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Ant navigation: resetting the path integrator

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Summary

Desert ants use path integration as their predominant system of long-distance navigation, but they also make use of route-defining and nest-defining visual landmarks. Such landmark-gained information might override the information provided by the path integrator, but nevertheless the path integrator keeps running. Here we show that only cues that are associated with the ant being inside the nest are able to reset the path integrator to zero state. Ants were captured at a feeder, i.e. without having run off their home vector, and were forced to enter the nest. On their next outbound run their walking direction differed by 180° from that of ants that had also been captured at the feeder but instead of having been forced to enter the interior of the nest were released at its entrance. Whereas these latter ants still ran off their home vector pointing in the feeder–nest direction (and by this departed from the nest in a direction opposite to the feeder direction) the former ants had reset their home vector to zero state, and had therefore been able to reload their learned feeder vector, and consequently departed from the nest in the feeder direction.

Owing to its egocentric nature the path-integrator is error prone. Hence, it is a suitable strategy to reset the path integrator if the ant has appeared at its final goal, the nest. Otherwise during consecutive foraging runs navigational errors would steadily increase.

Key words: path integration, orientation, *Cataglyphis fortis*.

Introduction

Desert ants (genus *Cataglyphis*) use path integration as their predominant means of navigation. Employing a skylight compass and some kind of proprioceptive odometer they continually update a path-integration vector that would lead them directly back to their starting point, e.g. the nest (for a review, see Wehner and Srinivasan, 2003). Once they have completed their inbound (home) run and arrived at the nest, their path integrator has again reached its zero state. However, as *Cataglyphis* ants have been shown to be able to return to an artificial feeder (e.g. Wehner, 1982) or to a natural feeding site (Schmid-Hempel, 1983; Wehner et al., 1983), along a straight (outbound) path, the information about the path-integration vector is not lost, but must reside in some kind of reference memory. Furthermore, particular (open-jaw) training experiments show that *Cataglyphis* never learns a feeder-directed (outbound) vector that is not the reverse of the nest-directed (inbound) vector (for details see Collet et al., 1999; Wehner et al., 2002).

Whatever the computational mechanism of the path integrator might be (for models, see Mittelstaedt, 1983; Hartmann and Wehner, 1995; Collett and Collett, 2000), the results of previous experiments can conveniently be described applying the following formalism (for conventions, see Andel and Wehner, 2004). Let us assume that the ants, having arrived at a feeding site, transfer the state of their path integrator to some kind of reference memory (reference vector **R**: **R**=+1 with the plus sign meaning **R** is pointing from the feeder to the nest, and with the value 1 indicating the straight-line distance between feeder and nest). Subsequently, while performing their homebound runs the ants are considered to continually compare the current state **C** of their path integrator (**C**=0 at the feeder) with the reference vector. If **C**=+1, i.e. **R**–**C**=0, the ants have reached the nest. Before setting out for a new foraging journey to the same feeding site, the ants reverse the sign of their reference vector (**R**=–1 with the minus sign meaning that **R** is pointing from the nest to the feeder) and walk until **R**–**C** has again become zero. Then they should have arrived at the feeding site.

The egocentric nature of the path-integration process makes it vulnerable to the accumulation of errors. This problem gets larger the longer the foraging journey lasts (Müller and Wehner, 1988). The ants compensate for this error-proneness of the path integrator by making additional use of route-defining and nest-defining landmarks (Collett et al., 1992; Wehner et al., 1996; Bisch-Knaden and Wehner, 2003; for Australian desert ants *Melophorus bagoti* see Kohler and Wehner, 2005).

