

R. Wehner · K. Gallizzi · C. Frei · M. Vesely

Calibration processes in desert ant navigation: vector courses and systematic search

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Abstract This study investigates the ability of desert ants to adapt their path integration system to an “open-jaw” training paradigm, in which the point of arrival (from the nest) does not coincide with the point of departure (to the nest). Upon departure the ants first run off their home vector and then start a systematic search for the nest. Even if they are subjected to this training-around-a-circuit procedure for more than 50 times in succession, they never adopt straight homeward courses towards the nest. Their path integration vector gets slightly recalibrated (pointing a bit closer to the nest), and their search pattern gets asymmetric (with its search density peak shifted towards the nest), but the bipartite structure of the inbound trajectory invariably remains. These results suggest (1) that the ants cannot learn separate inbound and outbound vectors (i.e. vectors that are not 180° reversals of each other), (2) that the recalibrated vector is dominated by the ant’s outbound course, (3) that the recalibration of the vector and the modification of the search geometry are fast and flexible processes occurring whenever the ant experiences a mismatch between the stored and actual states of its path integrator.

Keywords Ants · *Cataglyphis* · Path integration · Search strategy · Vector navigation

Introduction

The salt pans of North Africa are inhabited by only one species of ant, *Cataglyphis fortis*. These long-distance navigators leave their underground colonies for tens and even hundreds of meters using path integration as their main navigational means. Path integration (vector

navigation *sensu* Wehner 1983; Collett and Collett 2000; Wehner and Srinivasan 2002) provides the foraging ant with an ongoing estimate of its direction and distance from the nest, i.e. with a continually updated global vector that always points at the start of the ant’s foraging excursion, a tiny nest hole in the ground. This path-integration vector enables the ant to reach its point of departure along the shortest route. Later, its 180° reversal can be used for returning directly to the previously visited food site.

Beyond ants, path integration as defined in Mittelstaedt’s seminal papers (Mittelstaedt and Mittelstaedt 1973; Mittelstaedt 1983, 1985) has recently attracted much attention in other arthropods (e.g. crabs: Zeil 1998) mammals (e.g. rats and hamsters: McNaughton et al. 1996; Etienne et al. 1998) and humans alike (e.g. Loomis et al. 1993). In addition, it has stimulated quite some theoretical endeavours of sorts (Wittmann and Schwegler 1995; Hartmann and Wehner 1995; Benhamou and Séguinot 1995; Collett and Collett 2000; Mittelstaedt 2000). One reason for this revival of interest in path integration is certainly the notion that this navigational tool is used by insects and mammals not only as a short-term means of memorizing the starting point of an outbound path but also as a long-term frame within which landmark information is acquired and structured. If path integration serves that fundamental a function in animal navigation, it seems pertinent to ask – as we do in this account – how flexibly it can be adapted to various navigational needs.

One immanent property of any path integrator is its susceptibility to cumulative errors: the tip of the home vector is not sharply pointed, but becomes blurred the more the farther the animal has ventured into unfamiliar territory (for *Cataglyphis* ants see Wehner and Wehner 1986). Hence, path integration does not guide the animal exactly back to the start, but to some near-by location. Supplementary corrective mechanisms are needed for finally pinpointing the goal. In a landmark-free environment such as a vast salt pan, the systematic search programme as described by Wehner and Srinivasan

R. Wehner (✉) · K. Gallizzi · C. Frei · M. Vesely
8057 Zürich, Switzerland
E-mail: rwehner@zool.unizh.ch
Tel.: +41-1-6354830
Fax: +41-1-6355716

(1981) and Müller and Wehner (1994) provides *Cataglyphis* with the only corrective means. Hence, path integration and systematic search are two navigation modules that are employed by the salt-pan ant, *C. fortis*, one after another. Whenever the path integrator has reached its original state, but the ant has not yet arrived at the nest, the systematic search programme is switched on. If landmarks are available (as it is the case, for instance, in the habitats of *C. bicolor* and *C. mauritanicus*), landmark guidance offers an important additional way of correcting for accumulating errors in path integration.

In the present account we ask whether the two modes of navigation used by *C. fortis* in a landmark-free environment – steering vector courses and employing a systematic search strategy – are rigidly ordained behavioural routines, or whether they can be flexibly adapted to various environmental contingencies. One of these contingencies with which the ants are confronted within their salt-pan habitat are the prevailing winds which may blow off and on across the desert plain, but when they blow during the course of the day, their direction is rather constant (Wehner and Duelli 1971). As a consequence of these sometimes fairly strong winds *Cataglyphis* may get blown off the ground and displaced for a certain distance. Due to the resulting interruption of the path integrator, the ant's inbound (home) vector

does no longer point towards the nest, but towards a location that is shifted from the nest location by a vector equivalent to the displacement vector.

In the experiments described in this paper we have used an “open-jaw” training paradigm, in order to load the ant's path integrator with such displacement vectors, and asked whether and how the path-integration and the systematic-search system adapt to this interference. A similar experimental paradigm had already been applied in an early study in honey bees (Otto 1959), and in desert ants as well (*C. bicolor*: Wehner and Flatt 1972). It was systematically used in a recent investigation (Collett et al. 1999), in which *C. fortis* was not only displaced sideways from its feeding site, but was then also forced to perform its inbound (homeward) runs within an artificial channel guiding it directly back to the nest (Fig. 1A). Whereas this latter intervention creates a situation to which the ants will never be exposed during their foraging lives, in the present account we mimic the natural conditions by letting the animals home freely, i.e. by letting them first run off their home vector and then switch on their systematic-search programme (Fig. 1B). This experimental paradigm allows us to study the effects of passive displacement on either system, the path-integration and the systematic-search system.

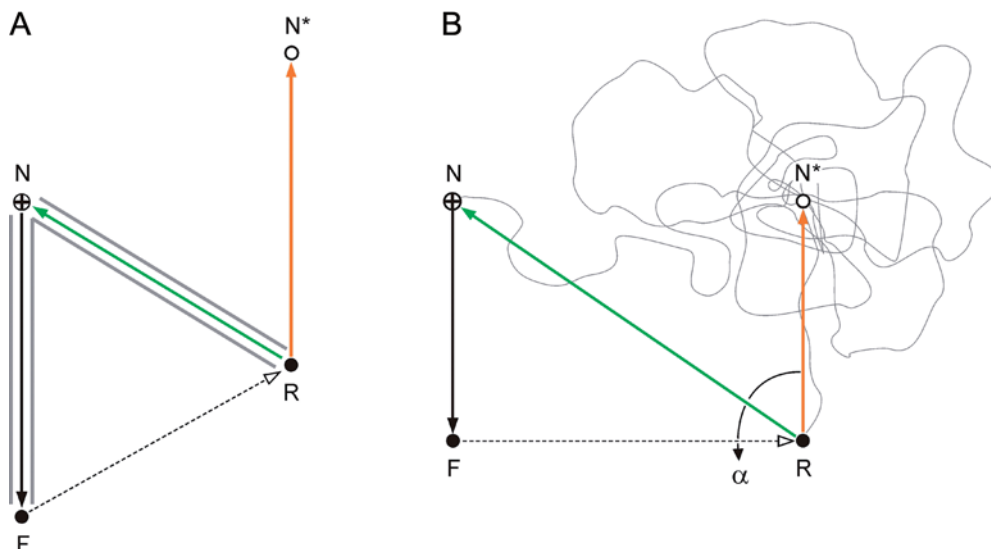
Material and methods

Experimental set-up

The experiments were performed near our *Cataglyphis* field station in a salt-pan area about 5 km north of Maharès in southern Tunisia. Since during winter time this area is regularly flooded by the sea and dries out again in the summer, the ground is left with an extremely flat, salty crust only scarcely covered by low halophilic shrubs (Heusser and Wehner 2002). The nearly complete lack of natural landmarks provides an ideal set-up for experiments on path integration.

