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Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial system of reference?

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Summary

Central-place foraging insects such as desert ants of the genus *Cataglyphis* use both path integration and landmarks to navigate during foraging excursions. The use of landmark information and a celestial system of reference for nest location was investigated by training desert ants returning from an artificial feeder to find the nest at one of four alternative positions located asymmetrically inside a four-cylinder landmark array. The cylindrical landmarks were all of the same size and arranged in a square, with the nest located in the southeast corner. When released from the compass direction experienced during training (southeast), the ants searched most intensely at the fictive nest position. When instead released from any of the three alternative directions of approach (southwest, northwest or northeast), the same individuals instead searched at two of the four alternative positions by initiating their search at the position closest to the direction of approach when entering the landmark square and then returning to the position at which snapshot, current landmark image and celestial reference information were in register. The results show that, in the ants' visual snapshot memory, a memorized landmark scene can temporarily be decoupled from a memorized celestial system of reference.

Key words: navigation, visual navigation, landmark guidance, celestial reference system, learning, insect, ant, *Cataglyphis fortis*.

Introduction

Desert ants of the genus *Cataglyphis* returning from a foraging trip to the nest use both path integration and visual landmarks as navigation tools for relocating the nest site (Wehner and Wehner, 1990; Collett, 1992; Wehner, 1992; Wehner et al., 1996). In its system of path integration, the ant computes the net distance and direction from the nest at each stage of its foraging journey and hence is, in principle, able to home from any point along a direct route (Wehner, 1982, 1992). To accomplish this task of path integration, the ant must register the courses selected as well as the distances travelled during the foraging run (Müller and Wehner, 1988; Wehner, 1992; Ronacher and Wehner, 1995; Hartmann and Wehner, 1995). In addition to path integration, the ants navigate by using familiar landmarks along the homing run as well as close to the nest location (for reviews, see Collett and Cartwright, 1983; Collett, 1992, 1996; Wehner, 1992; Wehner et al., 1996). Landmarks provide important information for pinpointing the nest when insects return after a foraging run (e.g. Wehner and Räber, 1979; Brunnert et al., 1994) and can be used for locating feeding sites (Cartwright and Collett, 1983, 1987; Cheng et al., 1987). Two-dimensional snapshots of landmark scenes have been shown to be retinotopically fixed (e.g. Wehner and Müller, 1985; Judd and Collett, 1998; see also Dill et al., 1993). In the natural habitat of desert ants, foragers are regularly forced to follow complex routes in a cluttered environment (Wehner et al., 1996). During such travels, the ants seem to use both global and local vectors defined by their path integration system, which interact with the availability and use of memorized landmarks (Collett et al., 1998). In familiar terrain, the ants seem to ignore the global vector that would lead them along a direct route back to the nest. Instead, they rely on local vectors and stored familiar landmark scenes. However, when the ant leaves the familiar area, the global vector assumes dominance and guides the ant back to the area of the nest, where other guidance strategies take over.

If available, landmarks provide the most obvious navigational cue used in the close vicinity of the nest. To investigate whether stored landmark views are spatially oriented within a celestial system of reference, we studied the searching behaviour of desert ants in relation to landmarks arranged around the nest (goal). The goal was located asymmetrically within a square array of four cylindrical landmarks so that there were four localities at which a stored snapshot could be matched with the current retinal images. However, it was only at one of these positions that the snapshot and the current retinal image were in register with the celestial

system of reference. In these experiments, we used ants that had returned from a foraging visit to a feeder located at a distant and fixed compass direction relative to the nest. The ants were released from four compass directions: from the training direction (0 °) and from three others of ±90 ° and 180 ° from the training direction. In the latter three cases, the closest hypothetical nest positions given by the landmarks were in conflict with the directional information given by celestial information. Hence, the experiments are designed to provide information about the extent to which a memorized visual snapshot scene can be coupled or decoupled from a celestial system of reference.

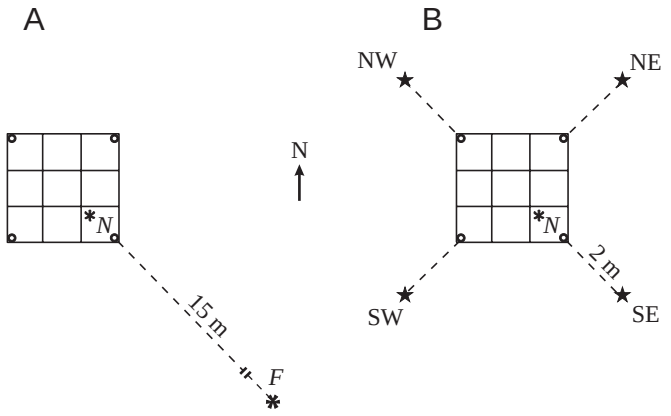

Fig. 1. Experimental arrangement used for training (A) and recording (B) the search trajectories during homebound runs in individually marked *Cataglyphis* ants. The ants were all trained to visit a feeder (*F*) located 16 m southeast from the nest entrance. The search trajectories of individual ants were then recorded for ants released in four different compass directions (NW, NE, SW and SE in B) in a separate test field. The nest (*N*) was located diagonally 100 cm northwest of the landmark in the southeast corner of the four-cylinder landmark square arrays. The side of the landmark square corresponded to a distance of 282 cm between the centres of the landmarks. The diagonal distance between the landmarks was 400 cm.

