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Local vectors in desert ants: context-dependent landmark learning during outbound and homebound runs

Abstract Desert ants, *Cataglyphis fortis*, associate nestward-directed vector memories (local vectors) with the sight of landmarks along a familiar route. This view-based navigational strategy works in parallel to the self-centred path integration system. In the present study we ask at what temporal stage during a foraging journey does the ant acquire nestward-directed local vector information from feeder-associated landmarks: during its outbound run to a feeding site or during its homebound run to the nest. Tests performed after two reversed-image training paradigms revealed that the ants associated such vectors exclusively with landmarks present during their homebound runs.

Keywords *Cataglyphis* · Landmarks · Local vectors · Spatial learning · Visual navigation

Introduction

During their long-distance foraging trips, *Cataglyphis* ants use path integration to return to the nest and, thereafter, to a previously visited feeding site (Wehner and Srinivasan 1981; Müller and Wehner 1988; Collett et al. 1999; Wehner et al. 2002). Since this self-centred system of navigation is prone to cumulative errors, the ants in addition use visual information derived from terrestrial landmarks to pinpoint the feeding site (Wehner 1970; Wolf and Wehner 2000) and the nest (Wehner and Räber 1979).

If information from path integration is eliminated experimentally, landmarks alone can guide the ants back to the nest (Wehner and Flatt 1972; Wehner et al. 1996). They can even override the global home vector derived

from path integration, if experiments are designed in which route-based courses and vector courses point in different directions (Sassi and Wehner 1997). In all these studies, sets of artificial landmarks strung together along the route between the nest and a feeder could have led the ants directly from one signpost to the next. The ants having passed one signpost would enter the catchment area of the next, etc. Moreover, it has recently been shown that *Cataglyphis* ants are able to associate local vectors with individual landmarks (Collett et al. 1998; Bisch-Knaden and Wehner 2001). These local vectors could substantially decrease the time spent for moving from one landmark, or set of landmarks, to the next.

In the present account, we test the ant's ability to learn local vectors associated with feeding-site landmarks during the feeder-arriving and the feeder-departing state of the ant's foraging journey. For example, ants of the genus *Formica* have more difficulties in solving a maze problem they encounter during their outbound path than they do during their homebound path (Schneirla 1934). We trained ants to experience a small array of feeder-associated artificial landmarks either exclusively during their outbound runs to a feeder or exclusively during their homebound runs. In the test situation, "zero-vector" ants (ants which had already run off their home vector, i.e. ants in which the arrant state of the vector matched the stored one) of either group were confronted with the landmarks within an unfamiliar area and tested there in their homebound state. Any differences in the recall of the appropriate local vectors would then depend on the preceding training condition.

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Material and methods

The experiments were performed at our *Cataglyphis* Field Station in the salt pan areas between the villages of Maharès and Chaffar (southern Tunisia). This area inhabited by the halophilic ant, *Cataglyphis fortis* was chosen for the experiments because it consisted of bare terrain largely devoid of any natural landmarks.

Hence, arrays of artificial landmarks were the only visual cues that could be used by *C. fortis* alongside the ants' path integration system.

Training procedure

In total, six colonies were used in the experiments. A feeding site was established 13 m to the south of each nest entrance. The feeder consisting of a piece of watermelon and some biscuit crumbs attracted 10–50 foragers per day, depending on nest size and nest activity.

Two training conditions A and B were applied that differed in the presence or absence of an array of artificial landmarks experienced by the ants while they were running back and forth between the nest and the feeder (Fig. 1). The angular height of the cylindrical landmarks (16.7° as seen from the midpoint between two landmarks) is similar to the ants' skyline within those parts of the desert habitat that are loosely covered with vegetation (mean ± SD; 20.2 ± 8.9° as seen from the center in between islands of vegetation; Heusser and Wehner 2002). The 2 m distance between the artificial landmarks is also in accord with the mean width (± SD) of natural landmark corridors (1.7 ± 0.7 m; lit. cit.).