The monogynous (one-queen) and monodomous (one-nest) colonies of *C. fortis* selected for this study were located in an open area with no vegetation within a range of at least 50 m. Overnight the colonies often reconstructed their subterranean system of

Fig. 1A,B. Open-jaw training paradigm applied for studying the calibration of the ant's global (path-integration) vector. The ants trained from the nest (N) to a feeder (F) are displaced from the feeder to the point of release (R); see *dashed arrow with open arrowhead*. From there they are either forced by a channel to walk directly back to N (**A** Collett et al. 1999) or allowed to return home under unconstrained conditions (**B** current investigation). N^* is the fictive location of nest as experienced by the ants after their first displacement. *Orange arrow*, inverse of the ant's immediately preceding outbound course; *green arrow*, the ant's inbound course (in **A**) or a hypothetical integrated inbound course leading from R directly to N (in **B**); *thin convoluted line* (in **B**) is an ant's trajectory as recorded after the animal's first displacement from F to R ; α is the angular deviation from direction $R \rightarrow N^*$ towards N



tunnels. This activity resulted in a funnel of sand around the nest entrance. As this funnel would have served as a landmark, it was carefully removed every morning.

Training procedure

The ants were trained to visit a feeder 5 m or 10 m south of the nest (Fig. 1B). The feeder consisted of a plastic bowl painted with Fluon (polytetrafluoroethylene) on the inside. This Fluon coating provided the container with a smooth surface and thus prevented the ants from escaping. The bowl was dug into the sand, so that the upper rim was level with the ground. This set-up had two advantages: the feeder could not serve as a landmark, and the ants could not return to the nest unless released by the experimenter. The feeder was filled with watermelon and small crumbs of biscuit (Saida, a sort of butter cookie). It was put into place around 9.30 a.m. and removed between 4.00 p.m. and 5.00 p.m. This time span coincided with the activity period of the foragers.

Test procedures

As we wanted to examine especially the time-course of the ant's navigation performances, it was important that all foragers used in the experiments had the same foraging history. Therefore only ants that had visited the feeder for the first time, and were then observed during all successive foraging trips, were included in the experiments. As an observer was present at the feeder during the whole activity period of the foragers, all foraging runs of the test animals could be recorded.

Upon their first arrival at the feeder the foragers were individually marked with a two-digit colour code. The colour dots were applied, with the help of a needle, to the alitrunk and the gaster. Afterwards the animals were captured in a small plastic tube and transferred to a release point 2.5 m, 5.0 m, 7.0 m, 7.5 m or 10.0 m east of the feeder. During this transport the tube was covered, so that the animals were prevented from seeing the surrounding landscape.

After release, the ants were tracked until they reached the nest. To facilitate the recording of the ants' trajectories a grid of 1-m squares (grid size: 25 m×25 m; emulsion paint Flash) was laid out on the ground. The paths of the animals were recorded on graph paper that also contained a rectangular grid (square size: 1.5 cm). Soon after the successful foragers each carrying a biscuit crumb in their mandibles had reached the nest, they left it again and returned to the feeder. Having arrived there, they were again displaced to the point of release and their home runs recorded. This procedure was continued for each individual ant throughout the whole day. The animals were not tested again the next day, because over night some quite substantial memory loss of directional information occurs (Ziegler and Wehner 1997). Due to this 1-day test procedure, the number of tests that could be performed with an individual ant depended on the ant's foraging activity: the more often the ant visited the feeder, the more it could be tested. The total number of tests performed per animal per day ranged from 18 to 55.

The animals displaced by 10 m rather than 7.5 m and 5.0 m had great difficulties in relocating their nest. Searching lasted up to 30 min and more. When the animals had finally reached the nest, they usually did not return to the feeder during the same day. Hence, as only a few data could be obtained with the 10-m tests, they are not included in this paper.

Even though we endeavoured to exclude the influence of any landmark information, we nonetheless could not rule out completely that in the training area some sort of signpost information (e.g. the presence of nestmate foragers around the nest opening) had been effective in guiding the ants. Therefore control experiments were performed in a test field 75 m north of the training area. The ants were captured at the feeder as usual and then transferred to the test field, where their "home runs" were tracked. The recordings were stopped after the ants had approached the fictive position of the nest, i.e. the point where the nest would have been had the ants been tested in the training area, for at least 1 m.

Data evaluation

After the path records had been digitized by using Gedit for DOS, sets of concentric circles were laid around the release point, and the ants' first crossings of each circle (crossover points) were determined. The evaluation of these sets of data followed the methods of circular statistics as outlined by Batchelet (1981). In particular, we applied the Rayleigh test for directedness (null hypothesis: uniform data distribution) and computed the Stephens confidence intervals, in order to check whether the mean direction of a sample differed significantly from an expected direction; 0° defines the direction from the point of release to the fictive position of the nest.

When circular statistics could not be applied as in the case of sets of dependent data (data obtained from successive runs of the same animal), linear statistical methods were used instead. As the Rayleigh test revealed that all data were strongly directed, the use of linear statistics seems to be legitimate: only in 2 out of 260 cases, in which the mean angles were calculated by using linear and circular methods, did the two values differ at all. A $Q-Q$ plot (Stahel 1995) showed that the data were not normally distributed and, hence, non-parametric tests had to be applied: the Friedman (rank analysis of variance) test for systematic differences within a data set; the Wilcoxon test and the Mann-Whitney U -test for evaluating the statistical significance between two sets of data (applied for sets of dependent and independent data, respectively; Köhler et al. 1992).

For analysing the search patterns, the search trajectories of all animals were overlaid in a graph. Using the software Gedit we then calculated the local search densities defined as the percentage of the total path length within a unit area of 1 m^2 .

Results

When *Cataglyphis* ants are displaced from a feeder to a near-by release site, they first run off their home vector computed during the outbound run and then commence a systematic search for the nest (Wehner and Srinivasan 1981; Wehner and Wehner 1986). Whenever the displacement distances are short, the ant's search trajectories will finally hit the goal (see for example Fig. 1B). If the experimental paradigm of training the ant to a feeder, displacing it to a near-by release point, and recording its homeward trajectory is repeated over and over again, the homing ant could adopt, in principle, one of the following three strategies: The direction of its inbound path could be (1) the 180° reversal of the immediately preceding outbound path, (2) the direction of the integrated former inbound path (integrated over the entire search), or (3) some intermediate direction between these two possibilities. Hypotheses 1 and 3 imply that the ants' straight inbound courses do not lead the animals directly back to the nest, so that in addition the ants must rely on their search strategy. If this turns out to be the case, we shall not only study the changes in the ants' vector courses, but shall also ask whether the ants transform the geometry of their search pattern in such a way that with increasing number of displacements the path lengths of the home runs get shorter.