In experiments designed to let the information provided by the path integrator compete with information gained by familiar landmarks, the latter is able to override the path integrator (Sassi and Wehner, 1997), but by itself does not reset it (Andel and Wehner, 2004). For example, in one experiment (Knaden and Wehner, 2005) the entrance to a nest of *Cataglyphis fortis* was conspicuously marked by an array of landmarks, a set of four large black cylinders positioned around the nest entrance. After the ants had been trained to shuttle back and forth between the feeder and the nest, they were displaced from the feeder to an unfamiliar test area. Upon release they immediately set off in their prior home direction and after having arrived at the vector-defined fictive position of the nest ($\mathbf{P}_{\mathrm{V}}$), started a systematic search for the non-existing nest. At this time, the familiar nest-defining landmark array was quickly installed some metres to the side of the fictive position of the nest. The ants directly headed for the landmarks and searched narrowly at the landmark-defined position ($\mathbf{P}_{\mathrm{L}}$) of the (again non-existing) nest. The question now was whether the search at the $\mathbf{P}_{\mathrm{L}}$ did reset the path integrator such that the position of the nest would now be defined by $\mathbf{P}_{\mathrm{L}}$ rather than by $\mathbf{P}_{\mathrm{V}}$. The answer was a clear no. After the landmarks were removed again, the ants did not continue their search at $\mathbf{P}_{\mathrm{L}}$, but switched back to $\mathbf{P}_{\mathrm{V}}$. Hence the landmarks had been clearly used by the ants as stimuli defining the position of the nest (as the ants' intensive search there had shown), but they had not been sufficient to reset the path integrator. What cues are finally involved in the resetting process? This is the question addressed in the present account.

The experimental paradigm to answer this question was to train ants to a feeder and then capture the ants at the feeder and release them into the nest directly. By doing this, the ants were not allowed to run off their home vector on their own and therefore entered the nest with a home vector at the normal feeder state. The following outbound runs should tell us, whether the stay in the nest resets the path integrator of the ants to zero-vector state and whether the ants were able to reload their vector pointing towards the feeder.

Materials and methods

Experiments 1 and 2

At our Maharès field site (Tunisia) we trained ants (*Cataglyphis fortis* Forel 1902) to a feeder (a piece of watermelon provided with some crumbs of biscuits) 8 m south of the nest entrance (Fig. 1A). The trajectories of ants were recorded by the use of a grid of lines painted on the flat ground at 1-m intervals, and by tracing the paths of the ants on paper sheets provided with a 100:1 reduction of the grid. We stopped the recordings when the ants started a systematic search, i.e. when they slowed down and turned by about 90° for at least 1 m. The trajectories were later digitized.

In Experiment 1 we examined whether the immediate vicinity of the nest, with all its surrounding characteristics, be they visual or olfactory, suffices to reset the ant's path integrator. The ants were captured at the feeder and released directly at the nest entrance, i.e. less than 2 cm away from it. Untreated ants that moved from the nest to the feeder served as controls.

In Experiment 2, ants that had been trained in the same way as the ones in Experiment 1 were again captured at the feeder, but now forced to enter the nest. They were placed under an inverted jar on top of the nest entrance. The jar was removed after the experimental animals had disappeared into the nest. It took more than 2 min before this could be achieved and all ants had finally entered the nest. We then removed the feeder and recorded the ants' paths when they left the nest for the first time after they had been forced to enter it. In the following we will refer to these ants as 'reset ants'. Again untreated ants that moved from the nest to the feeder served as controls.