Materials and methods

Experimental subjects and study area

Desert ants of the species *Cataglyphis fortis* inhabiting open salt-pan areas of the Saharan desert were used to investigate the mechanism of landmark navigation close to the nest site. The experiments were performed in the ants' natural habitat near the village of Maharès in southeast Tunisia (34.58°N, 10.50°E) in July–August 1997 and 1998. All ants used in the experiments were individually marked so that the numbers of foraging visits by the ants to an artificial feeder could be recorded for each ant prior to the experiments. New unmarked foragers were continuously captured at their first visit to the feeder, then colour-marked and released. The colonies were selected primarily on the basis of the absence of obvious nearby landmarks (the closest landmark, of maximum height 0.5 m, was located more than 40 m away). In the first experiment, the ants were trained to visit a single feeder located 16 m southeast of the nest (Fig. 1A). In the second experiment, the ants were trained to forage in four different compass directions at feeders located 15 m away from the nest entrance and in directions of 10 ° relative to a north–south and east–west axis respectively and with the nest located in the south–west corner of the four cylinder landmark square (cf. Åkesson and Wehner, 1997). In a third experiment we used the same locations of the four feeders as above, but trained the ants to locate the nest in the centre of the landmark square.

Observations at the feeder started prior to the time when the first ant appeared outside the nest entrance in the morning (between 08.00 and 08.30 h; Coordinated Universal Time+1 h) and continued until at least 16.00 h in the afternoon, when foraging activity decreased.

Experimental arrangement and procedure

We arranged a four-cylinder landmark square around the nest entrance such that the nest entrance was located asymmetrically relative to the centre of the landmark square (Fig. 1A). The landmarks used in the experiments were plastic cylinders, covered with black paper, of height 40.5 cm and diameter 22.5 cm. The side length of the landmark square was 282 cm (as measured from the centre of the landmarks). Correspondingly, the diagonal distance was 400 cm. Two of the sides of the landmark square were arranged parallel to the geographic north–south axis. The nest entrance was located inside the landmark square along a diagonal line 100 cm northwest from the landmark located in the southeast corner of the landmark square (Fig. 1A).

During the first 2 days of training, we captured as many ants as possible outside the nest entrance and marked them with a one-colour code (one colour for each day). On the following days, we marked the newly arriving ants individually with three colour dots on the thorax and abdomen. The colours allowed us to identify the experimental animals at a distance without capturing them. During the first day of marking ants, the four landmarks were installed around the nest. Two days later, we started to train individually marked ants to visit the feeder. During the experimental period in 1998, a stationary observer was present at the single feeder for the full day and recorded each visit by the individually marked ants at the feeder. Food was presented at the feeder only when the observer was present. This procedure allowed us to record the great majority of the foraging runs performed each day by all marked ants that visited the feeder.

After the ants had visited the feeder, they were captured at the nest, i.e. less than 1 m from the landmark closest to the nest (so-called zero-vector ants) and displaced inside a covered glass vial to a nearby test field where the same landmark arrangement as that present at the nest had been installed. The test field was located in an open area without any nearby landmarks. It covered 30 m×30 m and contained a grid made of thin white lines (grid width 1 m) painted on the ground. The grid was aligned parallel to the north–south axis.

In the test field, the first search trajectories of the marked ants were recorded after the animals had visited the feeder five times. The ants were released from four different compass directions relative to the landmark array, one of which coincided with the direction towards the feeder (southeast), while the others deviated by ±90 or 180 ° from this 0 ° direction (northeast, southwest, northwest). The release sites were located 2 m diagonally from the closest landmark (Fig. 1B). Each ant was tested several times from all four directions. The tests followed each other in random order, with three training-field foraging runs interspersed between individual tests. We released the ants with a piece of biscuit to boost their motivation to home for the fictive nest. The ants' search trajectories were recorded for 3 min each by an observer constantly changing his or her position relative to the searching ant while recording the ants' paths on graph paper.

Data analyses and statistics

The search trajectories of individual ants were digitized on a computer tablet (MbasaSoft GEDIT; Antonsen, 1995). On the basis of the pooled trajectories, the search density distributions were calculated for a selected area (3 m×3 m) around the nest. In Figs 7 and 8, the search densities pertaining to each experimental configuration are presented both pooled and separated for all four release sites. We also divided the 3-min tracking period into two half-periods (1.5 min each). The proportion of the time spent searching was computed for each of these two half-periods.