Vector courses

In a standard series of experiments individually marked ants were trained to a feeder (F) located 5.0 m to the

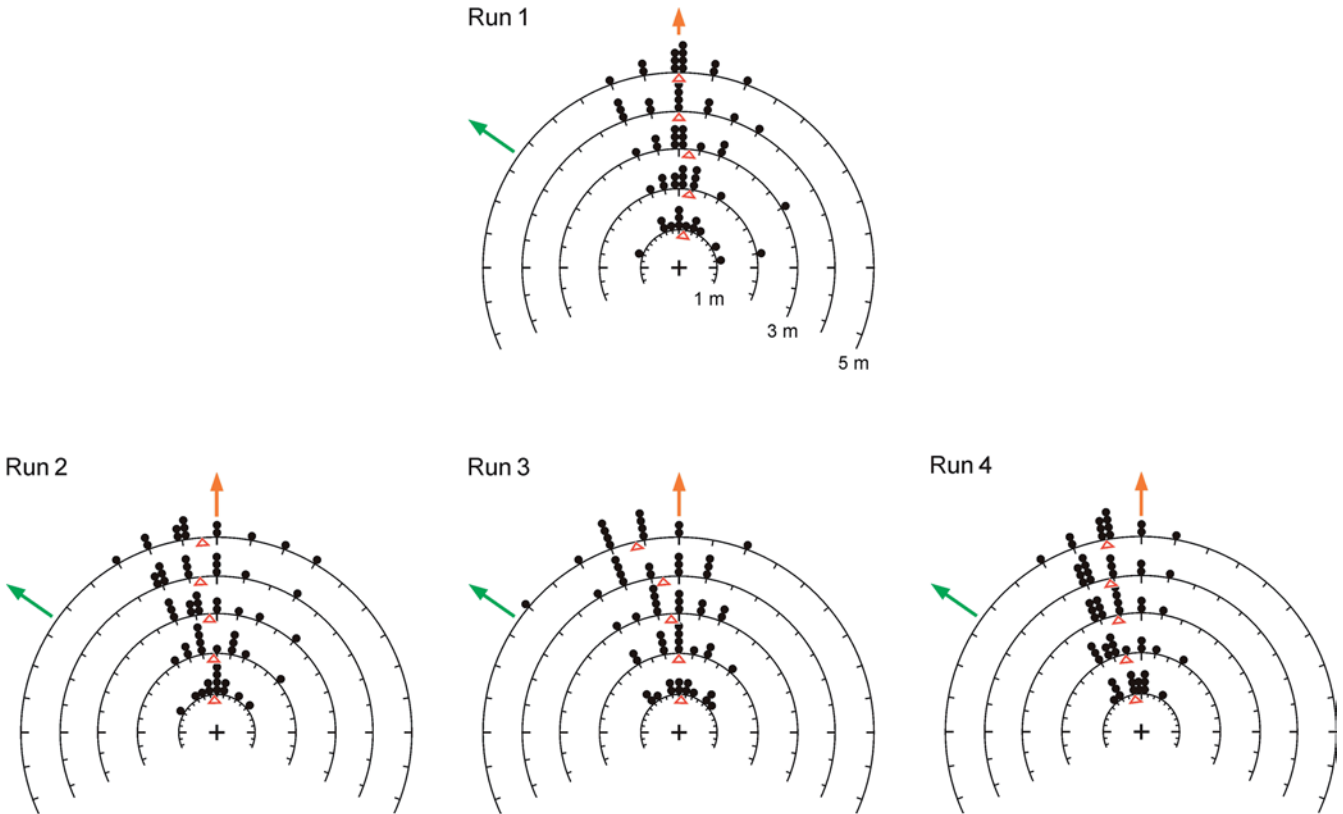


Fig. 2. Inbound courses of 13 individually marked ants after the first 4 consecutive displacements (training distance: 5.0 m, displacement distance: 7.5 m). + is the release point. The directions were recorded in bins of 10° . The *open red arrowheads* mark the means of the circularly distributed data. For conventions see Fig. 1B

south of the nest (N). We then displaced the ants in the dark by 7.5 m to the east to R and released them there (see Fig. 1B). If subjected to this experimental paradigm for the very first time, the ants should select a course that is the inverse of the outbound course (N→F), and walk for a distance that is equivalent to their predisplacement distance. Then, at about the fictive position N* of the nest, they should start their search programme, which sooner or later would lead them to the real nest N.

This is exactly what occurred. Having been displaced for the first time, the ants ran off in the direction of N* (Fig. 2, run 1), but when the training-around-a-circuit procedure was repeated time and again, the direction of the home vector turned towards the direction of the former (integrated) inbound courses, i.e. towards the direction of N (Fig. 2, runs 2–4). Up to the 3rd or 4th run the angular deviation α from $\alpha_0 = 0^\circ$ (the inverse of the immediately preceding outbound run) increased steadily and thereafter scattered around a constant value (Fig. 3). It seems as if the animals had learned very quickly to recalibrate their home vector, and that the home vector had reached a constant value after maximally four repetitions of the displacement paradigm.

In order to define the time-course of this recalibration process in more detail, we performed pair-wise statistical comparisons of the directions α chosen by the ants in runs 1–18. In particular, we compared the vector direction α_i of each run no. i with the vector directions of all other runs nos. j ($j > i$), e.g. α_1 versus α_2, α_3 etc., α_2 versus α_3, α_4 , etc. (Wilcoxon pair comparison test, $n = 26$ for each pair of α values). With a few exceptions (3 out of in total 75 pair-wise comparisons) significant differences

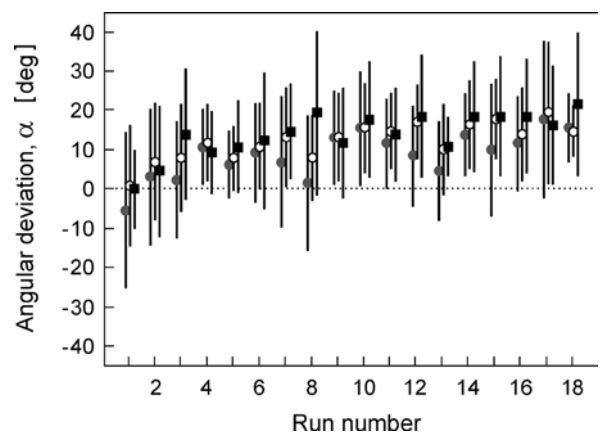


Fig. 3. Angular deviation, α , from direction R→N* (see orange arrows in Figs. 1B and 2) of runs nos. 1–18 of the same 13 individually marked ants, for which full data plots are given for runs nos. 1–4 in Fig. 2. The α values are given for distances of 3 m (*filled circles*), 4 m (*open circles*), and 5 m (*filled squares*) from the start. Values are means \pm SD (see Batschelet 1981)