The ants were exposed to different landmark panoramas during their outbound and homebound runs. To achieve this goal we captured the ants at the feeding site in a trap. The bait was placed in a plastic bowl (20 cm in diameter), with its inner edge brushed with Fluon that prevented the ants from escaping once they had entered the feeder. The individually marked ants were collected singly from the trap and displaced to a remote test area. In training condition A, the landmarks were present only during the ants' homebound runs performed within the test area. There the ants were released at the position of the fictive feeder relative to the landmark array, captured again after they had completed their homebound runs (characterized by the start of the systematic search as described by Wehner and Srinivasan 1981; Müller and Wehner 1994), and released into their colony. In the reverse training condition B, the ants performed their homebound runs

within the bare test area after having passed the landmark configuration during their outbound runs. Each ant performed five of these round trips before the test procedures started.

Test procedure

Individual ants were captured after they had completed their homebound runs within the test area. They were provided with a biscuit crumb and released singly at the position of the fictive feeder relative to the landmark configuration. The trajectories of the ants were recorded for 5 min each on graph paper (squares: 1 cm×1 cm) with the help of a white grid (squares: 1 m×1 m, grid dimensions: 25 m×25 m) painted on the desert ground. After the test, the ants were marked and transferred back to their nest. Each ant was tested only once.

Data analysis

The direction and the length of the longest path segment emanating from the landmark array were determined for each trajectory (Fig. 2). Due to the symmetrical arrangement of the landmarks, the ants had equal chances to leave the square array of landmarks at any of its four sides. Hence, if the ants did not associate any directional information with the landmark panorama, their probability of leaving the array at the 0°, 90°, 180° or 270° side should be 0.25 each. Chi-square tests were applied to test for this hypothesis. If the longest path segment was shorter than 1 m, the trajectory was excluded from this circular scatter analysis. Trajectories of ants that did not enter the landmark configuration during the 5-min recording time could not be analysed either. Nevertheless, in both latter cases, the trajectories were included in the search density diagrams (Fig. 3; see Results for further explanations).

In order to examine to what extent the ants' directional choices were affected by the training conditions, concentric circles (radii: 6, 8 and 10 m) were drawn about the point of release. The first intersections of the ants' trajectories with these circles were determined (see Results, Fig. 5). The *V*-test described by Batschelet (1981) was applied to test for the ants' tendency to cluster around the compass direction of the fictive nest (0° in Figs. 2 and 5).
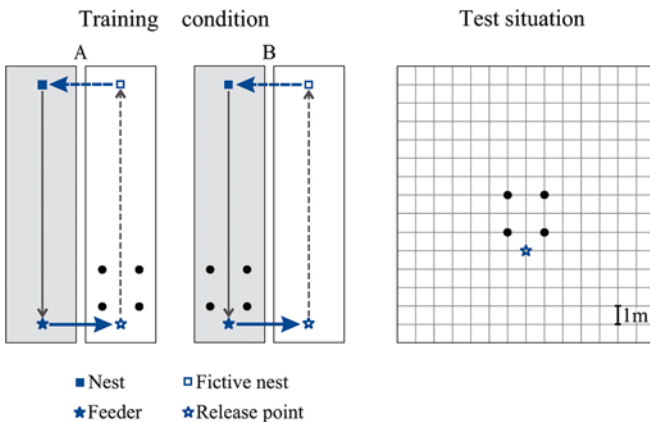

Fig. 1 Training conditions and test situation. During training, an array of four landmarks (each 20 cm wide and 30 cm high, *filled black circles*) was present near the feeder during either homebound (*A, broken arrows*) runs, or outbound (*B, solid arrows*) runs, respectively. The ants were captured at the feeder and transferred (*solid blue arrow*) from the training area (*grey*) to a remote area (*white*) called test area, because subsequently in this area the tests were performed. There they were released, captured again at the end of their homebound runs and transferred (*dashed blue arrow*) back to the nest. During tests, the ants were released within the test area at the position of the fictive feeder relative to the landmark array
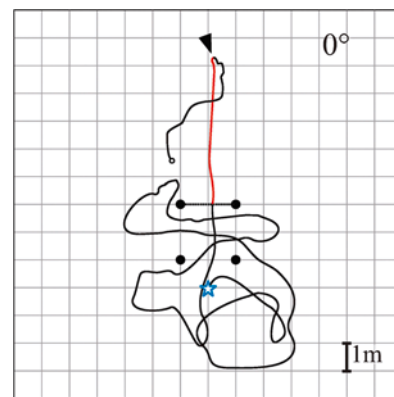