We analysed the number of positions at which the ants searched for the fictive nest entrance, i.e. where distinct peaks in the search density profiles occurred. Each search trajectory was evaluated visually, and the number of positions (0–4) at which the ant had searched for the nest was classified on the basis of the ants' turning behaviour. If the ant had stopped and turned at least once within a circle of 20 cm radius around the position of the hypothetical nest given by the landmark array at any of the four alternative positions, this was counted as searching for the nest. The majority of the ants, however, turned a number of times and returned several times to the same position to search for the nest. The median values resulting from these computations of the four alternative positions given by the landmark scene at which individual ants searched for the nest were compared for different experiments using the median test (Siegel and Castellan, 1988).

Results

As the goal was located asymmetrically within a square array of four identical landmarks, its geographical position was accompanied by three additional positions at which the ant could note its current landmark image with its stored one but could not place this in register with a celestial system of reference. By releasing the ants not only from the training direction (southeast), from which they would hit the (fictive) geographical location of the goal first, but also from these alternative directions (southwest, northwest, northeast), we were able to investigate the extent to which the ants are able to couple or decouple a memorised visual snapshot scene from a celestial system of reference.

In total, we recorded the search trajectories of 27 individually marked ants (release sites given in Fig. 1B; northwest N=16, northeast N=18, southwest N=20, southeast N=22). On the basis

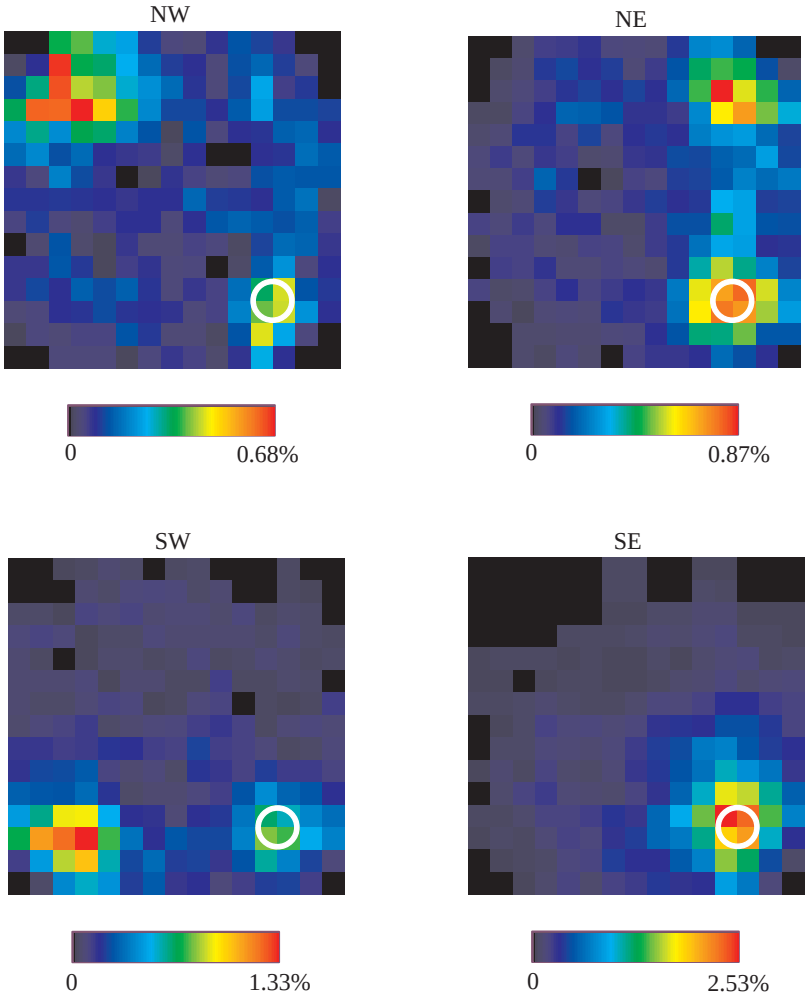

Fig. 2. Search density distributions for a group of individually tracked desert ants searching for the fictive position of the nest located within a four-cylinder landmark array. Search density distributions are given for releases from directions identical with (SE) or different from (NW, NE, SW) the training direction. If it lived long enough to complete the experimental period, each ant had been released from all four directions. An open circle depicts the position of the hypothetical nest. The sides of the square are 282 cm between the centres of the landmarks. The four cylindrical landmarks are positioned in each of the four corners of the search density square. Colour scales indicating the relative search densities in each 20 cm×20 cm square pixel are given beneath the distribution for each group. N=16 (NW), N=18 (NE), N=20 (SW) and N=22 (SE) ants.