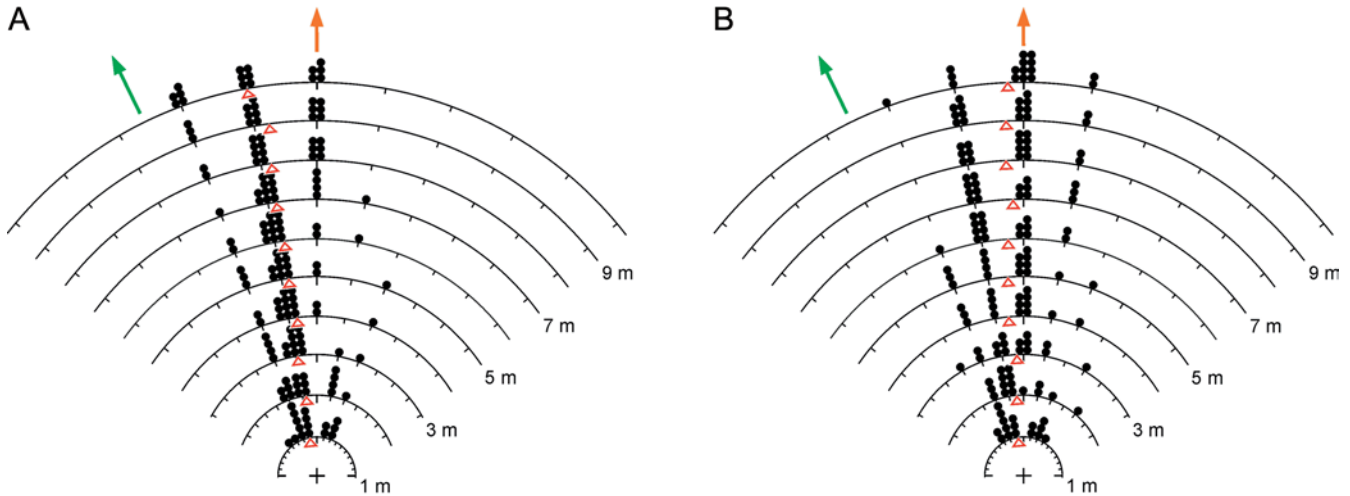


Fig. 4 **A** Inbound courses of 16 individually marked ants after 6 consecutive displacements (from F to R in Fig. 1B; distances N–F and F–R: 10.0 m and 5.0 m, respectively). **B** Inbound courses of the same 16 ants, which after their 7th foraging runs had returned directly to the nest (F→N in Fig. 1B) and were displaced again after their 8th foraging runs. The graph depicts the inbound courses of runs no. 8. All directional recordings are given in bins of 10°

($P < 0.05$) occurred only if the first run was included in the comparisons.

In a second set of experiments we compared the vector courses α of displaced ants with the vector courses α_C of control animals that had returned directly (without displacement) from the feeder to the nest. As expected, the homeward runs of the control animals did not deviate from 0° (95% confidence limits: $-3.30 < \alpha_C < +2.10$; $n = 20$). In various series of displacement tests (training distance N–F = 10.0 m; displacement distances F–R = 2.5 m, 5.0 m and 7.0 m) the ants' homeward courses α were compared, again in a pair-wise way, with α_C . Statistically significant differences ($P < 0.01$) resulted for all runs nos. ≥ 2 , i.e. if α_C was compared with α_2 , α_3 , etc., but they did never result for run no. 1, i.e. if α_C was compared with α_1 ($n = 33$, 58 and 31 for all pair-wise tests with F–R = 2.5 m, 5.0 m, and 7.0 m, respectively).

In conclusion, recalibration of the global home vector is a rather fast process apparently occurring every time the animal experiences a mismatch between the stored and the current state of its path integrator. Further support for this conclusion comes from experiments, in which a series of successive displacements was interrupted and the ant allowed to home directly from the feeder (F→N rather than R→N). If, thereafter, the ants were displaced again to the former release site R, their homeward courses were shifted back towards $\alpha = 0^\circ$ (compare Fig. 4A and 4B). Accordingly, one displacement following the direct homeward run shifted the homeward vector again off the α_0 direction. The same

Fig. 5A,B. Same experimental paradigm as in Fig. 4, but with 20 other ants tested within a far-off test area. **A** Inbound run no. 6 (after 6 consecutive displacements). **B** Inbound runs no. 8 (after the ants had performed their inbound runs no. 7 from the feeder directly back to the nest). The ants' directional choices are not significantly different from those of the control animals, which had constantly moved back and forth between the nest and the feeder, i.e. had never been displaced ($P = 0.714$, Mann-Whitney U -test), but in the former case (**A**) they are different from the controls ($P < 0.05$). R is the point of release within the test area. For further conventions see Fig. 1B

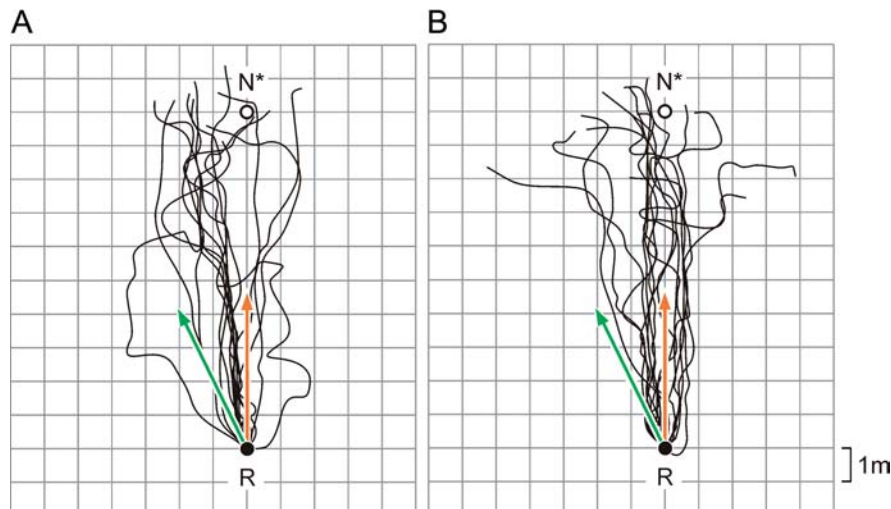
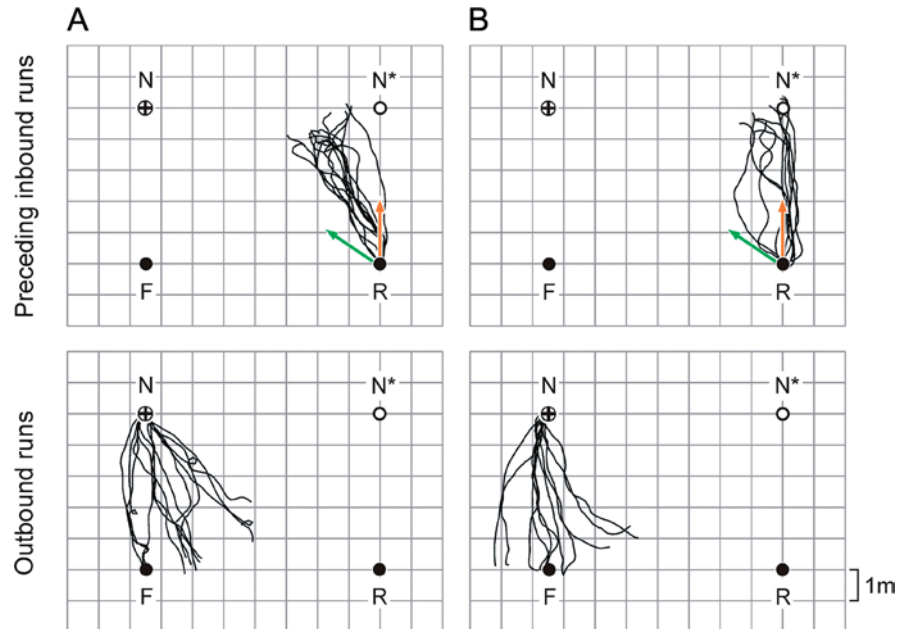


Fig. 6A,B. All inbound runs (*upper graphs*) and consecutive outbound runs (*lower graphs*) recorded in two individual ants. As a consequence of preceding displacements ant **A** recalibrated its path-integration vector (by about the same amount as did the majority of ants), but ant **B**, which had been subjected to exactly the same displacement paradigm, did not. The inbound runs of ants **A** and **B** are runs nos. 4, 5, 6, 7, 12, 13, 14, 23, 24, 29, 30, 31 and runs nos. 5, 6, 7, 28, 29, 30, 31, 32, 33, 34, 39, respectively