Fig. 2 Data analysis. Example of an ant that was released (*open blue star*) within the test area in front of the square array of landmarks (*filled black circles*). Its trajectory (*solid black line*) was recorded for 5 min (*small open circle*: end of recorded path). The longest path segment emanating from the landmark array (shown here in *red*) was determined. Its length was measured from the intersection of the trajectory with the corresponding side of the landmark array (*dotted line*) and the point where the ant made a sharp turn (*arrowhead*) back to the landmark configuration. *0°*, direction towards the fictive position of the nest as seen from the landmark array

Experiment A

Experiment A*

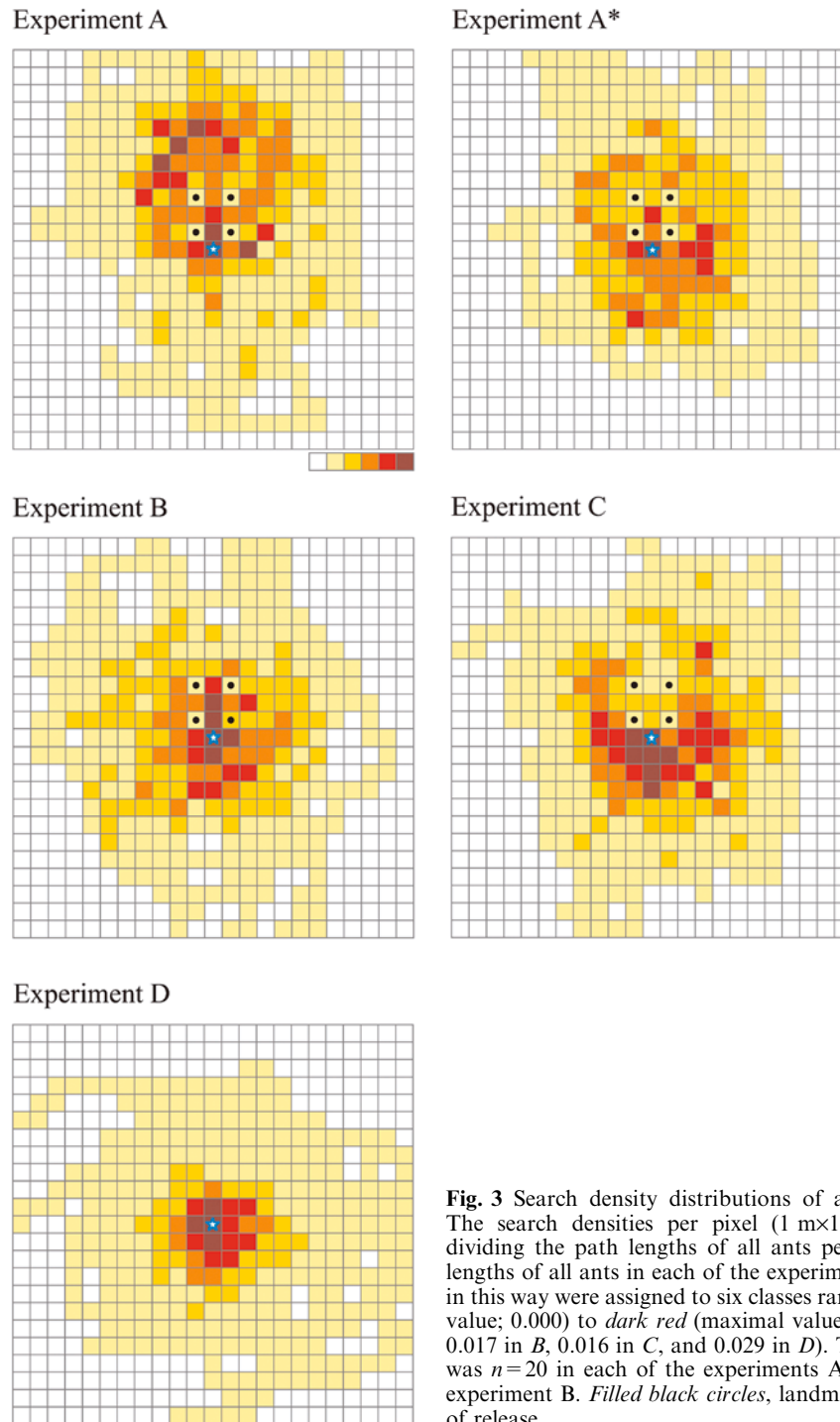

Experiment B

Experiment C

Experiment D

Fig. 3 Search density distributions of ants within the test area. The search densities per pixel (1 m×1 m) were determined by dividing the path lengths of all ants per pixel by the total path lengths of all ants in each of the experiments. The values obtained in this way were assigned to six classes ranging from *white* (minimal value; 0.000) to *dark red* (maximal value; 0.015 in *A*, 0.021 in *A**, 0.017 in *B*, 0.016 in *C*, and 0.029 in *D*). The number of ants tested was $n = 20$ in each of the experiments A, A*, C, D and $n = 19$ in experiment B. *Filled black circles*, landmarks; *open blue star*, point of release

Results

At which instant during their foraging round trips do the ants acquire local, landmark-associated vector information? In a first attempt to answer this question we trained the ants to encounter an experimental landmark array between their nest and a feeder exclusively during their homebound or outbound runs, respectively. Later homebound ants were tested within a desert plain far away from the training ground, where they did not experience landmark-based orientation cues other than those linked to the experimental array of landmarks.

If the ants were moved from the feeder to the test area, their global home vector derived from path integration would always have pointed in the compass direction of the fictive nest, irrespective of whether familiar landmarks were present or not (see Fig. 8 in Bisch-Knaden and Wehner 2001). Therefore, the

acquisition of landmark-based local vector information was tested in ants that had just completed their homebound runs from the feeder to the nest. Hence global vector information could not overshadow any local-vector information that had possibly been associated with the landmarks presented during training.