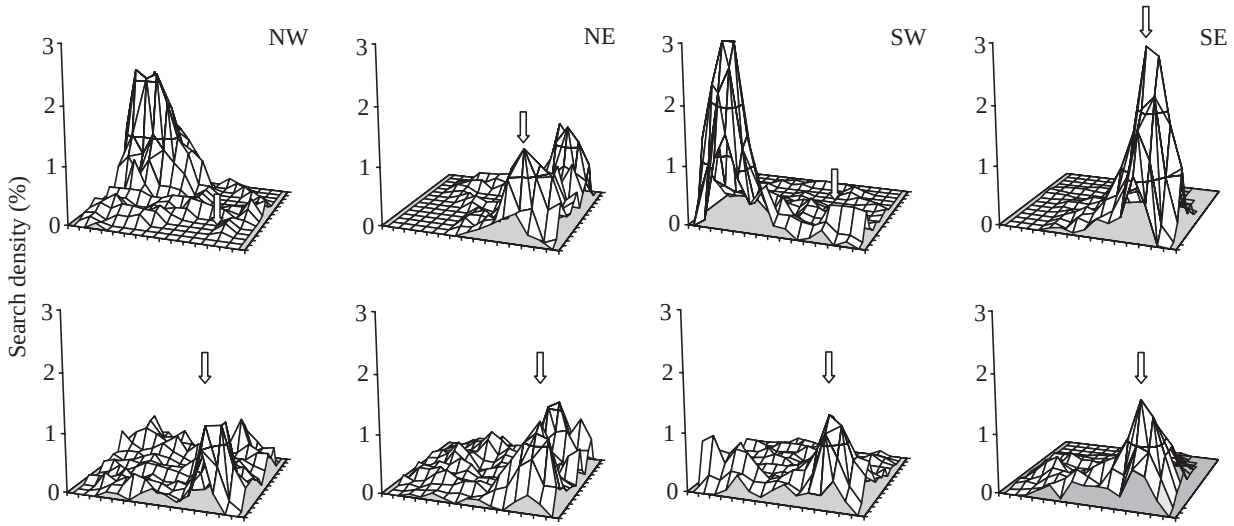

Fig. 3. Three-dimensional search density distributions of individually tracked desert ants searching for the nest located within a four-cylinder landmark square array. The fictive positions of the nest are depicted by open arrows. Data are given separately for the first and the second 1.5-min recording periods in the upper and lower graphs, respectively. The ants were released in four different compass directions relative to the landmark square (NW, NE, SW, SE). The four cylindrical landmarks are positioned in each of the four corners of the search density square. *N*=16 (NW), *N*=18 (NE), *N*=20 (SW) and *N*=22 (SE) ants. The same data are presented in Fig. 2 for the entire 3-min recording periods.

of these search trajectories, we calculated the relative search activities pertaining to all 225 20 cm×20 cm^2 pixels of the four-cylinder landmark array (Fig. 2). The search density distribution given in Fig. 2 (southeast) corresponds to searching performed by ants captured and released in the direction of approach from the feeder during training. There is a single high search density peak. In contrast, the search density distributions recorded for ants released at any of the other directions (Fig. 2, northwest, northeast, southwest) resulted in two obvious peaks, one located at the hypothetical geographical position of the nest and a second peak at that of the three other snapshot-matching sites that was closest to the site of release. The great majority of the ants started to search for the nest at the closest hypothetical nest position during the first half of the tracking period (1.5 min) and searched at the correct geographical position of the nest given by celestial and landmark information during the second half of the test period (Fig. 3). This behaviour was especially obvious in releases from southwest and northwest (Fig. 3). In three cases (northwest, southwest and southeast in Fig. 3), search intensities were slightly lower during the second half of the test period.

Individual ants released from directions different from the training direction most often searched at two positions [median=2 for all, *N*=16 (northwest), *N*=18 (northeast), *N*=20 (southwest); Fig. 4]. They usually changed to the correct position of the hypothetical nest during the second half of the search period. In contrast, ants released from the direction of training predominantly searched at only one position [median=1, *N*=22 (southeast)], i.e. the correct position of the (fictive) nest (median test, χ^2=15.2, d.f.=3, P<0.01; Fig. 4). Examples of search trajectories for two ants released from all four directions are given in Fig. 5. The only direction of release from which ants (*N*=2) were recorded never to enter the

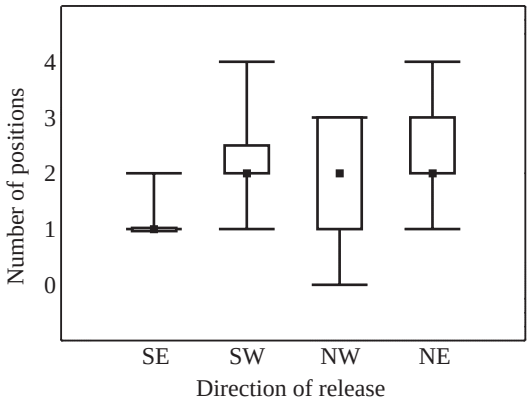

Fig. 4. The landmark panorama within the landmark square provided four alternative positions where the ants could search for the fictive nest. The box-plot representation depicts the median number of positions at which the ants were recorded searching for the nest. Median values (filled squares) are given for the four directions from which the ants had been released. Releases from southeast correspond to releases from the training direction. Limits for minimum and maximum values (lines above and below the boxes) and 25–75 % percentile ranges (open boxes) are given. *N*=16 (NW), *N*=18 (NE), *N*=20 (SW) and *N*=22 (SE) ants (same data pool as that represented in Fig. 2). For further information, see the text.

landmark array and search for the nest was at the release site northwest of the landmarks, which is located opposite to the direction towards the feeder (Fig. 4).