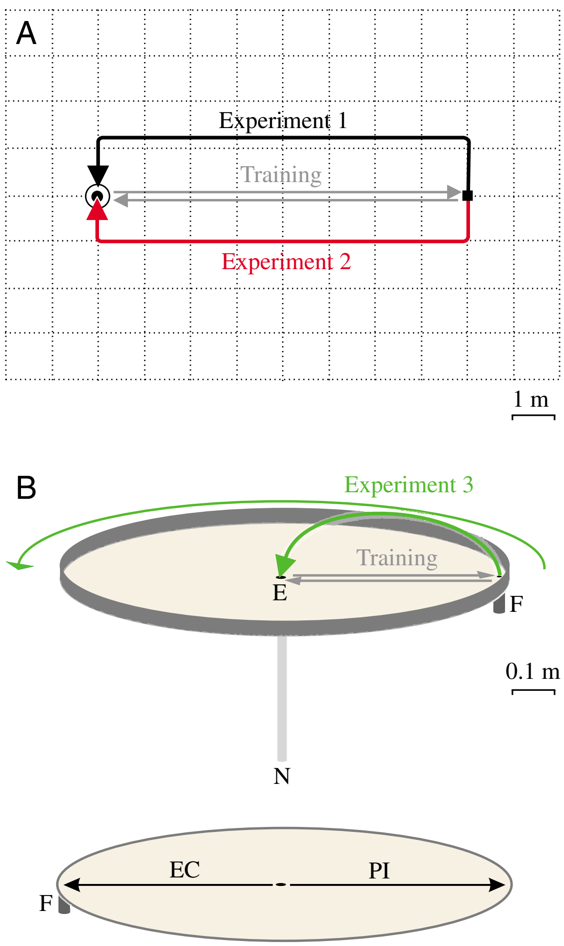

Fig. 1. Experimental design. (A) Training (grey arrows) and test situations in Experiments 1 and 2. Filled circle, nest entrance; open circle, close vicinity of the nest; filled black square, feeder, nest-to-feeder distance, 8 m. Experiment 1 (black arrow): ants were captured at the feeder and released close to the nest entrance; Experiment 2 (red arrow): ants were captured at the feeder and released into the nest entrance. (B) Training (grey arrows) and test situations in Experiment 3. N, natural nest entrance; E, nest entrance on the arena (diameter, 1 m) enforced by a metal tube; F, feeder trap. Experiment 3 (green arrows): ants were released from the feeder trap into the nest entrance and the arena was turned by 180° (lower diagram); PI arrow, walking direction defined by path integration (after a 180° turn of the arena); EC arrow, walking direction defined by arena-specific external cues.

Experiment 3

If in Experiments 1 and 2 the reset ants should actually head towards the feeder, they could do so by relying on familiar landmarks or odour cues present along their route from nest to feeder. In order to control for such effects and to test whether any potential feeder-heading behaviour of outbound ants was the result of information from the ant's path integrator, we designed an experimental set-up that allowed us to exclude any external cues. A circular wooden arena (1 m diameter, with a 5 cm grid marked on it) was placed on top of a *Cataglyphis* nest (Fig. 1B). The natural nest entrance was connected with the centre of the arena by a vertical metal pipe (diameter: 2 cm, length: 0.4 m), so that all nest-leaving ants entered the arena through this pipe. The inner walls of the pipe contained small twigs, so that the ants could easily ascend inside the pipe. A brown plastic barrier (height: 3 cm) at the outer border of the arena prevented the ants from escaping and excluded any view of landmarks. A feeder trap filled with biscuit crumbs was installed by connecting a screw top jar down under a hole (diameter: 1 cm, distance from nest: 0.48 m) in the arena. During training, the ants were allowed to leave the feeder trap by a paper ladder. Ants that had reached the feeder were individually marked by a two-colour code. When one to three ants continuously shuttled back and forth between nest and feeder, their runs to the feeder were recorded by a digital camcorder. The position of the camcorder was changed continuously in order not to be used as a landmark. We removed the paper ladder from the feeder and waited until the focus ants were trapped inside the feeder jar. The whole arena was turned by 180° in order to prevent the ants from using any arena attached orientation guides (as there might have been odours or small optical irregularities in the arena's ground or border). In order to prevent the ants from using proprioceptive cues when leaving the nest, we also changed the arrangement of the twigs within the pipe connecting the nest with the arena. We then carefully poured the ants out of the feeder glass directly into the metal pipe and video tracked the first emergence of the reset ants.

Experiment 4

Should the previous sets of experiments indeed show that the ants did reset their path integrator once inside the nest, Experiment 4 should help us to identify the nest-specific resetting cues. Ants that were trained and captured as those in Experiments 1 and 2 were now put into small cages placed directly into the nest entrance. These cages were small plastic tubes (diameter: 0.7 cm) with ends that were closed with metal mesh (mesh width: 0.8 mm). By placing these cages into the nest entrance, the ants were able to antennate with nestmates and to be exposed to possible nest-entrance specific odours (be they volatile or attached to the walls of the nest entrance). A black cover darkened the nest entrance and the cages. After 5 min the cover was removed and the upper mesh was opened. As soon as the ants left the cages, we removed the cages and recorded the trajectories of the ants as described above. Of course, in this experiment the ants captured at the feeder and put into the cages were not provided with food crumbs.