At this juncture, it might be worth mentioning that global vectors, unlike local vectors, have never been shown to be recalled by familiar landmark arrays (Collett et al. 1998). Instead, the global-vector path-integration system continuously operates while the animal is running and, hence, during the homeward runs, the global vector always points towards the nest (Sassi and Wehner 1997).

Landmarks present during homebound runs (experiments A and A*)

Ants that had passed the landmarks only during their homebound runs clearly preferred the direction towards the position of the fictive nest while they were searching (Fig. 3). However, 7 out of the total of 20 trajectories could not be analysed because the ants did not enter the landmark array during the recording time ($n=6$) or because their longest path segment emanating from the landmark array was shorter than 1 m ($n=1$). In the remaining 13 trajectories, the distribution of the longest path segments showed a significant preference for the compass direction of the fictive nest (in 10 out of the 13 paths; $P=0.0002$, X^2-test; Fig. 4). These path segments had a mean length ($\pm$SD) of 5.0 ± 1.2 m, $n=10$) and represented the local directional information (the "local vectors") that the ants had associated with the landmark configuration.

In experiment A, the ants had experienced the landmarks during five training homebound runs. How do they behave when they are exposed to the landmark array only during a single homebound run? We addressed this question in experiment A*. First, the ants were trained to visit the feeder without any landmarks en route. They then performed a single additional homebound training run in which they experienced the landmark array within the test area. Subsequent tests were performed in the usual way (Fig. 3). There was no tendency to search in the direction of the fictive nest as it was in experiment A. However, the ants searched more intensively inside the array than in tests following training without any landmark experience (experiment C, see section "Controls" below; mean relative search densities ($\pm$SD) inside the square array of landmarks: 3.0 ± 2.6 %, $n=20$ in experiment A* and 1.4 ± 1.8 %, $n=20$ in experiment C; $P=0.02$, Mann Whitney U-test). Hence, a single landmark encounter significantly alters the ants' search strategy in the test situation.

