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Landmark memories are more robust when acquired at the nest site than en route: experiments in desert ants

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Abstract Foraging desert ants, *Cataglyphis fortis*, encounter different sequences of visual landmarks while navigating by path integration. This paper explores the question whether the storage of landmark information depends on the context in which the landmarks are learned during an ant's foraging journey. Two experimental set-ups were designed in which the ants experienced an artificial landmark panorama that was placed either around the nest entrance (nest marks) or along the vector route leading straight towards the feeder (route marks). The two training paradigms resulted in pronounced differences in the storage characteristics of the acquired landmark information: memory traces of nest marks were much more robust against extinction and/or suppression than those of route marks. In functional terms, this result is in accord with the observation that desert ants encounter new route marks during every foraging run but always pass the same landmarks when approaching the nest entrance.

Introduction

While foraging over tens of metres, desert ants (*Cataglyphis* spp.) use landmarks as navigational aids in various ways. For example, as also shown by Collett et al. (1993) and Chittka et al. (1995) for honeybees, *Cataglyphis* can supplement its path integration system, i.e. its continuously updated global vector, by local vector information associated with familiar landmarks (Bisch and Wehner 1998; Collett et al. 1998). In addition, it can use landmarks to navigate along familiar routes (Wehner et al. 1996), to pinpoint its nest entrance (Wehner and Rüber 1979), or to relocate a feeding site (Wolf and Wehner

2000). Obviously, the foragers can activate separately acquired landmark memories and apply them in adaptive ways. In the present account, we focus on the storage characteristics of the same landmark information acquired during different stages of the ants' foraging journeys: en route when the ants have just left a foraging site, and when they are finally approaching their permanent goal, the nesting site.

Materials and methods

The experiments were performed within a saltpan area near Maharès in southern Tunisia. Foraging desert ants were trained under two experimental conditions which coincided in the distance between the nest and a feeding site (13 m) but differed in the location of an array of artificial landmarks (four black cylinders, each 20 cm wide and 30 cm high, placed at the corners of a 2×2 m² square. This array of landmarks was installed before the training started and was either arranged symmetrically around the nest entrance ("nest marks", see Fig. 1A), or placed close to the feeder along the direct route to the nest ("route marks", see Fig. 1B). The ants travelled back and forth between their nest and the feeder for at least one whole day, i.e. on average 30 times (Åkesson and Wehner 2002), before the test procedures started.

In the control tests, individual ants were captured at the end of their foraging round trips close to the nest entrance, provided with biscuit crumbs and released near an array of landmarks identical to the one used during training (Fig. 1C). The ants' trajectories were recorded for 3 min (nest marks) or 5 min (route marks) each on graph paper, i.e. on scaled down versions of a grid of white lines painted on the ground. The ants were colour-marked after the test in order to test them only once.

In the critical tests, the ants trained under either experimental condition had to perform a single foraging trip without landmarks. Nevertheless, the ants approached nest and feeder in a straight way. Having completed this landmark-free training run they were captured close to the nest and released within the test area as described above. Nest-mark and route-mark experiments were performed with the same nests in different years during the months of July and August.

The trajectories of the ants were digitised, and the resulting search densities inside the square array of landmarks were computed. The differences between these intra-square search densities obtained in the critical and control experiments provided a measure of the robustness of the landmark memory stores in the nest-mark and route-mark conditions. In the route-mark condition, we additionally recorded the directional choices made by the ants

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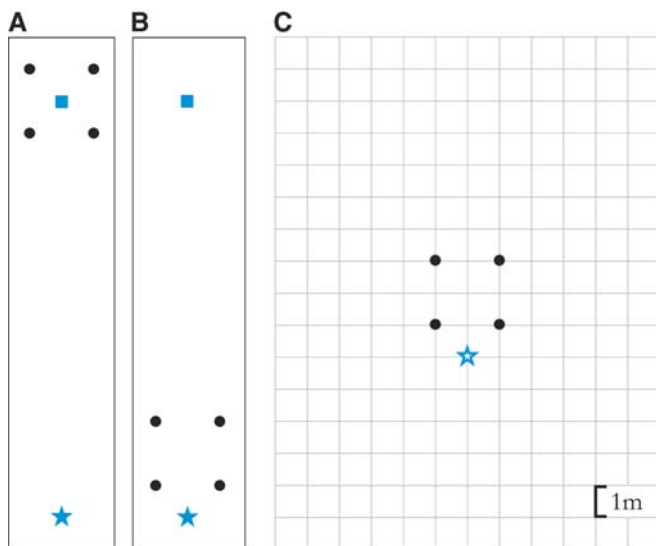