Data analysis

For Experiments 1, 2 and 4, we cut the trajectories at their first crossing of a fictive 6-m circle around the nest entrance. The sinuosity of the runs was computed by dividing the ant's path length by the bee-line distance between nest and recording circle, i.e. by 6 m. Directionality (with nest-to-feeder direction being defined as 0°) and sinuosity of the experimental animals were compared with the corresponding data of the control animals (circular statistics: Rayleigh test and Watson-Williams test; linear statistics: Student's *t*-test).

In Experiment 3, the trajectories were cut at their first transgression of a 0.4 m circle around the nest entrance. An ant's last outbound run performed before the reset was taken as a control and its sinuosity and directionality were compared with those of the first run after the reset. As there are no tests available for paired circular data, we used the same circular statistics as above and the paired Student's *t*-test for the linear statistics.

Results

Does the close vicinity of the nest reset the path integrator?

In Experiment 1 we tested whether the direct vicinity of the nest suffices to reset the path integrator of the ants to zero state. The 15 ants that were taken at the feeder and were released near the nest entrance never entered the nest directly. Rather, they headed towards the fictive nest as defined by their path integrator, ran off their home vector and started a systematic search for the nest within an 8.1±1.4 m distance from the real nest (the nest–feeder distance was 8.0 m). By this they differed dramatically from the untreated ants that were tracked on their way from the nest to the feeder (Fig. 2; test ants, N=15; mean direction, 180°; r=0.992; Rayleigh test: P<0.001; control ants, N=40; mean direction, 4°; r=0.936; Rayleigh test: P<0.01; difference between both groups, Watson-Williams test: P<0.001). Hence, the close vicinity of the nest with all its possible cues such as nest odour, nest surrounding landmarks, and nestmates rushing in and out the entrance hole is not able to reset the ant's path integrator. Is the inside of the nest able to do so?

Do reset ants still follow their home vector after they have been inside of the nest?

Ants were captured at the feeder and, without having performed their inbound runs were placed directly into the nest (reset ants). Within 6 h, 17 of the 20 reset ants left the nest again. The directions of their well-directed trajectories (Fig. 2; mean direction, 0°; N=17; r=0.914; Rayleigh test: P<0.001) in Experiment 2 did not differ from those of the control ants, either in mean direction or in standard deviation (Watson-Williams test, P>0.05), but revealed a higher sinuosity of 1.95±0.59 (compared with 1.09±0.15 in the control; Student's *t*-test: P<0.0001). None of the ants headed

