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Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, *Cataglyphis fortis*

Abstract In foraging and homing, desert ants of the genus *Cataglyphis* employ two different systems of navigation: a vector-based or dead-reckoning mechanism, depending on angles steered and distances travelled, and a landmark-based piloting mechanism. In these systems the ants use either celestial or terrestrial visual information, respectively. In behavioural experiments we investigated how long these types of information are preserved in the ant's memory, i.e. how long the ants are able to orient properly in either way. To answer this question, ants were tested in specific dead-reckoning and piloting situations, whereby the two vector components, direction and distance, were examined separately. The ability to follow a particular vector course vanishes rapidly. Information about a given homing direction is lost from the 6th day on (the time constant of the exponential memory decay function is $\tau = 4.5$ days). The homing distances show a significantly higher dispersion from the 4th day on ($\tau = 2.5$ days). Having learned a constellation of landmarks positioned at the corners of an equidistant triangle all ants were oriented properly after 10 days in captivity, and 64% of the ants exhibited extremely precise orientation performances even when tested after 20 days. Thus, the memory decay functions have about the same short time-course for information on distance and direction, i.e. information used for dead-reckoning. In contrast, landmark-based information used in pinpointing the nest entrance is stored over the entire lifetime of a *Cataglyphis* forager.

Key words Navigation · Dead-reckoning · Piloting · Memory · Ants

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Introduction

While foraging, *Cataglyphis* ants individually make long excursions in order to find food. Having grasped their bait they return directly to their nest and do not retrace their outbound paths. Displacement experiments show that the ants use a path integration or dead-reckoning system (Müller and Wehner 1988; Wehner 1992). To accomplish this task, the animals must evaluate angles steered as well as distances travelled. During their outbound runs they are continually computing a vector pointing towards the nest. However, as cumulative errors arise during this egocentric way of navigation, backup systems are needed for finally pinpointing home. Piloting by familiar landmarks serves such a function (Wehner and Räber 1979; Wehner et al. 1996). Once a home vector has brought an ant close to its nest, the entrance is located by means of visual landmarks. Experiments on ants (Wehner and Räber 1979) and bees (Cartwright and Collett 1983) suggest that the insect is "drawn" to its goal by a process of image matching. It moves so as to maximize the fit between its present retinal image and its "snapshot" memory of the landmarks as seen from the nest entrance. Low shrubs, stones and small elevations of the ground form natural landmarks that can be used in piloting. The effective angular height at which they appear above ground (as seen from the nesting site) can be smaller than 2° [see Fig. 6 in Wehner et al. (1996)].

The duration of an outbound run lies within the range of tens of minutes (K. Selchow and R. Wehner, unpubl. obs.). During this time period the home vector is continually updated and finally used for homeward orientation. Once the ant has returned to its nest, the memory of the homing vector is reset to zero. If immediately thereafter the ant is replaced to the feeding site, from which it just has returned home, it searches in all directions rather than selects again the homeward course. Nevertheless, information about the particular vector is certainly stored in some higher order memory,

at least 180 deg reversed, because after a successful foraging run *Cataglyphis* usually searches for food in the same area, it has visited during the preceding foraging trip, even if in the absence of landmarks it can rely only on vector information.

In this study we investigated the question of how long the information about (i) the home vector and (ii) the landmark array can be stored in and retrieved from the ant's long-term memory. In particular, we tested how long the ants were able to orient properly by using either type of information. To accomplish this task we experimentally exploited particular dead-reckoning and piloting situations. In the former the two vector components, direction and distance, were examined separately.

Materials and methods

Cataglyphis fortis is an endemic species of the salt pans (chotts and sebkhas) of Tunisia and Algeria (Wehner 1983). The experiments described here were carried out in alluvial plains near the village of Maharès (34.56° N, 10.50° E).

Individually marked ants were trained to a feeder positioned at a distance of either 12 or 15 m from the nest. They were captured after they had grasped their bait and transferred to a small glass flask. In control tests they were released immediately on a test field or in a test channel, and the run was recorded in full spatial detail [for methods see Wehner (1982)] for 5 min. Subsequently the ants were kept individually under natural light conditions, fed with water and sugar and then released after a particular number of days within half an hour of the same time of day at which they had been trained. All transports occurred in the dark. The mean mortality rate during captivity was 3 per cent per day.

