exp. Psychol. Anim. Behav. Process.* **37**, 420-435.

Zeil, J. (1993a). Orientation flights of solitary wasps (*Cerceris*, Sphecidae, Hymenoptera). I. Description of flight. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **172**, 189-205.

Zeil, J. (1993b). Orientation flights of solitary wasps (*Cerceris*, Sphecidae, Hymenoptera). II. Similarities between orientation and return flights and the use of motion parallax. *J. Comp. Physiol. A* **172**, 207-222.

Zeil, J., Hofmann, M. I. and Chahl, J. S. (2003). Catchment areas of panoramic snapshots in outdoor scenes. *J. Opt. Soc. Am. A* **20**, 450-469.