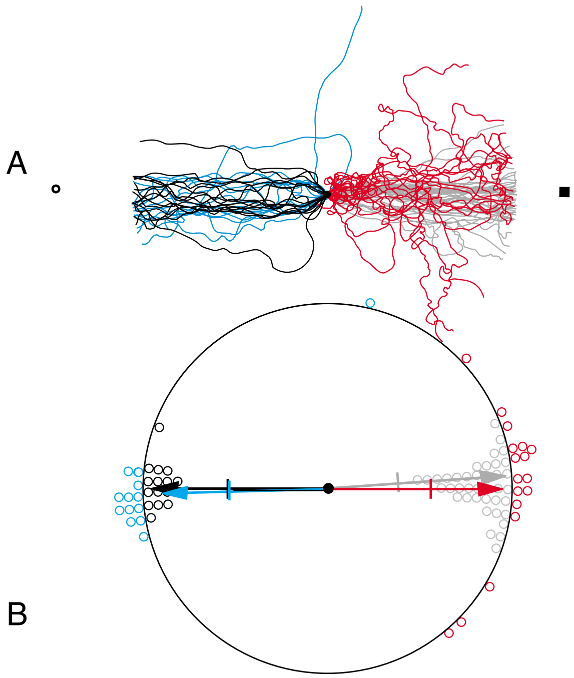

Fig. 2. Experiments 1, 2 and 4. (A) Filled circle, nest entrance; open circle, position of fictive nest when path integrator has not been reset; square, position of feeder or fictive feeder when path integrator has been reset. Black lines, trajectories of ants released close to the nest (*N*=15); red lines, trajectories of ants reset into the nest (*N*=17); blue lines, trajectories of ants released in cages into the nest entrance (*N*=16); grey lines, trajectories of control ants, heading to the feeder (*N*=40). All runs were cut to the first transgression of a 6 m circle around the nest entrance. (B) First intersections of trajectories with a 6 m circle around the nest entrance. Open circles, first intersections; black, Experiment 1; red, Experiment 2; blue, Experiment 4; grey, control; arrows give the mean direction and the directionality with the radius of the large circle meaning a maximum concentration with *r*=1 and the marker denoting the border of significance with *P*=0.01.

in the direction opposite to that of the feeder, as was the case in Experiment 1, in which the ants did not enter the inside of the nest but were released close to it. Hence there must be cues inside the nest that enable the ants to reset their path integrator. The result that reset ants in Experiment 2 showed a preference direction towards the feeder indicates that the path integration vector pointing towards the feeder had been reloaded, or it could just be due to the guidance by landmarks, which the ants had learned during their preceding foraging journeys. Experiment 3 was designed to test whether the path integrator sufficed to guide the ants towards the feeder, even though the ants had not yet performed the return from the feeder.

Are the feeder-directed runs of reset ants caused by path integration alone?

Again we placed ants from the feeder directly into the nest. Now, however, any possible guidance cues such as odours or landmarks were excluded by the use of a turnable circular arena, which had the nest entrance in the centre and the feeder at its border (Fig. 1B). The result was as clear-cut as before: as in Experiment 2 the reset ants showed a clear preference direction towards the feeder (Fig. 3A, outbound runs under control condition: mean direction, 356°; *N*=20; *r*=0.887; Rayleigh test: $P<0.001$; outbound runs after reset: mean direction, 6°; *N*=20; *r*=0.66; Rayleigh test: $P<0.001$; difference between groups, Watson-Williams test: $P>0.5$). Because of the turning of the arena, the preference direction exhibited by the reset ants was directly opposite to any possible arena-bound cues. Therefore, the ants' directional choices must have been exclusively mediated by the ants' path integrator. One could have expected that the missing or even misleading external cues could have resulted in a higher sinuosity of the reset ants. However, this was not the case. There was no difference in the sinuosity values between ants tested under both conditions (control condition: 1.5±0.5; reset condition: 1.29±0.12; Student's paired *t*-test: *P*=0.13).