Test procedures

Direction (angular component of vector)

Ants trained to a particular feeding site were tested on a field with a grid of white lines painted on the hard desert ground (mesh width 1 m). This test area was located several hundred meters apart from the nesting site, so that any visual influence of the latter could be avoided. The runs were recorded on sheets of graph paper provided with a rectangular grid of lines. The grid was identical to the one painted on the floor, but reduced in scale (1:67).

Data evaluation followed the statistical methods for circular distributed data as provided by Batschelet (1981). Circles corresponding to distances of 3, 5 and 7 m from the point of release were drawn around the latter site, and the angular positions were recorded at which the ant's trajectories crossed these circles for the first time. In all these angular distributions mean vectors characterized by mean angles $\bar{\Phi}$ and lengths r were computed. The home component v, i.e. the component of the mean vector with respect to the homeward direction, provides a measure of the concentration of the angular data around $\bar{\Phi}$ and was tested using the V test. In the present account only data of the 5-m circle are presented.

In the control groups the ants were released and tested immediately after training. In the first and the second group the ants were provided with or without a homeward vector, respectively. In all other tests the ants were released after a captivity period of 1, 2, 4, 6, 8 or 10 days.

Distance (linear component of vector)

A 12-m channel and a 25-m channel aligned in parallel were used for training and testing, respectively. The narrow plastic channels consisted of several pieces of 1 m length that could be connected firmly by clamps (Müller and Wehner 1988). One end of the training channel was placed directly at the nest site. A fence placed around the nest entrance and equipped with an opening leading into the channel induced the ants to enter the channel. The ants walked on a horizontal wooden platform mounted within the channel and covered by a mixture of sand and rubber. The channel prevented the ants from systematic errors in path integration and excluded any orientation by landmarks. The ants were able to see only the sky and hence to derive directional information from skylight cues. Inside the channel they were trained to a feeder 12 m from the nest entrance, captured and released either immediately or after 2, 4, 6, 8 or 10 days of captivity in the test channel. There the homing distances were recorded by determining the points at which the ants terminated their straight homeward runs and turned around by 180° [start of the search pattern; Wehner and Srinivasan (1981); Wehner and Wehner (1990)]. As the range of the data points obtained this way was limited due to the experimental setup, the median quartile test (Sachs 1994) was used for statistical analysis.

Landmark skyline

A set of three artificial landmarks consisting of small black cylinders 20 cm high and 12 cm wide was centred around the entrance of a *Cataglyphis fortis* colony. The landmarks were positioned at the corners of an equidistant triangle and at a distance of 1 m from the nest entrance. After having been trained to a feeder 15 m from the nest the individually marked ants were allowed to collect food and hence to learn the particular landmark constellation around the nest for at least 2 days. Then they were captured at the nest entrance after they had completed a foraging excursion, transferred to a glass flask and released in the test area (the same test-grid area as the one used in the vector-direction experiments) either in control experiments immediately thereafter or after a captivity period of 10 or 20 days. In the test area the same landmark constellation was arranged but turned around by 180° so as to "decouple" landmark and skylight information. The ants were released at 1-m distances from the centre of the triangular array of landmarks, and their search trajectories were recorded.

To distinguish "oriented" from "non-oriented" runs, a circular area (radius 0.25 m) around the fictive nest position was chosen which the ants had to enter at least twice within a time period of 5 min, in order to be regarded as "oriented". To allow for a more detailed evaluation of the data the ants' trajectories were digitalized by computer, and relative search densities per square pixels of test area were computed. Pixel size was chosen to be 0.25 m². The grid was shifted so that the hypothetical nestsite was positioned in the middle of the central square.

Wherever possible exponential memory decay functions $y = e^{a*x}$ (x in days) were fitted to the data by using a non-linear, user-specified regression of the "StatSoft Statistica" program.