Fig. 1 Training (A, B) and test (C) situations. During training an array of cylindrical landmarks (filled black circles) was placed around the nest (A, blue square), or near the feeder (B, blue asterisk). After at least 1 day of training, individual ants returning from the feeder were captured close to the nest and displaced to a remote test area (C). There they were released (open blue asterisk) in front of an array of landmarks identical to the one used during training. A white grid painted on the plain ground helped in recording the ants' trajectories

when leaving the square array. Four concentric circles (radii: 4, 5 and 6 m) were drawn about the point of release, and the first intersections of the ant's trajectories with each circle were determined. The Rayleigh test (Batschelet 1981) was applied to test for directed distributions of these intersection points, and 95% confidence intervals were determined to test for the ants' tendency to walk in the direction of the fictive nest.

Results

Cataglyphis ants were trained to experience a configuration of conspicuous landmarks either arranged symmetrically around the nest entrance ("nest marks") or placed close to the feeder ("route marks"). Tests were performed with homing ants that were captured close to the nest entrance. At that time, their path integration system is almost reset and, therefore, cannot interfere with any potential local landmark memories.

In the nest-mark training paradigm, the ants persistently searched at the fictive position of the nest after they were transferred to an unfamiliar test area where they encountered a replica of the landmark array used during training (control tests: Fig. 2A_{co}; mean search density within the array of landmarks: 53.9%, SD=15.7%, $n=10$). In the subsequent critical tests, the ants performed a landmark-free training run immediately preceding the tests. The result was clear-cut: the removal of the landmarks during the last training run did not affect the ants' search behaviour at all (Fig. 2A_{cr}). As in the control tests, the ants stayed inside the landmark configuration for most of their search time (mean search density: 59.5%,

Table 1 Directional choices of ants that had been trained with route marks

Test condition	Distance from point of release		
	4 m	5 m	6 m
Control tests	1.1°±45.2°	1.1°±25.1°	15.5°±30.0°
Landmarks always present during training	($n=20$)	($n=20$)	($n=17$)
Critical tests:	56.1°±67.9°	30.8°±72.0°	21.4°±69.7°
Last training run without any landmarks	($n=20$)	($n=20$)	($n=20$)

Mean angular positions ± angular deviation (corresponding to S.D.) at distances of 4, 5 and 6 m from the point of release (see Material and Methods). n , sample size (number of ants tested). **Bold numbers** mean that the angular positions are not randomly distributed ($p<0.05$, Rayleigh test) and that the 95%-confidence interval includes the direction towards the fictive position of the nest (0°)

SD=11.2%, $n=10$; for the difference between critical and control tests: $P=0.4$, Mann-Whitney U test).