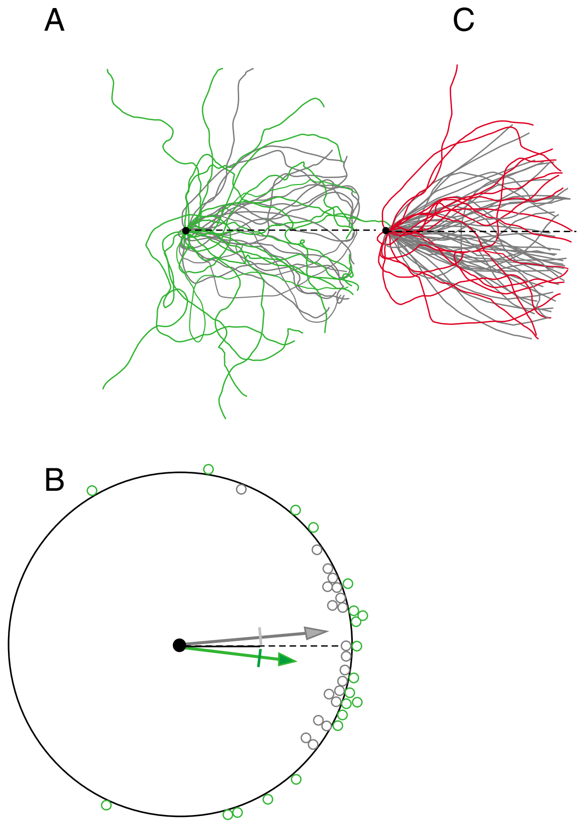

Fig. 3. (A) Outbound runs of ants leaving the nest in Experiment 3. Green (grey) lines, trajectories of ants in reset (control) condition [*N*=20 (20)]; filled black circle, nest entrance; all runs were cut to the first transgression of a 0.4 m circle around the nest entrance. (B) First intersections of trajectories with a 0.4 m circle around the nest entrance. Open green (grey) circles, first intersections in reset (control) condition, arrows give the mean direction and the directionality with the radius of the large circle meaning a maximum concentration with *r*=1 and the marker denoting the border of significance with *P*=0.01; broken line, nest-to-feeder direction. (C) Outbound runs of ants in Experiment 2 cut at 0.4 m. Red (grey) lines, trajectories of ants in reset (control) condition [*N*=17 (40)].

Which are the nest-bound cues that reset the path integrator?

Having shown that cues inside the nest did reset the ant's path integrator, we tried to specify these cues by conducting Experiment 4. The ants were trained as in Experiments 1 and 2, and were again captured at the feeder, but were now released into small cages positioned in the nest entrance hole that allowed antennal contacts with the walls of the nest entrance and with nestmates, for 5 min. Such contacts were in fact observed. After the cage had been opened, the ants could have either followed their home vector (i.e. the path integrator had not been reset by the ants' stay in the nest entrance), or they could have moved directly into the nest (the path integrator had been either reset or at least overridden by the nest cues), or they could have headed directly towards the feeder (the path integrator had been reset, and the feeder vector had been reloaded).

The ants behaved according to the first hypothesis. When they were allowed to leave the cage, only 4 out of 20 ants directly entered the nest, while 16 ants behaved as the ants had done in Experiment 1: they exhibited their home vector and ran for 7.2±2.2 m (N=16) towards the fictive nest (mean direction, 181°; N=16; r=0.917; Rayleigh test: P<0.001). Obviously, the intensive antennal contacts with nestmates and with the material of the entrance hole had not been sufficient for resetting the path integrator, even if the ants were exposed to this situation for 5 min in darkness, as is typical for the nest interior.

Discussion

In recent research on insect navigation, studies on path integration have often held centre stage (for reviews, see Wehner, 1992; Collett and Collett, 2000; Wehner and Srinivasan, 2003). In keeping with the formalism outlined in the Introduction, ants frequently returning to the same feeding site acquire a reference vector **R** pointing towards the feeder when the ants are at the nest and pointing at the nest when the ants are at the feeder. They then move from either nest or feeder until the current state **C** of their path integrator has reached the state defined by the reference vector, i.e. until **R**–**C**=0. What, however, happens when the ants have run off, say, their home vector, i.e. when their path integrator is at zero state, but the nest has not been reached yet, but is reached only later?

In order to address this question we asked whether nest-bound cues were able to reset the path integrator even if **R** does not yet equal **C**.

As we expected from our previous work cues associated with the close vicinity of the nest did not suffice to reset the ant's path integrator. When ants were captured at the feeder and released close to the nest, they followed their still existing home vector (**C**=0) and departed from the nest (Fig. 2A). Actually, one of the 15 ants even stumbled into the entrance hole of the nest, but hurried out immediately and ran off its home vector.

However, when we changed the experimental paradigm just by the detail that now the ants were forced to enter the nest entrance instead of being released close to it, the result changed dramatically. In Experiment 2 all ants that reappeared within 6 h at the nest entrance now headed towards the feeder, that is, had turned their running direction by 180° compared to the one of their former home vector (Fig. 2A). One could argue that in this time period the vector information had decayed. This, however, is extremely unlikely as it has been shown that vector information lasts for more than 2 days (Ziegler and Wehner, 1997). Repeating this experiment on a circular arena that was free from visual landmarks confirmed that this directionality was the result of path integration and not guided by any external cues (Fig. 3). In terms of the model described above, the ants had now reset their current vector **C** from 0 (feeder state) to 1 (nest state), while the reference vector **R** had remained constant.