Results

Direction

While the animals of the control group ran straight to the hypothetical site of the nest (N) before they started to search around (Fig. 1), the trajectories of the animals kept 1–4 days in captivity were widely distributed, though clearly concentrated in the 180°-sector containing the fictive position of the nest. Finally, the runs of the 6-day group are quite evenly distributed around the release site and therefore resemble the data of the con-

Fig. 1A–D Search trajectories of the vector-direction experiments. The ants were released in the test field either immediately after training (**A**, control) or after having been kept in isolation for a 2-day (**B**), 6-day (**C**) or 10-day (**D**) period. *N* indicates the fictive position of the nest entrance. The *cross of heavy lines* marks the point of release
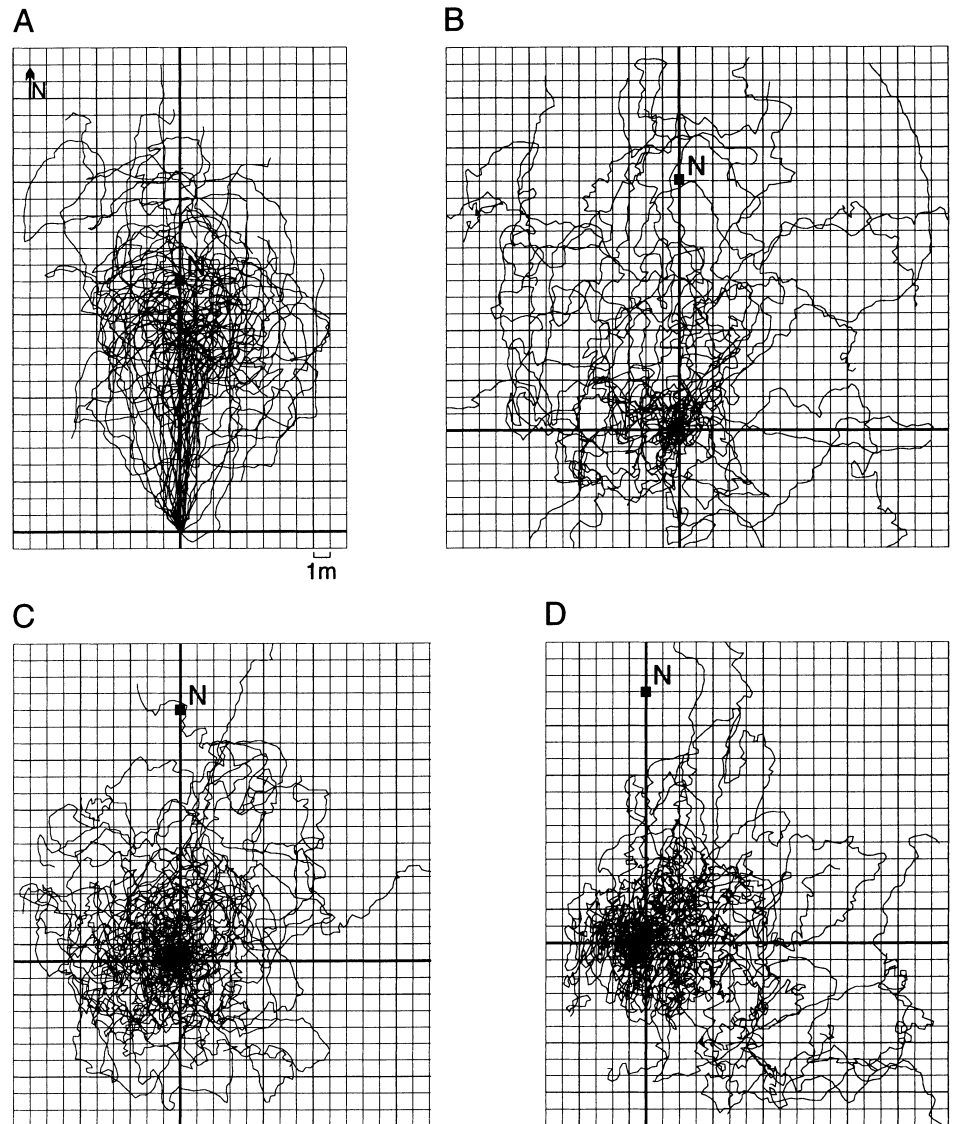
trol group without a stored vector. After 8 and 10 days the ants showed, in addition, a slight tendency to head to the east. The source of this systematic deviation is unknown.