We also compared the number of positions at which the ants searched for the nest after different lengths of training: (i) after five to maximally 14 recorded natural foraging runs performed on the same day and (ii) after a training period lasting for at least 3 days. For individual ants, the mean number of visits to

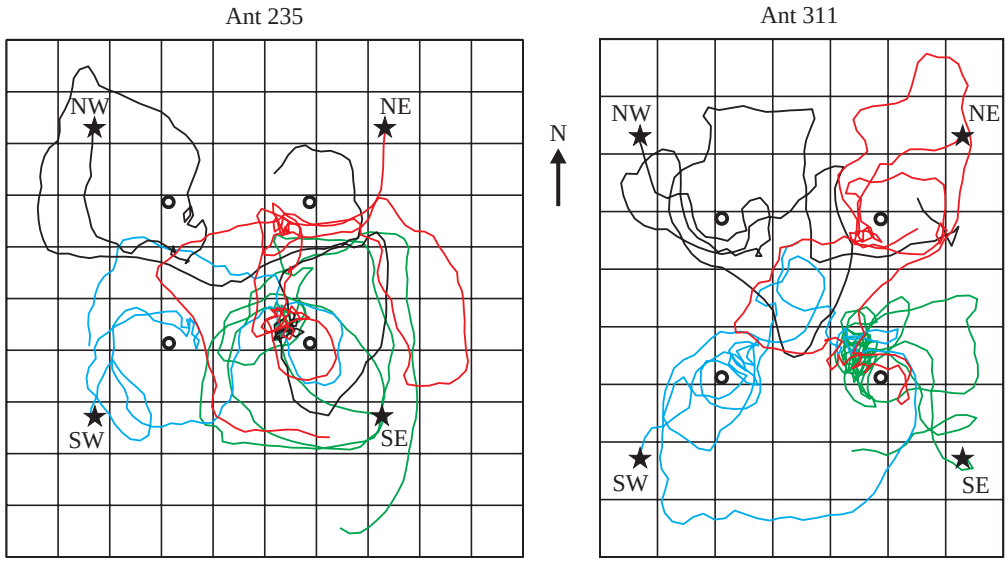

Fig. 5. Examples of searching trajectories for two ants recorded after releases from four different compass directions after a short training period (see text). Open black circles indicate the positions of the landmarks; stars represent the sites of release. The green lines indicate the search trajectories of ants released from southeast, i.e. from the direction from which they had approached the nest during training. According to the criteria used to define the number of search positions, ants 235 and 311 both exhibited four search positions.

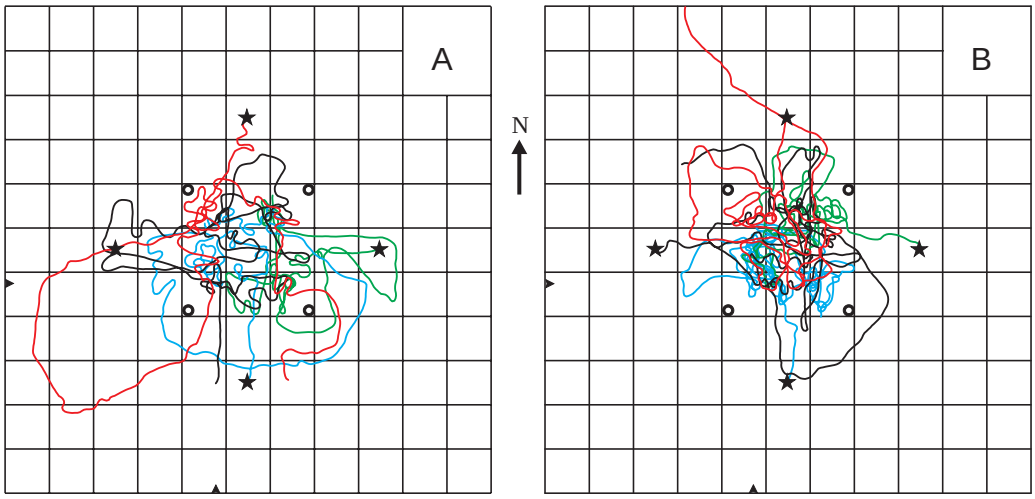

Fig. 6. Examples of the trajectories of eight ants (four in A and four in B) searching for the nest within a four-cylinder landmark array recorded after releases from four different compass directions. All ants were released from the direction of training after at least 3 days of training. Open circles indicate the positions of landmarks; stars denote the sites of release; the black arrowheads at the edge of the grid point to the fictive position of the nest. Each search trajectory selected by an individual ant is represented by a coloured line.