As a result of the standard procedures applied in experiment A some trajectories had to be excluded from the scatter analysis (5 ants did not enter the landmark array, and in 3 ants the longest path segment emanating from the landmark array did not exceed 1 m). For the remaining 12 ants, the longest path segments were evenly distributed in all four directions ($P=0.3$, X^2-test; Fig. 4). Nevertheless, those path segments pointing towards the fictive nest (mean length $\pm$SD; 5.4 ± 2.2 m, $n=4$) were significantly longer than those pointing in the other three directions (2.3 m ±0.9 m, $n=8$; $P=0.007$, Mann Whitney U-test).

The comparison of experiments A and A* shows the build-up of landmark-based local vector information from run no. 1 to run no. 5. The mean lengths of the local vectors did not differ in experiments A* and A in which the ants experienced the landmarks during one or five successive training homebound runs, respectively ($P=0.7$, Mann Whitney U-test). Continuous training instead resulted in a larger number of tested ants that exhibited distinct local vectors (20% in experiment A* versus 50% in experiment A; $P<0.05$, X^2-test).

Landmarks present during outbound runs (experiment B)

If the ants had been exposed to the landmarks only during their outbound runs (Fig. 3), 10 out of the 19 test trajectories recorded could not be analysed. Either did

Fig. 4 Directional choices of ants within the test area. For each 5-min trajectory the longest path segment emanating from the square array of landmarks and exceeding 1 m in length is displayed. *Filled black circles*, landmarks; *open blue square*, position of fictive nest relative to the landmark array; *open blue star*, point of release
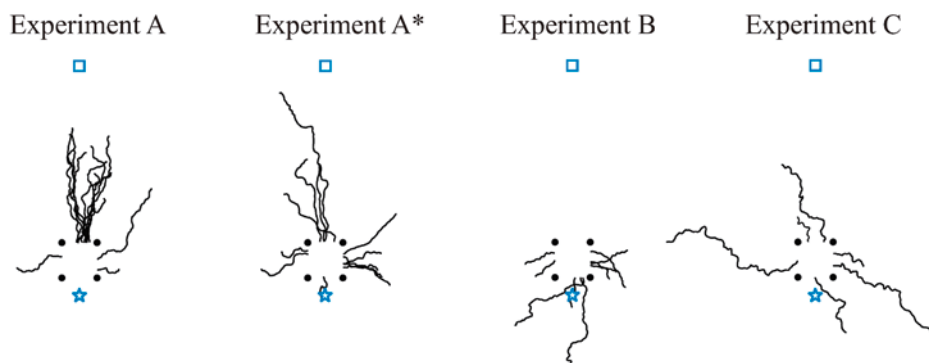
the ants not enter the landmark array ($n = 7$), or their longest path segments emanating from the landmark array were shorter than 1 m ($n = 3$). The nine remaining path segments were distributed randomly ($P = 0.3$, X^2-test; Fig. 4). In contrast to experiments A and A* described above, none of the ants was able to associate a local vector with the landmarks.

Controls (experiments C and D)

Two additional experiments were performed to test for a possible tendency of the ants to prefer a particular direction relative to the landmark array, and to reveal hidden orientation cues potentially present within the test area. In the first experiment, the ants while being trained to visit the feeder had not seen any landmarks at all (experiment C, Fig. 3). In the test situation, the majority of these ants seemed to avoid the landmarks: 12 out of 20 ants tested did not enter the landmark array. For another 2 ants, the longest path segment emanating from the landmark array was shorter than 1 m. In the remaining six trajectories, the path segments were randomly distributed ($P = 0.9$, X^2-test; Fig. 4). In the second experiment, the ants were trained to experience the landmarks for a full day during both their outbound and homebound runs and were released within the bare test area ($n = 20$, experiment D; Fig. 3). In this case, their search was not biased in any direction but was closely centred on the point of release. The results of these two control experiments confirm that the ants neither exhibited any innate landmark-associated preferences

nor rely on distant landmark cues that might have been present in the test situation.