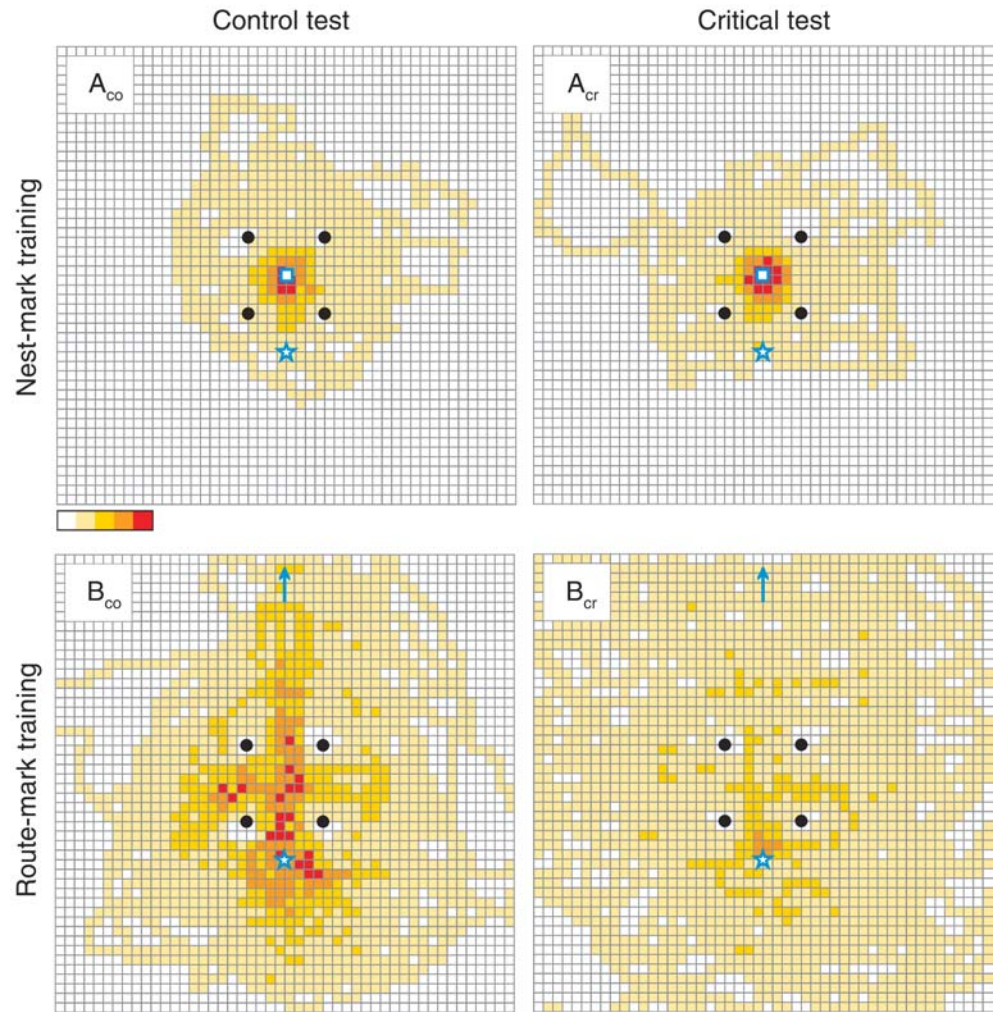
The route-mark training paradigm, in contrast, exhibited striking differences between the control tests and the critical tests (Fig. 2B_{co}, B_{cr}). In the control tests, the ants left the landmark array preferentially in the direction of the fictive nest. In the critical tests, however, after the ants had performed just a single training run with the landmarks being absent, this tendency had almost vanished (Table 1), and the ants' search trajectories were spread widely and associated only weakly with the landmark array. The mean search density within the landmark array was significantly smaller than in the control tests (5.1%, SD=4.0%, $n=20$, in the critical tests vs 11.5%, SD=5.7%, $n=20$, in the controls; $P<0.001$, Mann-Whitney U test).

Discussion

There is a wealth of information on context-dependent learning in foraging honeybees and ants. For example, in a binary choice paradigm, in which honeybees have to discriminate between two visual stimuli A and B, they can learn the visual discrimination A+B- at one place (e.g. a feeding site) and A-B+ at another place (e.g. the nesting site or another feeding site; Collett et al. 1997; Srinivasan et al. 1998).

The present account addresses a different question. An identical visual stimulus (a square array of four cylindrical landmarks) is presented either around the nesting site or en route close to the feeding site. After the animals have learnt to use these arrays of landmarks as navigational aids – to pinpoint the location of the nest entrance or to determine in what direction to start from the feeder, respectively – they have to perform one foraging journey without any landmarks. If tested thereafter, they are still able to use the array of landmarks to locate the nesting site, but they are no longer able to use the very same landmarks as route marks guiding them home.