the feeder was 29.2±27.1 (mean ± S.D.; N=29) per day (S. Åkesson and R. Wehner, in preparation). These experiments with different lengths of training were performed to investigate whether the coupling between landmarks and celestial compass cues becomes weaker as training time proceeds. Ants of the long-training group, each trained to one of four different feeders, searched for the nest at more than one position when released from the direction of training (median=3, minimum=1, maximum=4, N=26, Fig. 6) compared with ants of the short-training group (southeast, see above and Fig. 4; median test, χ^2=13.5, d.f.=1, P<0.001). Furthermore, the number of positions at which the ants searched for the nest did not depend on the location at which they had been released (in the training direction or from any of the other three compass directions) for the group of ants that had been allowed a training period of at least 3 days (median test, χ^2=0.007, d.f.=1, P>0.05).

In a companion training paradigm, the ants had to locate the nest in the centre of a four-cylinder landmark square. This experiment was designed to create an unambiguous landmark situation and to test whether in such a situation an experimental rotation of the landmark array relative to the celestial system of reference had any effect. The ants searched intensely at the (only one) fictive position of the nest when released from any of four alternative compass directions (training landmark array depicted in inset of Fig. 7; cf. Åkesson et al., 1998), and the search density profiles centred at the fictive position of the nest were only slightly broader when the landmark arrays had been rotated by 45 ° (Fig. 8).

Discussion

Desert ants returning from a foraging journey reliably rely on landmark cues to pinpoint the nest entrance. Ants have already been shown to use stored two-dimensional images, which are retinotopically fixed, to locate the nest entrance

(Wehner and Müller, 1985; Judd and Collett, 1998). Here, we ask the questions whether these stored images are spatially oriented within a celestial system of reference and, if so, whether they can be decoupled from it (e.g. Collett, 1992). We designed experiments in which ants could locate the nest asymmetrically within a square array of four cylindrical landmarks. Only at one of four alternative positions were the landmark snapshot and the current retinal image in register with the celestial system of reference. Do the ants search only there, or do they also search at the other three locations at which the current panorama image could be matched to the stored but not to the celestial coordinates?

Ants released at a site coinciding with the direction of training exhibited high search intensities at the fictive position of the nest, demonstrating their ability to learn to use an array of landmarks and to place it correctly into the celestial frame of reference. However, when the same individuals were released from directions other than the direction of training, they most often searched for the nest at two of the four alternative positions within the four-cylinder landmark array: first at the position closest to the point of release, where landmarks and skymarks were out of register, and then at the 'true' position of the nest. This behaviour indicates that the memorised landmark image can temporarily be decoupled from the celestial system of reference. An alternative explanation of the ants' search behaviour might be that they perform a stereotyped search by following fixed routes followed by brief pauses and turns. Such search behaviour might at first glance be supported by the observations of ants returning to the nest after short training periods (Fig. 5), in which some ants seem to make a brief pause at the end of the return route rather than following more intense searching and turning at the hypothetical nest. However, a stereotyped search strategy, with fixed routes mixed with brief turning, was not observed for ants recorded after a longer training period (Fig. 6), suggesting that they were indeed searching at the alternative positions of the fictive nest, with the celestial system of reference temporarily decoupled from the landmark image.

Honeybees have been shown to store landmark patterns with reference to compass cues (Dickinson, 1994; Collett and Baron, 1994; Fry and Wehner, 2002). Dickinson (1994) trained honeybees to locate the site of a feeder near a cylindrical landmark when the bees were given access to the natural clear sky during training and testing. The bees' visits to four alternative positions relative to the landmark were then recorded; they were able to