Statistical data are given in Table 1. Up to a 4-day captivity period the ants' directional choices are clustered around the home direction (V test: $P < 0.01$). Captivity periods of 6 or more days resulted in random orientation (V test: $P > 0.01$). Nevertheless, even then the home components exceeded by far the ones of the vectorless animals, i.e. of ants that previously had not been trained to a particular feeding site. In all oriented groups (V test: $P < 0.01$) the true home directions lay within the confidence limits of $Q = 0.99$ of the mean angle.

The exponential function $y = e^{-0.23 * x}$ (x in days; $R = 0.84$) could be fitted for the data of all experiments. This function yields a time constant of $\tau = 4.5$ days (Fig. 2).

Table 1 Results of the vector-direction experiments. For all test groups sample size N (number of individuals tested), mean orientation angle $\bar{\Phi}$, home component v and the significance level P as inferred from the V test are given. The latter test indicates whether the null hypothesis (random angular distribution) can be rejected, or whether the angular data are uniformly grouped around the home direction. The accuracy of grouping is given by the home component $v \leq 1.0$

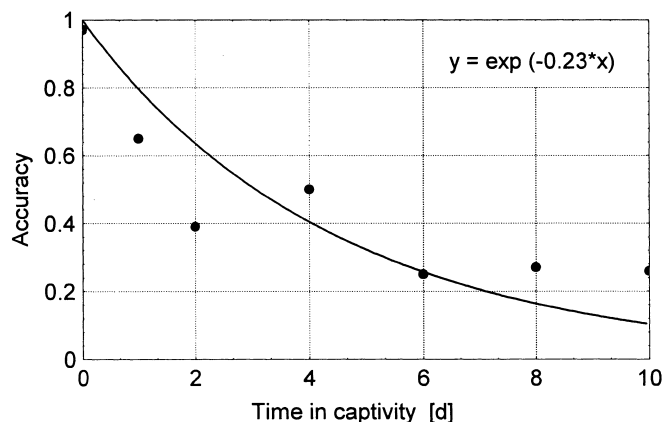| Time in captivity	Sample size N	Mean angle $\bar{\Phi}$	Home component v	P (*V test*)
0	33	2°	0.97	$P < 0.01$
1	27	21°	0.65	$P < 0.01$
2	26	−8°	0.39	$P < 0.01$
4	24	18°	0.50	$P < 0.01$
6	33	−22°	0.25	$P > 0.01$
8	22	33°	0.27	$P > 0.01$
10	23	58°	0.24	$P \gg 0.01$
Zero-vector	24	−64°	0.10	$P \gg 0.01$

Fig. 2 Exponential decay function fitted to the data of the vector-direction experiments. As a measure of the directional accuracy, the length v of the home component (see Table 1) is plotted against the number of days the ants have spent in captivity

Distance

Earlier experiments (Wehner 1982; Müller 1989; Schäfer and Wehner 1993) have shown that plastic channels, though a very unnatural environment, do not disturb the ant's ability to measure distances quite precisely. Inde-

pendent of training distance which varied in the range of 10–30 m, the mean homing error was at most 0.5 ± 2.0 m. In the control experiment (12-m training distance) the deviation of the median was slightly higher (0.9 ± 1.6 m). The ants used in all experiments were taken from the same nest.

The results are summarized in Table 2 and Fig. 3. In the control group and the 2-day group the positions at which the ants made their first 180° turn are clustered around the hypothetical nestsite. After longer periods of captivity these turning points are spread out more and more over the entire length of the channel. Many ants turned back after a short walk or ran through until the end of the channel. Captivity periods of 4 or more days led to first-turn distributions that were significantly different from the ones of the control group (Median quartile test: $P < 0.01$). The changes in the scatter of the first-turn data are well reflected in the increasingly larger median of the absolute deviations of the ants' first-turning points from the hypothetical nestsite. In Fig. 4 the reciprocals of these medians are taken as a measure of how accurately the ants are still able to gauge distance. The exponential function $y = e^{-0.41*x}$ (x in days; $\tau = 2.5$) fits the data sufficiently well (regression coefficient: $R = 0.99$).