Fig. 2 Search densities of the ants within the test area. In the control tests, the ants had been trained continuously in either the nest-mark (A_{co}) or the route-mark (B_{co}) situation (see Fig. 1). In the critical tests (A_{cr} and B_{cr}) the landmarks had been absent during the last training run. The search trajectories of the ants were recorded for 3 min (**A**) or 5 min (**B**). Then, the relative search densities per pixel ($0.25 \times 0.25 \text{ m}^2$) were determined by dividing the path lengths of all ants per pixel by the total path length of all ants in each of the tests. These values were assigned to five classes ranging from *white* (minimal value; 0.000) to *red* (maximal value; 0.022 in **A**, 0.004 in **B**). These maximal values were obtained in the control tests and served as reference values in the critical tests. *Filled black circles*, cylindrical landmarks; *open blue asterisk*, point of release; *open blue square*, position of fictive nest in **A**; *blue arrow*, direction of fictive nest in **B**



The former result is in line with the long-term retention (for at least 20 days) of nest-mark memories in *Cataglyphis* ants (Wehner 1981, Fig. 64; Ziegler and Wehner 1997). In the critical route-mark tests, however, the question arises whether the visual snapshot and the local vector associated with it have been completely erased from memory after a single landmark-free training run, or whether the landmark information was just suppressed by a more recently acquired one, in our case by the single experience of “no landmarks present”. In a small-scale binary choice paradigm designed for bumblebees, Chittka (1998) trained the bees to associate turns to the right or left when the bees encountered a blue or yellow marked entrance, respectively. After intercalated reversal trainings, the time course of relearning the first training schedule was significantly different from that of the initial training. Chittka (1998) argues that the previously learnt visual information was temporarily suppressed rather than deleted from memory. In the landmark navigation experiments described in the present account, we cannot yet decide between these two possibilities. Hence, “robustness” can mean one (or both) of two possible memory characteristics: long-lasting

stability of stored information or resistance against suppression by novel information.

The high robustness of stored nest-mark information and the low robustness of stored route-mark information in desert ants might be based on intrinsic differences in storing information about places (nest marks) or directions (route marks). Nevertheless, as to the functional significance of the observed differences, the structure of the ant’s space-use pattern offers a plausible explanation. First, note that during the short life span of a *Cataglyphis* forager (6.1 days in *C. bicolor*, Schmid-Hempel and Schmid-Hempel 1984) the landmark constellation within the ant’s foraging grounds does not change. Furthermore, the nests we worked with were located at the same places for at least 5 years and, therefore, nest relocations seem to be extremely rare. Finally, each forager restricts its searching activities to a small sector of the area surrounding its nest (Wehner 1987). This means that homing ants always approach the nest from the same direction and hence face the near-by landmarks from the same vantage point. Due to these foraging characteristics, there is almost never any need for the ants to relearn a new landmark panorama around their nesting site. This

does not apply, however, for route marks experienced close to a feeding site. In *C. bicolor*, the average width (50°) and length (30 m) of an ant's foraging sector results in an area of about 420 m² (Wehner et al. 1983). In *C. fortis*, the corresponding values are 30°, 24 m, and about 160 m², respectively (K. Selchow and R. Wehner, unpublished data). Within this search area, the location of the ant's food items, arthropod carcasses, is spatially and temporarily unpredictable. Hence, the animals will start successive home runs from different locations characterised by different landmark configurations. The previously stored local vectors will have to be replaced by new ones. In the present research, the competing new information was "no landmarks between feeder and nest". Obviously, in our critical route-mark tests, but not in the nest-mark tests, this most recent information has caused the ants to disregard the previously stored landmark information completely.

As during its entire foraging life an ant sticks to the same club-shaped foraging sector, it passes landmarks located close to the nest far more frequently than landmarks farther away from it. Therefore, one might conclude that memory traces of landmarks are the more robust against extinction and/or suppression the closer they are to the nest. In support of this conclusion, let us emphasise again that in our experiments the number of reinforcements was the same for both the nest marks and the route marks.

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