When the ants were transferred to dark cages and exposed there to nest odour and antennal contacts with nestmates, their path integrator was not reset. We, therefore, cannot yet define the decisive cues that cause the resetting process inside the nest.

In hamsters, Etienne et al. (2004) showed that an episodic view of a learned landmark array is able to reset the animal's path integrator. As the hamster's path integration system is based completely on idiothetic cues, path integration in hamsters is much more susceptible to cumulative errors (Mittelstaedt and Mittelstaedt, 1973; Benhamou et al., 1990). In a similar experiment, Knaden and Wehner (2005) exposed *Cataglyphis* ants to a situation in which the position, at which the ant's path integrator was at zero-state, did not coincide with the position of the nest as marked by the familiar landmark panorama (see Introduction). Contrary to what was observed in the hamsters, the landmarks did not suffice for resetting the path integrator. This result again underlines the predominant role path integration based on external (celestial) compass cues plays in *Cataglyphis*. As our present data show, only cues bound to the inside of the ants' colony are able to reset the path integrator.

What might be the ultimate reason for the reset of the path integrator inside the nest?

The egocentric nature of path integration results in a progressive accumulation of errors when foraging journeys last too long (Mittelstaedt and Mittelstaedt, 1973; Müller and Wehner, 1988; Wehner and Wehner, 1990). Because of these errors, at the end of the journey the position of the nest, as defined by the path integrator, might not coincide with the actual position of the nest. As long as the accumulated errors do not become too large, the ants will at least reach the vicinity of the nest, where they will then be guided home by the aid of nest-surrounding external cues. However, when being guided to the nest by these cues, the path integrator is still running (Andel and Wehner, 2004), so that when the ants finally enter the nest, the path integrator is not at zero state anymore. Let us now assume that there would be no reset occurring within the nest: as the reference vector pointing from the nest towards the feeder is always the reverse of the reference vector pointing from the feeder towards the nest (Collett et al., 1999; Wehner et al., 2002), the next foraging trip would not point exactly at the feeder, but would be affected by the errors that had accumulated during the ant's last inbound journey. Therefore, on consecutive foraging trips path integration errors would steadily increase, and the information about the nest–feeder (and feeder–nest) vector would increasingly deteriorate. Hence, during a forager's lifetime repeated calibrations of the path integrator are indispensable. As the nest provides an ant with specific and clearcut visual, tactile, olfactory and social cues, it is certainly the best place at which the path integrator could be reset reliably.

Dyer et al. (2002) describe that when bees are captured at a feeder to which they have been trained before and released there 3 h thereafter, their vanishing directions depended on the filling state of their crops. With their crops filled the bees headed towards the nest, whereas they headed in the direction opposite to the nest, when their crops were only partially filled or empty. As to the latter group, Dyer et al. (2002) suggested "that the bees had determined that they were home and needed to fly toward the food, ...", i.e. that they had reset their current vector to the nest state. This suggestion would imply that the bee actually being at the feeder behaved as if it were at the nest. Rather, we prefer the alternative hypothesis put forward by Wehner (2003) that the bees having not yet been completely successful at the feeder, and hence still being in their foraging mode, would continue to venture out further in the former foraging (nest-to-feeder) direction. This hypothesis is strongly supported by the foraging strategy of *Cataglyphis* ants (Wehner et al., 2004). Almost every ant returned to a site from which they have retrieved a food item in the immediately preceding foraging run. If next time they are unsuccessful there, they continue their search in the former foraging direction. In terms of the path integration concept mentioned above this means that the ant's path integrator keeps running, i.e. the current vector **C** increases. Finally, if the ant has found a food item at a new site, the state of the path integrator defines a new reference vector **R**. In summary, the ant's path integrator keeps running throughout. There is no need to assume that the animal resets its path integrator to the nest state when it leaves the feeder unsuccessfully. Furthermore, in a particularly well designed experimental paradigm Andel and Wehner (2004) showed that it is next to impossible to reset the ant's path integrator, as long as the ant is outside the nest.