Table 2 Results of the vector-distance experiments. The homing distance median and median absolute deviation (MAD) as well as the median of the absolute deviations of the ant's first turning points from the hypothetical position of the nest are given in meters (m). The last column represents the statistical differences between any particular test group and the control group as computed by means of the median quartile test

Time in captivity	Sample size N	Homing distance: Median and MAD (m)	Median of the absolute deviations (m)	P (Median quartile test)
0	31	12.9 ± 1.6	1.1	–
2	26	12.8 ± 2.2	2.5	$P \gg 0.05$
4	28	10.4 ± 3.7	3.6	$P < 0.01$
6	34	12.7 ± 8.1	8.2	$P < 0.001$
8	35	7.1 ± 5.6	7.3	$P < 0.001$
10	28	5.4 ± 4.0	8.8	$P < 0.001$

Fig. 3 Results of the vector-length (walking-channel) experiments, in which the ant's accuracy of gauging distance travelled was tested. Box-plot representations. The Y-axis indicates the distances travelled by the ants in the test channel. Release site and starting point: 0 m; training distance: 12 m
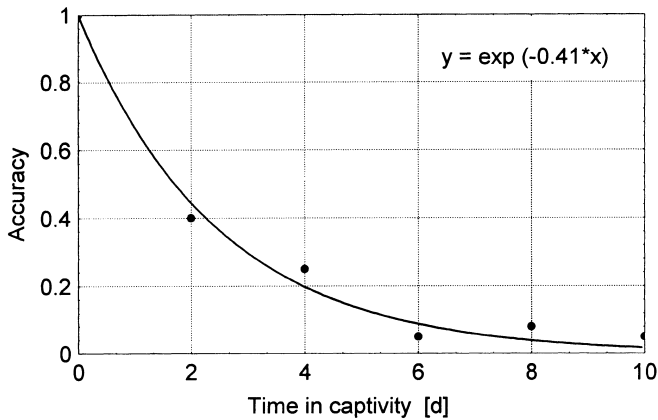
y = exp (-0.41*x)
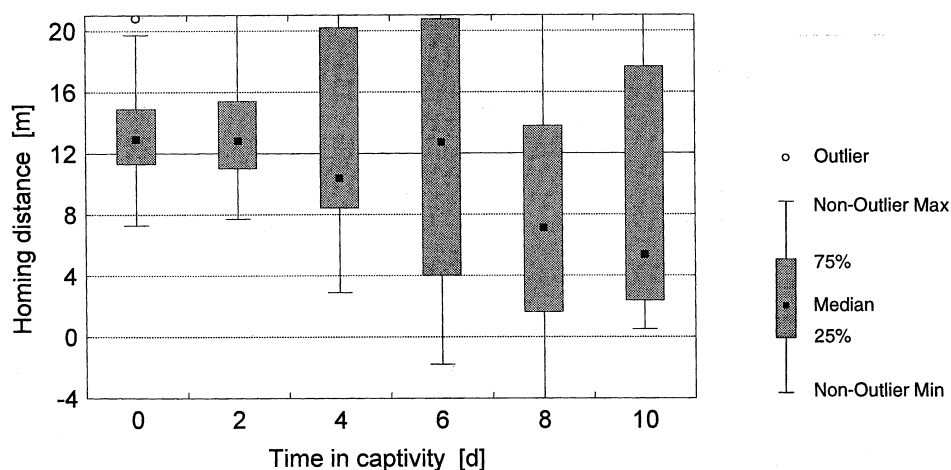
Fig. 4 Exponential decay function fitted to the data of the vector-length experiments. The accuracy with which the ants gauge distances travelled (ordinate) is given by the reciprocal of the median of the absolute deviations of the ants' first-turning points from the hypothetical position of the nest. Relative values: an accuracy of 1.0 corresponds to the deviation exhibited by the control group