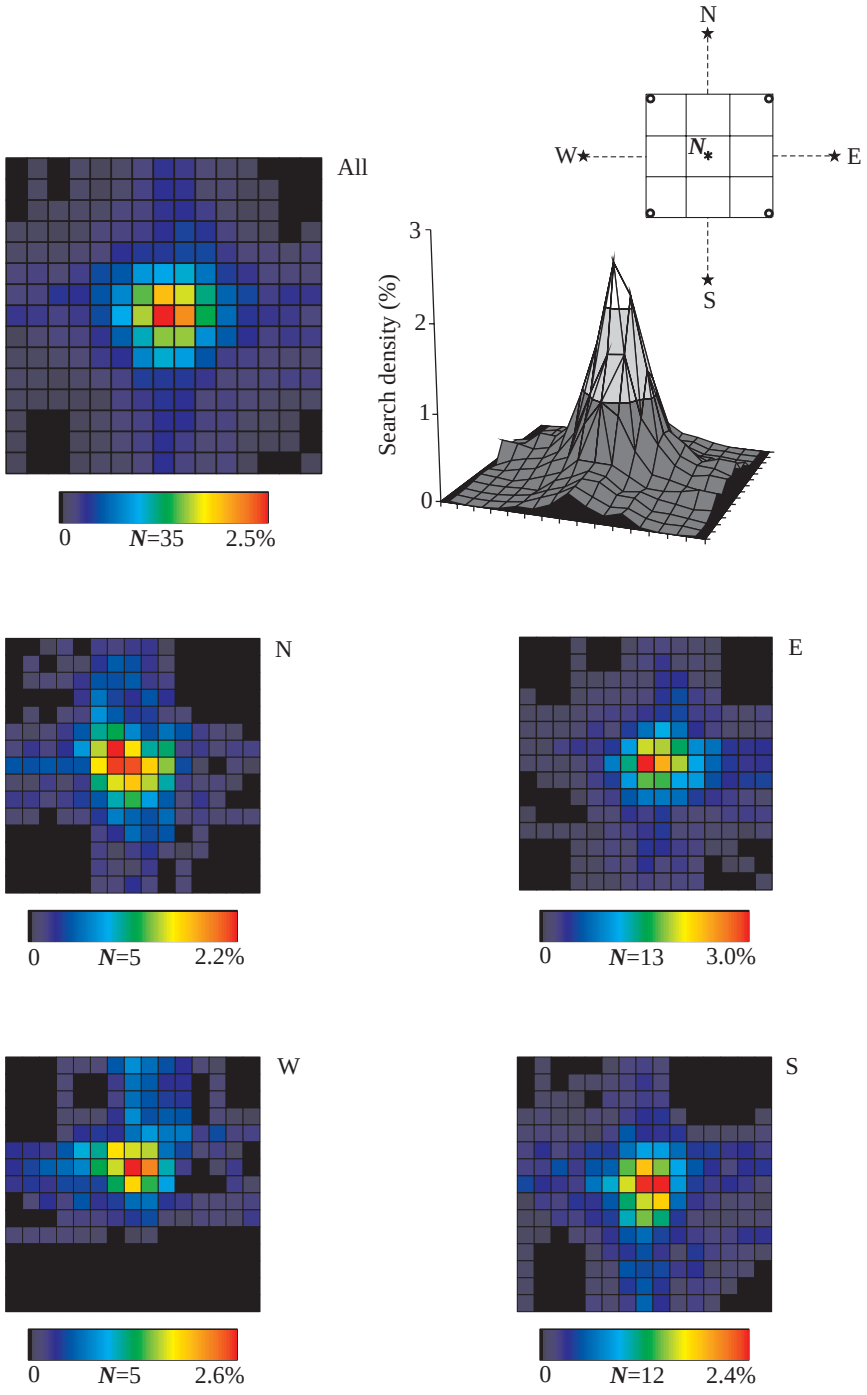

Fig. 7. Search density plots for experiments in which the ants were trained to locate the nest in the centre of a four-cylinder square array of landmarks (open circles in inset). Search densities recorded during 3-min periods are given for data from all release sites combined (All) as well as separately for different release sites (N, E, S, W). The density of search activity is given as a percentage for each 20 cm×20 cm square pixel (*N*=225 squares) within the four-landmark array. The inset shows the configuration of landmarks (open circles) and release sites (stars) used during training and testing. *N*, nest.

determine the fictive position of the feeder only when celestial cues were available, but not when the sky was completely covered by clouds. These experiments indicate that the bees are able to store landmark images relative to a celestial system of reference (Dickinson, 1994), as previously suggested by Lindauer (1960). However, Collett and Baron (1994) reported that honeybees were able to locate a feeder relative to landmarks even if celestial cues were absent as long as magnetic cues were available. Their experiments suggest that the Earth's magnetic field could also provide compass information for bees.

One could argue that the external system of reference shown to be effective in our experiments was provided by distant landmarks rather than by skylight information. In the salt-pan environment, in which the experiments were performed, this possibility can be almost completely ruled out. As seen from the nest entrance, the largest (isolated) landmark subtended 0.7°, and the few isolated landmarks that could be seen in the test field were even lower and in completely different positions. Hence, in all likelihood, it is a skymark system that the ants used as a frame of reference in our experiments. Distant landmark panoramas have been shown to be used as a navigational guidemark by homing wood ants, *Formica japonica* (Fukushi, 2001). However, in these experiments, the upper skyline of the surrounding trees, which was the important part of the landmark scene, was much higher (subtending >20°) than in our experiments (subtending <2°, see also Wehner et al., 1996). Furthermore, in our experiments the configuration of the natural distant landmarks differed between the training and test areas.