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References

Andel, D. and Wehner, R. (2004). Path integration in desert ants, *Cataglyphis*: how to make a homing ant run away from home. *Proc. R. Soc. Lond. B* **1547**, 1485-1489.

Benhamou, S., Sauvé, J. P. and Bovet, P. (1990). Spatial memory in large-scale movements: efficiency and limitation of the egocentric coding process. *J. Theor. Biol.* **145**, 1-12.

Bisch-Knaden, S. and Wehner, R. (2003). Landmark memories are more robust when acquired at the nest site than en route: experiments in desert ants. *Naturwissenschaften* **90**, 127-130.

Collett, M. and Collett, T. S. (2000). How do insects use path integration for their navigation*? Biol. Cybern.* **83**, 245-259.

Collett, M., Collett, T. S. and Wehner, R. (1999). Calibration of vector navigation in desert ants. *Curr. Biol.* **16**, 1031-1034.

Collett, T. S., Dillmann, E., Giger, A. and Wehner, R. (1992). Visual landmarks and route following in desert ants. *J. Comp. Physiol. A* **170**, 435-442.

Dyer, F. C., Gill, M. and Sharbowski, J. (2002). Motivation and vector navigation in honey bees. *Naturwissenschaften* **89**, 262-264.

Etienne, A. S., Maurer, R., Boulens, V., Levy, A. and Rowe, T. (2004). Resetting the path integrator: a basic condition for route-based navigation. *J. Exp. Biol.* **207**, 1491-1508.

Hartmann, G. and Wehner, R. (1995). The ant's path integration system: a neural architecture. *Biol. Cybern.* **73**, 483-497.

Knaden, M. and Wehner, R. (2005). Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator? *Anim. Behav.* doi: 10.1016/j.anbehav.2005.03.030

Kohler, M. and Wehner, R. (2005). Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: How do they interact with path-integration vectors? *Neurobiol. Learn. Mem.* **83**, 1-12.

Mittelstaedt, H. (1983). The role of multimodel convergence in homing by path integration. *Fortschr. Zool.* **28**, 197-212.

Mittelstaedt, H. and Mittelstaedt, M.-L. (1973). Mechanismen der Orientierung ohne richtende Aussenreize. *Fortschr. Zool.* **21**, 46-58.

Müller, M. and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.

Sassi, S. and 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. (1983). Foraging ecology and colony strtucture of two sympatric species of desert ants, *Cataglyphis bicolor* and *Cataglyphis albicans.* Dissertation, Universität Zürich.

Wehner, R. (1982). Himmelsnavigation bei Insekten. Neurophysiologie und Verhalten. *Neujahrsblatt Naturforsch. Ges. Zürich* **184**, 1-132.

Wehner, R. (1992). Arthropods. In *Animal Homing* (ed. F. Papi), pp. 45-144. London: Chapman and Hall.

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *J. Comp. Physiol. A* **189**, 579-588.

Wehner, R. and Srinivasan, M. V. (2003). Path integration in insects. In *Biological Basis of Navigation* (ed. K. Jeffery), pp. 9-30. Oxford: Oxford University Press.

Wehner, R. and Wehner, S. (1990). Insect navigation: use of maps or Ariadne's thread? *Ethol. Ecol. Evol.* **2**, 27-48.

Wehner, R., Harkness, R. D. and Schmid-Hempel, P. (1983). Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). Stuttgart, New York: Fischer.

Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: Coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.

Wehner, R., Gallizi, K., Frei, C. and Vesely, M. (2002). Calibration processes in desert ants navigation: vector courses and systematic search. *J. Comp. Phys. A* **188**, 683-693.

Wehner, R., Meier, C. and Zollikofer, C. (2004). The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. *Ecol. Entomol.* **29**, 240-250.

Ziegler, P. E. and 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.