Landmark skyline

In contrast to vector information, information about the landmark skyline around the nesting site prevails over the entire lifetime of a *Cataglyphis* forager. The search density profiles exhibit highly sharpened peaks at the fictive position of the nest irrespective of whether the ants are tested immediately after training (Fig. 5A) or

10–20 days later (Fig. 5B). In the control tests 10.2% of the total path length recorded during the 5-min test period occupy the central square (nest-site square) of the recording grid. Surprisingly the value of the 10-day captivity group (12.4%) even exceeds the one of the control group, while the 20-day captivity group showed only an insignificantly smaller value (9.5%) than the control group.

A closer inspection of the data of the 20-day captivity group allows for the discrimination of what could be called "oriented" and "non-oriented" runs (based on the criteria described in Materials and methods). In the latter, the trajectories were often very straight and did not show any sign of the search-loop pattern described by Wehner and Srinivasan (1981). Several factors could have led to this result. The "non-orienters" might not have learned the landmark constellation properly; their memory store might have been extinguished during the captivity period, or the motivation of the ants to reach the nest might have deteriorated during that period. The latter is the most likely hypothesis. The "oriented" ants spent 14.5% of their walking time rather than 10.2%, as the controls do, within the central square. [During searching the ants walk with constant speed – see Fig. 7 in Wehner and Srinivasan (1981) – so that the relative measures of path length and search time are equivalent.] It seems that the longer the ants are kept in captivity, the more intensively they search, if they search at all, around the target point.

Fig. 5A, B Three-dimensional search density profiles (*left*) and two-dimensional search density plots (*right*) of ants tested in the landmark (piloting) paradigm: **A** control: ants tested immediately after training; **B** 20-day test group: ants tested 20 days after training. Square size is 0.25 m² and 1.0 m² in the 3-D and 2-D representations, respectively. The peak of the 3-D plots is positioned at the fictive site of the nest. In the 2-D plots the nest site is marked by the heavy-line cross wire. The three cylinder forming the landmark array around the nesting site are indicated by *black dots*
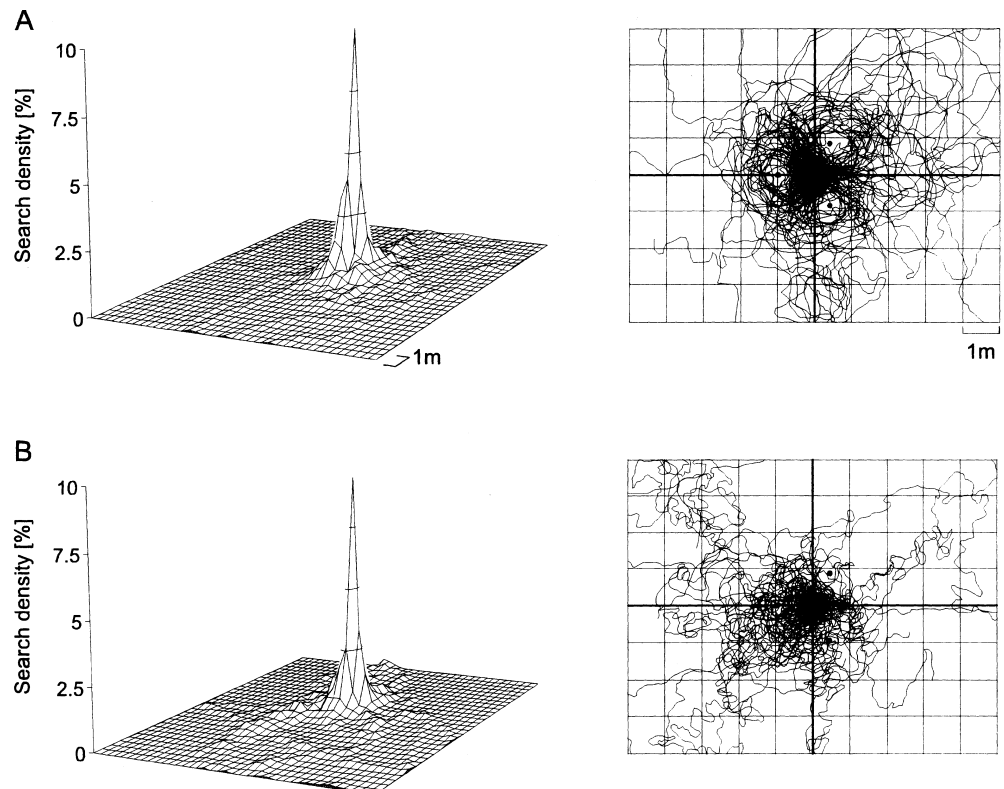
Discussion