Ants that did not exhibit distinct landmark-associated local vectors

Landmark-associated local vectors were only found in tests following training condition A. Nevertheless, even in this situation, there were a number of ants that did not exhibit a distinct local vector ($n = 10$ and $n = 16$ out of 20 trained ants in experiments A and A*, respectively). Moreover, none of the ants was able to do so in tests following training condition B. Have all these ants really been unsuccessful in associating any nestward-directed information with the conspicuous array of landmarks? To answer this question, we analysed the data in some more detail. In particular, we evaluated the spatial use of the area around the landmark array in the ants mentioned above, i.e., in those that had not exhibited local vectors in experiments A and A* (Fig. 5, left diagram). Furthermore, we compared the corresponding data of experiment B and control experiment C (Fig. 5, right diagram). We did so by determining the circular distribution of vanishing directions (at distances of 6, 8, and 10 m) from the point of release.

In experiments A and A*, most of the ants that had not exhibited distinct local vectors nevertheless associated directional information with the landmark array experienced during training. While searching, they favoured the direction towards the fictive nest as they were leaving the point of release. This "biased search" might be another example that the ant's search density profile is not always invariably radially symmetric, but can be modified by previously acquired information (Wehner et al. 2002). Such was not the case in experiments B and C (Table 1). Obviously, the landmark information acquired during the outbound runs was not associated with homebound local-vector information.

Nevertheless, the spatial use of the area within the square array of landmarks differed markedly between

Fig. 5 Search behaviour of ants that did not exhibit local vectors pointing towards the fictive position of the nest. *Coloured dots* represent the first intersections of the trajectories of the ants with concentric circles (radii: 6, 8 and 10 m) centred about the point of release (*open blue star*). *Left diagram*: experiment A (*yellow*, $n = 10$) and experiment A* (*red*, $n = 16$); *right diagram*: experiment B (*blue*, $n = 19$) and experiment C (*green*, $n = 20$). *Filled black circles*, landmarks; $0°$, direction of the fictive position of the nest relative to the landmark array
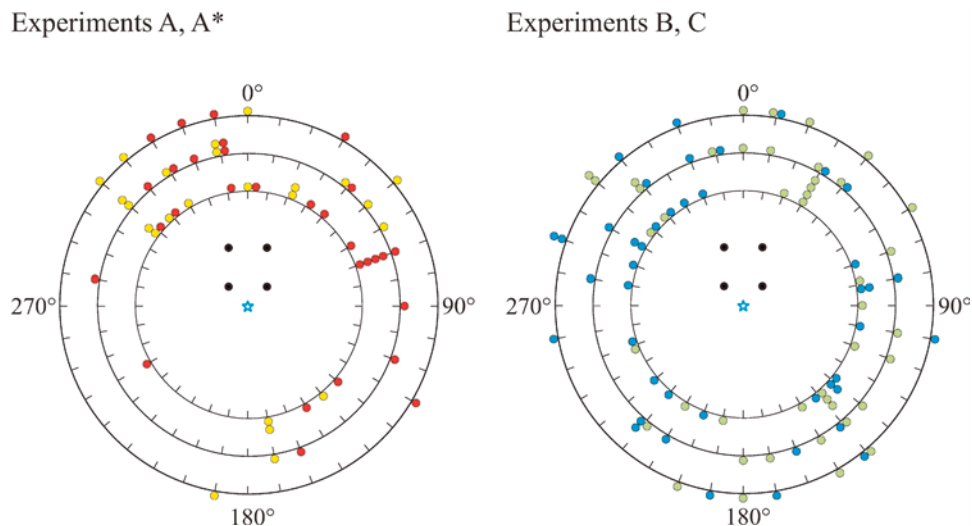

Experiments A, A*

Experiments B, C

Experiment	Distance from point of release		
	6 m	8 m	10 m
A	$P < 0.1$ (10)	$P < 0.01$ (9)	$P < 0.1$ (5)
A*	$P < 0.05$ (14)	$P < 0.05$ (11)	$P < 0.05$ (5)
B	$P \gg 0.1$ (19)	$P \gg 0.1$ (13)	$P \gg 0.1$ (10)
C	$P \gg 0.1$ (19)	$P \gg 0.1$ (16)	$P \gg 0.1$ (11)

experiments B and C (see Fig. 3). In the former case, in which the ants had seen the landmark array during their outbound training runs, they searched significantly more intensively inside the array than they did in the latter case, in which they had been confronted with the landmarks for the first time (mean relative search densities ($\pm$SD) inside the square array of landmarks: 3.8 ± 3.9 %, $n = 19$ in experiment B and 1.4 ± 1.8 %, $n = 20$ in experiment C; $P = 0.036$, Mann Whitney *U*-test). Obviously some information about the feeder-associated landmarks had been acquired during the outbound run, but nestward-directed local vector information had not been linked to it.