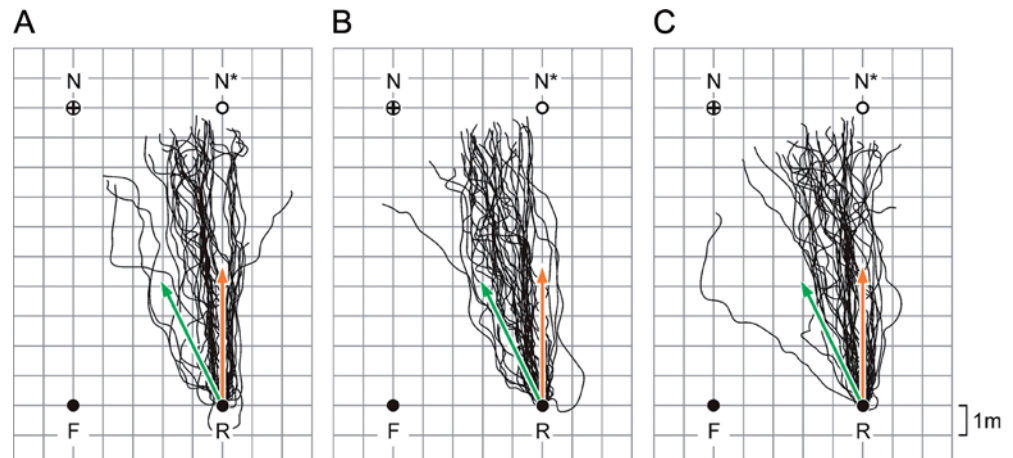
behaviour was observed when the ants were released within the far-off test field rather than at R within the training area (Fig. 5). Never did the ants' mean vector courses depend on whether the animals had been released in the test or in the training area.

Having discussed the time-course of the recalibration process to quite some detail, let us now ask what level – what value of α – does the recalibration process finally reach? Somewhat surprisingly, even when the displacement paradigm was repeated for more than 30 times, the vector courses stabilized rather quickly. One example of this time-course is shown in Fig. 3. The final value of α is quite small (total mean $9.6 \pm 2.0^\circ$, mean \pm SD) and significantly different from the vector courses predicted by the first two hypotheses. It is also different from the prediction derived from observations by Collett et al. (1999) that recalibration resulted in a course that was intermediate between the (experimentally disrupted) outbound and inbound courses. In the latter case the ant should have selected values of $\alpha = 28^\circ$ (the bisector

between the two directions) or, more properly, $\alpha = 36^\circ$ (the mean vector). Both predictions differ highly significantly from the ants' mean courses (9.6°).

For technical reasons, it is much more difficult to record outbound trajectories than inbound ones. In Fig. 6A and B two examples are presented in which the outbound courses are compared with the immediately preceding inbound courses. In either case the inbound and outbound courses are the inverse of each other. The ant, whose trajectories are portrayed in Fig. 6A, selected courses that deviated from $\alpha = 0^\circ$ by about the same amount as the courses did in the majority of ants, whereas the ant in Fig. 6B was special: In spite of being displaced repeatedly, it invariably selected a homeward course that was the inverse of the preceding outbound course, i.e. coincided with α_0 . The behaviour of this ant again shows that recalibration is a rather flexible process depending on a number of largely unknown contextual variables. For example, in one additional series of experiments (training distance N–F = 10.0 m,

Fig. 7. Inbound courses of 38 individually marked ants after their 2nd (A), 3rd (B), and 4th (C) displacement. For conventions see Fig. 1B



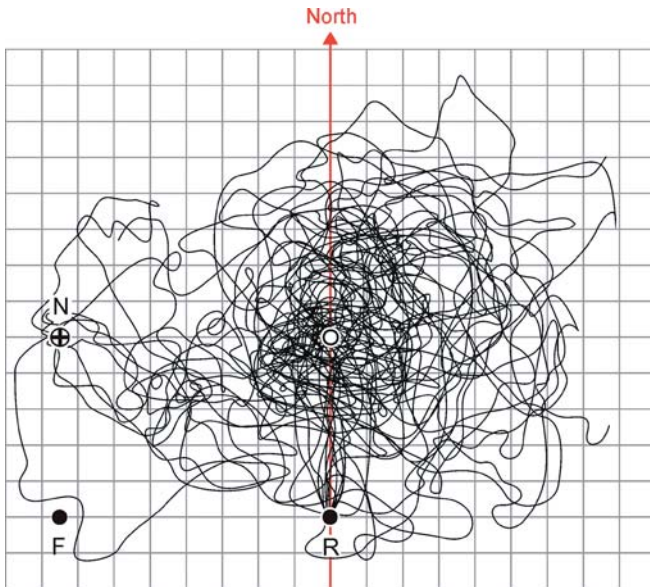


Fig. 8. Inbound runs performed by 13 ants after they had been displaced from the feeder (*F*) to the release point (*R*) for the first time (runs no. 1). The search density is distributed equally to the east and west of the north-south meridian passing through *R*. For conventions see Fig. 1B

displacement distance $F-R=5.0$ m) the vector courses of the ants displaced for the second time (second runs) fell into two groups. Some ants still adhered to the 0° direction, while others had already shifted their homeward courses towards the direction of the fictive nest. After the third and fourth displacement, and after all following displacements, this distinction was gone (Fig. 7).

Systematic search

Why do the ants having experienced the displacement paradigm in up to 55 successive outbound and inbound runs recalibrate their global vector by an angular amount that is so much smaller ($\alpha=9.6^\circ$) than that expected on the basis of the prediction by Collett et al. (1999) ($\alpha=36^\circ$)? Whereas in the latter study the displaced ants had been forced by a channel device to return straight to the nest, the current investigation mimicked natural conditions more closely: the ants were free to home in whatever way they wanted. They did so by invariably employing two mechanisms in succession: first, selecting a global vector course (as described in the previous section), and second, relying on a systematic-search programme. Let us now consider the latter.

Displaced for the first time (runs no. 1), the ants, having arrived at the fictive position N^* of the nest, display a systematic-search pattern that is centred about N^* and exhibits a radially symmetric search density profile (Fig. 8). However, it is already after the second displacement (runs no. 2), and all following displacements, that the search density profile gets directionally

biased towards the location of the nest, *N* (Fig. 9, red signatures). Consequently, the length of the entire homeward trajectory, which is dominated to about 90% by the search trajectory, decreases dramatically between runs nos. 1 and 2. After run no. 2 it reaches a constant level (Fig. 9, green signatures). Even then, however, it is still more than four times as long as the direct path from the point of release to the nest would be ($R-F: 9.0$ m; mean length of the recorded paths of runs no. 18: 37.2 m).

As the homeward runs described until now have been performed in the training area, one cannot be sure whether the observed change in the geometry of the search pattern is due completely to an internal change in the ant's search programme, or whether it is influenced in addition by nest-site specific signposts. Even though the latter argument is rather unlikely, because the *C. fortis* nests selected for these experiments have been located within bare salt-pan ground completely devoid of any conspicuous landmarks, it cannot be discarded completely. Therefore, additional experiments were performed in which the ants had to display their search pattern within a far-off test area. After having undergone five displacements in the training area (runs nos. 1–5), the ants were allowed to return from the feeder directly to the nest (runs no. 6). However, shortly before vanishing into their underground galleries, they were captured and transferred to the test area. Upon release, they immediately started their systematic search. The search trajectories were recorded for 5 min each. Then the ants were captured again and returned to the nest. This procedure (outbound run $N \rightarrow F$, return run $F \rightarrow N$, capture at *N*, transfer to test area, recording of search trajectories, transfer back to *N*) was successively repeated three times.