The main result of the present account can be summarized as follows: the time-courses of memory decay differ highly significantly between vector-based (dead-reckoning) and landmark-based (piloting) systems of navigation. In the former the orientation ability decays with time constants of $\tau = 4.5$ days (angular vector component) and $\tau = 2.5$ days (linear vector component). In the latter the ants still remember a specific landmark constellation around the nest entrance after 20 days of captivity [see also Fig. 64 in Wehner (1981) for a pilot experiment performed in *Cataglphis bicolor*]. This period by far exceeds the normal duration of an ant's foraging life (7.3 days; Selchow 1991).

Menzel (1968) showed that honey bees which had received just one reward had forgotten a colour signal after 6 days. In contrast, after three rewards they did not show any reduction in their correct choice behaviour during a period of 13 days. It was only the number of rewards that led to this difference in the duration of the memory store. In *Cataglyphis* a homeward-bound vector is built up anew whenever an ant starts to move in a new foraging direction. As these directions may change from one foraging excursion to another, vector memories may be based on single reinforcements. On the other hand, the landmark constellation surrounding the nesting site is experienced invariantly, whenever the ants leave or approach the nest. In our experiments, however, the ants had been trained to a particular (fixed) feeding site, so that they had experienced the home vector repeatedly (often more than 20 times) during the 2-day training period. This experimental paradigm might have consolidated their vector memory. Nevertheless vector information vanished rather rapidly.

In the present account, acquisition functions (learning curves) were not recorded for the three parameters tested. All experimental animals had visited the feeder, or returned to the nest, for two full days. From earlier studies (I. Flatt, F. Räber, M. Müller, R. Wehner, unpubl. obs.) we know that a constant level of accuracy is reached in vector navigation and in piloting by landmarks after maximally four visits to a feeder and returns to the nest, respectively. Hence, the experimental procedures used in the present study had certainly led to saturation of acquisition for all components of navigation. Even though possible over-training effects have not been studied in particular, control tests performed before the experimental retention period started always revealed maximal accuracy of performance.

Let us now turn to the difference in the time-course found in the memory decays of the two vector components, the angular and the linear one, with $\tau = 4.5$ and 2.5 days, respectively. Although the memory information used in measuring directions and gauging distances might be different, i.e. visual and idiothetic information might contribute in different ways to the assessment of direction and distance, the information finally gained about the angular and linear components of movement is used inseparably in path integration (Müller and Wehner 1988). Therefore, it is unlikely that the two kinds of information are treated separately in whatever kind of memory store might be involved. The differences found in the two time constants τ are certainly due to the necessarily different ways of how the accuracy values of the angular and linear components of movement were computed in either case.