Discussion

Desert ants are known to associate homeward-directed vector memories with the landmark panorama along familiar routes (Collett et al. 1998). We now asked at what temporal stage during a foraging journey such local-vector information is acquired: during the ants' outbound or homebound runs. Hence, we applied two reversed-image training paradigms: a close-to-feeder array of artificial landmarks was present either exclusively during the ants' homebound runs (experiment A) or exclusively during their outbound runs (experiment B). In identical test situations, the A-ants associated local vectors with the symmetrically arranged landmarks, but the B-ants did not.

It is indeed likely that homeward-directed local vectors associated with landmarks close to the feeder are learned exclusively during the ants' homebound runs. During the outbound run an ant does not yet know, whether or not its foraging journey will be successful, i.e., if the same landmarks will be encountered on the homebound run. Furthermore, in integrating a circuitous outbound path the ant would acquire an homebound vector leading it over novel territory. Even though during the subsequent foraging journey it usually would return to a previously visited feeding site (Wehner 1987), it would usually do so along a different route (Wehner et al. 1983). Consequently, ants returning to the nest will encounter sequences of landmarks that might differ substantially from the ones seen during their outbound runs. Furthermore, even if an ant returned

exactly along the route taken during the outbound run, in general it will not be able to predict the landmark views to be encountered during its homebound run from the ones encountered during its outbound run. This is because in an arbitrary set of landmarks view-based information depends on the direction from which the landmarks are approached. In global vectors, the 180° reversed states can be predicted from each other, but in landmark routes, they cannot. The learning of nestward-directed local vectors might therefore be restricted to the return part of a foraging trip.

As the comparison between the results of experiments A and B show, *Cataglyphis* had learned homeward-directed local vectors exclusively during its homebound runs. However, had the ants been unable to memorize any directional information linked to the landmarks seen during their outbound runs? A similar question was raised in experiments with foraging honeybees. When the bees had to choose between a colour seen on arrival at a food source and a different colour seen on departure, they clearly preferred the former (Menzel 1968; Grossmann 1970). Does this mean that they did not learn the colour of the feeder they were departing from? A subsequent study revealed that they are well able to do so. If they were transported passively to a reward site and, hence, saw its colour exclusively on departure, in binary choice tests the choice frequency for this colour was almost 100% (Lehrer 1993). The observed preference for the colour seen on arrival over that seen on departure might simply occur because the choice tests can be performed only on arrival at the feeder (see also Lehrer and Collett 1994). Therefore, the test situation by itself favours the retrieving of the colour information acquired in the analogous training situation.

Correspondingly, it might well have been that in training condition B the ants had learned a local vector pointing towards the feeder rather than one pointing towards the nest. However, such a feeder-directed vector memories could only be revealed if an appropriate test paradigm were applied. The ants should be tested in the nest-departing, food-arriving state, i.e., they should be captured during their outbound runs and then released within the test area without carrying a reward. This kind of experiment, however, is difficult to perform for both conceptual and technical reasons. Conceptually, one cannot predict whether a nest-departing ant is heading

for a familiar feeding site or intends to further search in its foraging sector (Wehner et al. 1983; Schmid-Hempel 1984). Technically, *Cataglyphis* ants that are disturbed during their foraging runs often do not continue to forage but return immediately to the nest.

As the insect's motivational state is decisively important in acquiring and using vector information (Menzel et al. 1998; Bisch and Wehner 1999; Dyer et al. 2002), we exclusively tested ants that had been captured at the end of their homebound runs and were carrying a food item. The results obtained in this way are clear-cut: at the feeder homeward-directed vector memories are acquired only while the ants are performing the homebound parts of their foraging journeys. In some ants, even one (immediately preceding) homeward run suffices for obtaining this information.

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