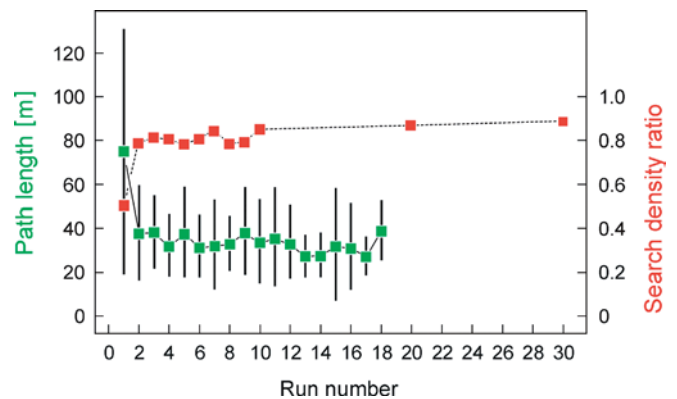


Fig. 9. *Green signatures:* path lengths of the ants' inbound runs after 18 consecutive displacements (for experimental design see Fig. 1B; the distances $N-F$ and $F-R$ are 5.0 m and 7.5 m, respectively). Values are means \pm SD. *Red signatures:* the ants' search area (i.e. the area covered by the ants' search trajectories) lying westwards (nestwards) of the north-south meridian of *R* divided by the ants' total search area (computed for search densities > 0.01). Search density within a particular pixel of space (pixel size: 1 m^2) is defined as an ant's path length within that pixel divided by the ant's total path length. Runs no. 1 are depicted in Fig. 8

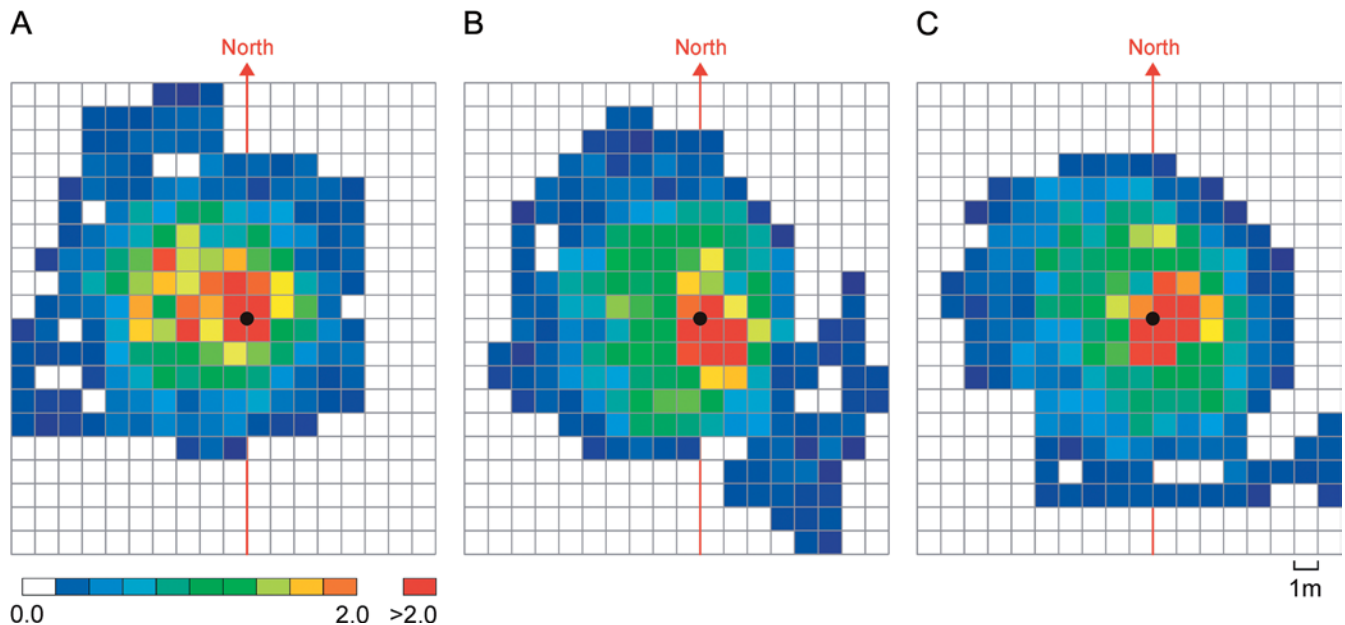


Fig. 10. **A** Search densities of 16 ants after 5 consecutive displacements (from F to R in Fig. 1B) and one direct homeward run (from F to N in Fig. 1B). At the end of these last inbound runs (runs no. 6) the animals captured just before they vanished into the nest were transferred to a far-off test area and released there. The *black dot* marks the point of release. **B, C** Search densities of the same 16 ants, which after their 7th and 8th foraging runs were again permitted to return to the nest directly (from F to N in Fig. 1B). They were captured, in the same way as in **A**, before entering the nest and transferred to the test area. In **A** the search densities to the east and west of the north-south axis passing through the release site are significantly different from a symmetric east-west distribution ($P < 0.001$, χ^2 -test), but in **B** and **C** they are not ($P > 0.3$)

The data shown in Fig. 10 reveal two important results: First, the ants have responded to the displacement paradigm by adopting an asymmetric (nest-direction biased) search pattern (Fig. 10A). Second, if the displacement paradigm is interrupted and the ants are allowed to return from the feeding site directly to the nest, the search density profile becomes symmetric again (Fig. 10B and C). Hence, the rapid adaptation to a new homing situation that we had observed in the recalibration of the path integrator occurs in the readjustment of the search programme as well.

Discussion

Path integration (vector navigation: Wehner 1983; Collett and Collett 2000; Wehner and Srinivasan 2002; for a full review of path integration in arthropods see Wehner 1992) is the cataglyphid ant's predominant mode of navigation. In landmark-free territory such as the large North African salt-pans (e.g. Chott el Djerid, Chott Rharsa and Chott Melrhir) inhabited by populations of *C. fortis* this mode of navigation is the only way at all, by which the animals can obtain positional in-

formation. But even in cluttered environments, in which individual ants adopt fixed, multi-segment paths, and in which they are never able to walk straight back and forth between nesting site and feeding grounds, the global vector resulting from path integration is computed continually. It surfaces immediately when the animal is displaced to landmark-free terrain (Wehner and Srinivasan 1981; Wehner and Wehner 1986). At times, navigation by landmarks and landmark-associated local vectors may over-ride vector navigation (Bisch and Wehner 1999; Collett et al. 1999), but even then the path integrator keeps running (Sassi and Wehner 1997).