Cartwright and Collett (1983) made a detailed study of the characteristics of the reference system by which honeybees use their memorised landmark panoramas to locate the site of a feeder. They rotated an asymmetrical array of three landmarks by 30–90° and found that the bees responded to these shifts by changing their search position only if the landmarks were rotated by a substantial amount (>45°) relative to the training configuration. The authors concluded that the bees do define the landmark scene with respect to external coordinates, but that they do so with a certain degree of imprecision (Cartwright and Collett, 1983). Their findings agree well with our observations that the search density profile centred above the fictive position of the nest was only slightly broader when the landmark array had been rotated by 45° (Figs 7 and 8).

In conclusion, the most important result of the present experiment is that ants can store images of panorama skylines with a celestial system of reference, but that they are also able to decouple their snapshot memories from this frame of reference. The experiments further suggest that this decoupling might be facilitated over time, such that, after some days of training, desert ants prioritize the current landmark memories and to a certain extent ignore the conflicting celestial information experienced when searching for the nest.

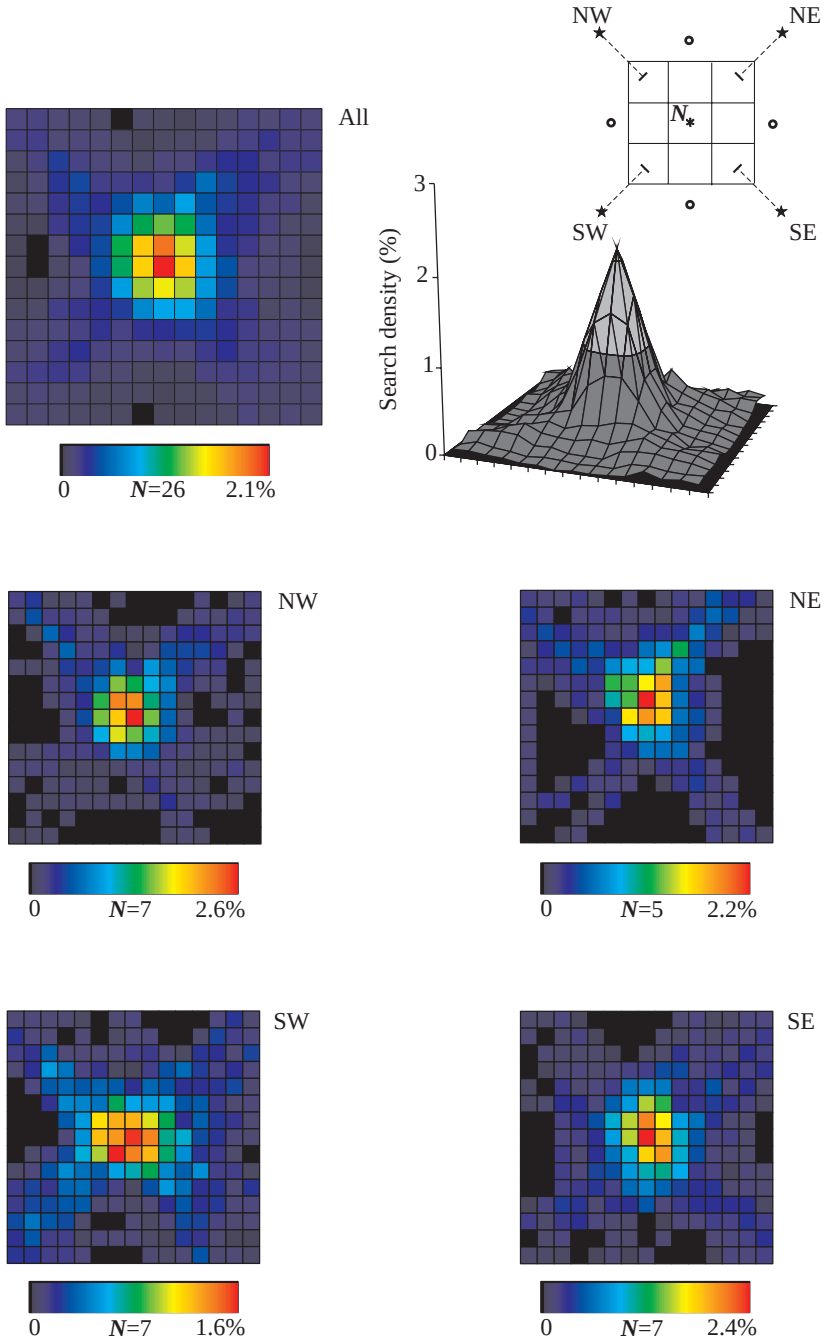

Fig. 8. Same experimental paradigm as in Fig. 7 but with the landmark array used for testing rotated by 45° relative to the training situation (for the latter, see inset in Fig. 7). *N*=27 ants each released from all four points of the compass. For further explanation see Fig. 7. *N*, nest.

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