Our data indicate that home-vector information is lost from memory within about 2–4 days. The very good fit of the exponential function to the distance-component data strongly favours this conclusion. This result is quite reasonable. A vector built up anew during each foraging run and thus changing from one run to another does not need to be stored over the entire lifetime of a *Cataglyphis* forager, whereas landmark-based information about the final goal, the nest, should be. If the same 3-cylinder landmark configuration surrounds the feeding rather than the nesting site, the trained animals learn the food-centred array as accurately as it has been described above for the nest-centred array, but fail to concentrate their search activities around the fictive position of the feeding site already after a retention period of 24 h. This failure, however, can be correlated with a decay of motivation, as the readiness to accept the food particles to which the ants have been trained decays with the same time-course as the search density peaks flatten. Hence, 24 h after training animals which had been kept outside the colony during this time interval are no longer motivated to return to a feeding site (H. P. Loch and R. Wehner, unpubl. obs.), but as shown above they always remain motivated to return home. The latter is also reflected in the walking speeds which do not decrease during the whole experimental period. The median values and lower/upper quartiles (in m $\cdot$ s^{-1}) are 0.22, 0.08/ 0.31 for the controls, 0.21, 0.15/0.26 for the 2-day captivity time, 0.19, 0.15/0.22 for the 6-day captivity time and 0.22, 0.16/0.23 for the 10-day captivity time. The walking speeds of all animals tested after various captivity periods do not differ from those of the controls ($P = 0.60$, $P = 0.16$ and $P = 0.97$ for captivity periods of 2, 6 and 10 days, respectively, vs. controls; Mann-Whitney-U test).

The time-dependent loss of landmark-based orientation at the feeding site also excludes the possibility that the ants run towards the centre of the landmark configuration simply as a consequence of some spontaneous preference. In additional control experiments naive ants, which had not been trained to the 3-cylinder configuration but were tested in the same way as the trained animals, did not move at all towards the centre of the configuration, but concentrated their searches about the point of release (I. Flatt and R. Wehner; H. P. Loch and R. Wehner; unpubl. obs.).

Taken together, these arguments prove that in "home-based" (rather than "food-based") animals motivation to return to the site of the colony did not decay during the retention times used in this study. On the

other hand, we cannot decide on the basis of the experimental paradigms described here whether the decay in performance of vector-based navigation is actually due to a decrease in storage content or in the possibility to retrieve the stored information.

Unfortunately, not much is known about the dynamics of memory stores of navigational information in other hymenopterans. Red wood ants, *Formica rufa*, have been reported to memorize a landmark-based route for at least a week and the azimuthal position of a light source for 5 days. Four feeding sites can be learned at once and memorized for at least 1 day (Jander 1957). Experienced *Formica rufa* ants that had stayed underground over a hibernation period of 210 days chose the same foraging course as before the winter break. Landmarks were used as orientational cues (Rosengren 1977; Rosengren and Fortelius 1986). This performance probably represents the maximum memory period known in hymenopterans. Honey bees, *Apis mellifera*, can return from a feeding site to the hive after having been kept in captivity for 2 and 4 days (Uchida and Kuwabara 1951). Anecdotally, Lindauer (1963) observed bees returning to the same feeding places after a winter break of 173 days. This period is comparable to the one found by Rosengren and Fortelius (1986) in wood ants. As honey bees and wood ants may remain faithful to particular feeding sites, if these sites provide sufficient food supply for extended periods of time, this finding is ecologically understandable.

The fact that central place foragers such as bees and ants can store landmark-based site and route information for time periods that exceed their normal life spans as foragers, but that vector-based (egocentric) information is stored for rather short periods of time, might have important consequences for the general organization of spatial information within the insect's central nervous system. First, let us point out that in our experiments vector information might still have resided in the ant's working memory (rather than having been transferred to some higher memory store), because prior to the test the ants had not returned to their central place, i.e. had not reset their vector navigation system to zero. One might argue that it is only then that vector information is transferred from the working memory to a higher-order "spatial memory". Keeping in line with this argument, the memory decay functions unravelled in the present account might tell us something about how long vector information can stay within the working memory, but not how stable a higher-order vector store might be. In this context, it is worth to mention a more recent finding. If ants are displaced after they have returned to the nesting site, i.e. after they have emptied their working memory store and potentially transferred the vector information to a higher-order store, they are not able to recall this information when released again at the feeding site – even if the feeding site is surrounded by a conspicuous array of landmarks (Loch and Wehner 1996). Experiments of that kind are crucial for our understanding of what navigational mechanisms underlie the map-like behaviour observed in bees and ants [for discussions see Cartwright and Collett (1987); Wehner and Menzel (1990); Wehner et al. (1996); Dyer (1996); Menzel et al. (1996)], especially for answering the question whether central place foragers label their landmark memories for particular locations within their foraging range with the corresponding vectors pointing home.

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