Furthermore, path-integration vectors are not short-lived navigational tools used merely for the instant returns to nesting or feeding sites, and being extinguished thereafter. Instead, they are stored at some higher than working-memory level. For example, when individual ants are held in captivity, or when they refrain from foraging for a number of days, they are still able to recall their former vector and use it to compute the direction to a previously visited goal (e.g. Ziegler and Wehner 1997). As *Cataglyphis* foragers exhibit strong sector fidelity (Wehner et al. 1983; Wehner 1987), the global vector may persist over the ant's entire – though short (Schmid-Hempel 1984) – foraging lifetime. Observations of individually marked ants have shown that a forager leaves its nest always in more or less the same direction, but that it does not find its booty (an arthropod corpse) exactly at the site where it had been successful before (Wehner et al. 1983; Schmid-Hempel 1984). Hence, the vector pointing from the nest to the foraging site must be recalibrated whenever the animal has moved to a new goal.

We have studied this recalibration process by training the animals to different outbound and inbound routes, so that the states of the vector at the feeder and at the nest are no longer 180° reversals of each other (open-jaw

training paradigm). In former experiments (Collett et al. 1999) this “decoupling” of inward and outward courses has been achieved by forcing the animals to walk in channels (Fig. 1A). In the present displacement paradigm the ants were permitted to select their homeward paths freely (Figs. 1B and 11). The results differ markedly. Whereas in the former (forced-detour) case the ants when later tested under unconstrained conditions selected homeward courses that were intermediate between the inbound and outbound courses to which they had been trained, in the latter case their homeward courses were much closer to the inverse of their outbound courses (Fig. 11).

Before we shall discuss possible reasons for these discrepancies, let us first point at the conformities: the ant’s inbound and outbound vectors are always the inverse of each other. We never succeeded in training the ants to acquire separate inbound and outbound vectors differing by angles others than 180° (see Wehner and Flatt 1972). If experimental paradigms are applied that cause the ants to experience a mismatch between the result of path integration on their return route and the result on their outward route, recalibration occurs. This recalibration results in systematic deviations of the ants’ trajectories from both their inbound and their outbound courses.

Let us now turn to the differences in the amount of recalibration that have been found in the two experimental paradigms mentioned above: the forced-detour (applied by Collett et al. 1999) and the free-homing paradigm (applied in the present account).

One possible reason for these differences could lie in the potentially different time spans over which the animals had been trained. One could argue, for instance, that the more training runs an animal had performed,

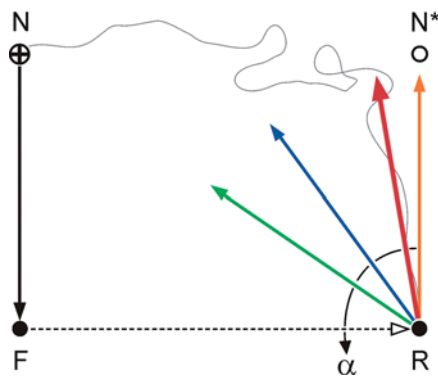


Fig. 11. Experimental paradigm (compare Fig. 1B) and main results. *N*, nest; *N**, fictive position of nest (for ants displaced from *F* to *R* for the first time); *R*, point of release; *dashed arrow*, displacement vector; α , angular deviation from direction $R \rightarrow N^*$; *orange arrow*, inverse of the ant’s immediately preceding outbound course; *green arrow*, vector pointing from *R* to *N*; *blue arrow*, vector course predicted by Collett et al. (1999), who had applied the experimental paradigm sketched out in Fig. 1A; *heavy red arrow*, mean vector course exhibited by the ants when subjected to the experimental paradigm of Fig. 1B; *thin convoluted line*, an ant’s trajectory after the animal has been displaced repeatedly (up to 50 times)

the more would its homeward course α approach the mean vector of the outbound and inbound vectors. Collett et al. (1999) started their experiments only after 4 days of training. However, as in their study the ants had not been labelled, nothing can be said about the number of displacements an ant had experienced prior to the experiment. The turnover rate in the life history of *C. fortis* is rather high, so that many ants might have arrived at the feeder at the 4th day of “training” for the first time in their foraging life. In contrast, in the present study the ants were labelled individually and their consecutive inbound and outbound paths recorded continuously. This fine-grain temporal analysis clearly showed that vector recalibration got stabilized, i.e. that α reached a constant value, already after the first, second or at the latest fourth displacement. No further change in the recalibrated vector occurred when training was continued for another 20–50 displacements. The conclusion that recalibration is a rapid process is further supported by experiments in which *Cataglyphis* responded immediately – from one homeward run to the next – to changes in the displacement paradigm (Figs. 4, 5).

If recalibration is so rapid a process indeed, why then is it incomplete? Why have the ants when tested in unconstrained homing situations put so much more weight on their outbound rather than their inbound courses? One could argue that unequal calibration had occurred along the outward and inward paths. By assigning proper weighting factors to the calibration processes occurring at the feeder and the nest one would be able to quantitatively simulate the experimental results. Obviously, the ants had placed more emphasis on the outbound than the inbound path, i.e. calibration had been stronger at the food site than the nest site. Note that the latter is a fixed goal, but that the former – the food sites within the ant’s search sector – are shifting targets. Furthermore, even though we had taken special care to perform the experiments within an extremely featureless salt-pan environment, some kind of visual signpost along the nest-to-feeder route might have reinforced the ant’s outbound path (see Otto 1959 for honey bees). Finally, as the displaced ants had to search for the nest for quite some time, but had to spend much less time to locate the feeding site on their next foraging journey, this difference in search time is another factor correlated with the unequal weighting at the nest and the feeder.

In any way, when displaced ants are free to home under unconstrained conditions, they adopt a two-step strategy: path integration and systematic search. As shown in Fig. 9, the latter becomes asymmetric, i.e. is directed towards the start of the open-jaw round-trip journey, already after the ant has experienced this training paradigm for the first time. As the asymmetry of the search density profile develops equally well in the training and the test area, it cannot be due to nest-site specific signposts. Instead, the asymmetry represents a compass-mediated shift of the ant’s search activity in the direction of the goal. This directional bias of the search

pattern (Fig. 9, red signatures) decreases the ant's search time significantly (Fig. 9, green signatures). Finally, it is the directional bias of the ant's successful search that feeds back into the vector-navigation system and causes the ant's global vector to deviate from the direct courses leading from the nest to the feeder and from the release point to the fictive position of the nest. However, this deviation is only moderate and far below what one would expect if equal weighting of the vector calibration process had occurred after the ant's arrivals at the nest and at the feeder.

Obviously, the inbound paths of the displaced ants are not integrated into one uniform inbound vector. A slight recalibration of the global vector – its inbound state as well as its inverse, the outbound state – does occur (according to hypothesis 3), but once this slightly recalibrated vector has been nullified, and the goal has not been reached yet, control is taken over by the systematic-search programme. Note that the path integrator keeps running also during the tortuous search phase following the straight vector of the ant's inbound trajectory (Wehner and Srinivasan 1981; Müller and Wehner 1994), but that path integration does not occur uniformly over the entire homeward run.

Furthermore, vector calibration is a rather flexible process. Some animals do not recalibrate their vector at all, and hence behave according to hypothesis 1 (see for example Fig. 6B in this paper and Fig. 7 in Wehner and Flatt 1972, in which the same experimental paradigm has been applied), and other animals exhibit delayed recalibration responses (Fig. 7). In the majority of cases, however, recalibration is a rapid process occurring every time the animal experiences a mismatch between the result of path integration on the return route and the result on the outward route (Figs. 4, 5). In detail, this mismatch means that at the end of, say, a homeward run the difference between the stored global vector and the state of the actual vector, i.e. the result of the continuously running vector subtraction process, is not zero.

Let us finally return to the systematic-search system and its experience-mediated asymmetry. As shown by experiments, in which the present training-and-test paradigm has been applied to the one-dimensional rather than the two-dimensional spatial domain (Cheng and Wehner 2002), this asymmetry can develop quite independently of vector recalibration. Within an array of channels aligned in parallel *C. fortis* was trained to different outbound (6 m) and inbound (12 m) distances. When the ants were later tested for the length of the resulting vector, recalibration had not occurred: the length of the resulting vector, in both its inbound and its outbound state, corresponded to the length of the outbound vector experienced during training. However, even though the ants did not recalibrate their global vector, they nevertheless changed their (linear) search pattern by searching farther from the start in the direction of the nest than did the controls. The one-dimensional search pattern had become asymmetric, as

had the two-dimensional pattern studied in the present account (Fig. 9, red signatures; Fig. 10A).

In conclusion, foraging *Cataglyphis* ants that have been shifted off their course – e.g. that have been experimentally displaced to the side – first run off their home vector and then apply a systematic-search strategy, which finally enables them to return to the start of their foraging journey. If they are displaced repeatedly and consistently by the same displacement vector, they transform their originally symmetric search pattern into an asymmetric one. The search-density peak is shifted towards the goal, and the length of the search trajectory, i.e. the search time, is decreased substantially. This acquired spatial asymmetry of the search programme induces vector recalibration to occur: the end of the vector path – the start of the search trajectory – is shifted towards the goal, so that search time is decreased further. However, this recalibration is incomplete in the sense that the resulting vector is not the mean of the (experimentally disconnected) outbound and inbound vectors. Obviously, the ant does not compute its homeward vector by integrating over its entire homeward path. Even after more than 50 consecutive repetitions of the displacement paradigm, the ant's homeward paths maintain their bipartite structure: a straight vector path is followed by a convoluted search trajectory.

Of course, in terms of minimisation of search time, the optimal solution would be to adopt a straight homeward path (hypothesis 2; green arrow in Fig. 11) by decoupling outbound and inbound vectors. However, such decoupling has never been observed: outbound and inbound vectors are always the inverse-sign states of the same global vector, irrespective of whether vector recalibration does not occur at all (Fig. 6B, Wehner and Flatt 1972), is incomplete (Fig. 6A) or complete (Collett et al. 1999). These different outcomes of the recalibration process clearly show that vector calibration is a flexible process. It is also a fast process. It instantly occurs whenever the animal having arrived at a familiar place – the nest or the feeder – encounters a mismatch between the stored and the actual state of its path integrator.

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References

- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Benhamou S, Séguinot V (1995) How to find one's way in the labyrinth of path integration models. *J Theor Biol* 174:463–466
- Bisch S, Wehner R (1999) Context-dependent retrieval of local vectors in desert ants. *Proc Neurobiol Conf Göttingen* 27:429
- Cheng K, Wehner R (2002) Navigating desert ants (*Cataglyphis fortis*) learn to alter their search patterns on their homebound journeys. *Physiol Entomol* (in press)

- Collett M, Collett TS (2000) How do insects use path integration for their navigation? *Biol Cybern* 83:245–259
- Collett M, Collett TS, Wehner R (1999) Calibration of vector navigation in desert ants. *Curr Biol* 16:1031–1034
- Etienne AS, Maurer R, Berlie J, Reverdin B, Rowe T, Georgakopoulos J, Séguinot V (1998) Navigation through vector addition. *Nature* 396:161–164
- Hartmann G, Wehner R (1995) The ant's path integration system: a neural architecture. *Biol Cybern* 73:483–497
- Heusser D, Wehner R (2002) The visual centring response in desert ants, *Cataglyphis fortis*. *J Exp Biol* 205:585–590
- Köhler W, Schachtel G, Voleske P (1992) *Biostatistik. Einführung in die Biometrie für Biologen und Agrarwissenschaftler*. 2. Aufl. Springer, Berlin Heidelberg New York
- Loomis JM, Klatzky RL, Golledge RG, Cicinelli JG, Pellegrino JW, Fry PA (1993) Nonvisual navigation by blind and sighted: assessment of path integration ability. *J Exp Psychol Gen* 122:73–91
- McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, Knierim JJ, Kudrimoti H, Qin Y, Skaggs WE, Suster M, Weaver KL (1996) Deciphering the hippocampal polyglot: the hippocampus as a path integration system. *J Exp Biol* 199:173–185
- Mittelstaedt H (1983) The role of multimodal convergence in homing by path integration. *Fortschr Zool* 28:197–212
- Mittelstaedt H (1985) Analytical cybernetics of spider navigation. In: Barth FG (ed) *Neurobiology of arachnids*. Springer, Berlin Heidelberg New York, pp 298–316
- Mittelstaedt H (2000) Triple-loop model of path control by head direction and place cells. *Biol Cybern* 83:261–270
- Mittelstaedt H, Mittelstaedt ML (1973) Mechanismen der Orientierung ohne richtende Aussenreize. *Fortschr Zool* 21:46–58
- Müller M, Wehner R (1994) The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J Comp Physiol A* 175:525–530
- Otto F (1959) Die Bedeutung des Rückfluges für die Richtungs- und Entfernungsangabe der Bienen. *Z Vergl Physiol* 42:303–333
- Sassi S, Wehner R (1997) Dead reckoning in desert ants, *Cataglyphis fortis*: can homeward-bound vectors be reactivated by familiar landmark configurations? *Proc Neurobiol Conf Göttingen* 25: 484
- Schmid-Hempel P (1984) Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 14:263–271
- Stahel W (1995) *Statistische Datenanalyse. Eine Einführung für Naturwissenschaftler*. Braunschweig, Wiesbaden
- Wehner R (1983) Celestial and terrestrial navigation: human strategies – insect strategies. In: Huber F, Markl H (eds) *Neuroethology and behavioral physiology*. Springer, Berlin Heidelberg New York, pp 366–381
- Wehner R (1987) Spatial organization of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara Desert) and *Ocymyrmex* (Namib Desert). In: Pasteels JM, Deneubourg J-L (eds) *From individual to collective behavior in social insects*. Birkhäuser, Basel, pp 15–42
- Wehner R (1992) Arthropods. In: Papi F (ed) *Animal homing*. Chapman and Hall, London, pp 45–144
- Wehner R, Duelli P (1971) The spatial orientation of desert ants, *Cataglyphis bicolor*, before sunrise and after sunset. *Experientia* 27:1364–1366
- Wehner R, Flatt I (1972) The visual orientation of desert ants, *Cataglyphis bicolor*, by means of terrestrial cues. In: Wehner R (ed) *Information processing in the visual systems of arthropods*. Springer, Berlin Heidelberg New York, pp 295–302
- Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J Comp Physiol* 142:315–338
- Wehner R, Srinivasan MV (2002) Path integration in insects. In: Jeffery K (ed) *The biological basis of navigation*. Oxford University Press, Oxford (in press)
- Wehner R, Wehner S (1986) Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. *Monit Zool Ital* 20:309–331
- Wehner R, Harkness RD, Schmid-Hempel P (1983) Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Akad Wiss Lit Mainz Abh Math Naturwiss Kl*. Fischer, Stuttgart
- Wittmann T, Schwegler H (1995) Path integration – a network model. *Biol Cybern* 73:569–579
- Zeil J (1998) Homing in fiddler crabs (*Uca lacteal annulipes* and *Uca vomeris*: Ocypodidae). *J Comp Physiol A* 183:367–377
- Ziegler PE, Wehner R (1997) Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, *Cataglyphis fortis*. *J Comp Physiol A* 181:13–20