

## Do familiar landmarks reset the global path integration system of desert ants?

M. Collett<sup>1</sup>, T. S. Collett<sup>2,\*</sup>, S. Chameron<sup>3</sup> and R. Wehner<sup>4</sup>

<sup>1</sup>Department of Zoology, Michigan State University, East Lansing, MI 48824, USA, <sup>2</sup>School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK, <sup>3</sup>Laboratoire Ethologie Expérimentale et Comparée, CNRS – FRE 2413, Université Paris Nord, 99, avenue Jean-Baptiste Clément, 93430 Villetaneuse, France and <sup>4</sup>Department of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

\*Author for correspondence (e-mail: t.s.collett@sussex.ac.uk)

Accepted 26 November 2002

### Summary

It is often suggested that animals may link landmark memories to a global coordinate system provided by path integration, thereby obtaining a map-like representation of familiar terrain. In an attempt to discover if desert ants form such associations we have performed experiments that test whether desert ants recall a long-term memory of a global path integration vector on arriving at a familiar food site. Ants from three nests were trained along L-shaped routes to a feeder. Each route was entirely within open-topped channels that obscured all natural landmarks. Conspicuous artificial landmarks were attached to the channelling that formed the latter part of the route. The homeward vectors of ants accustomed to the route were tested with the foodward route, either as in training, or with the first leg of the L shortened or extended. These ants were taken from the feeder to a test area and released, whereupon they performed a home vector. If travelling the latter part of a familiar route and

arriving at a familiar food site triggers the recall of an accustomed home vector, then the home vector should be the same under both test conditions. We find instead that the home vector tended to reflect the immediately preceding outward journey. In conjunction with earlier work, these experiments led us to conclude in the case of desert ants that landmark memories do not prime the recall of long-term global path integration memories. On the other hand, landmark memories are known to be linked to local path integration vectors that guide ants along a segment of a route. Landmarks thus seem to provide procedural information telling ants what action to perform next but not the positional information that gives an ant its location relative to its nest.

Key words: familiar landmark, memory, global path integration system, desert ant, *Cataglyphis fortis*.

### Introduction

Many insects use some form of an odometer and compass to monitor changes in their position (for reviews, see Wehner and Wehner, 1986; Wehner, 1992; Collett and Collett, 2000). An insect can obtain a record of its current distance and direction from a starting point by continuously updating a path integration (PI) accumulator. In honeybees and desert ants, it is thought that a forager initialises a global PI accumulator at its nest, and updates this accumulator until it decides to return to its nest, for instance on finding food (Wehner and Wehner, 1986; Collett and Collett, 2000). The use of this global PI information can be seen in the ‘global vectors’ of the desert ant *Cataglyphis* (sp.) when it follows straight trajectories of the appropriate direction and distance from a food site back to the nest (Wehner and Srinivasan, 1981; Müller and Wehner, 1988) and from the nest back to a food site (Schmid-Hempel, 1984; Collett et al., 1999; Wolf and Wehner, 2000). The appropriate global vectors are produced even in unfamiliar territory, providing proof that the guidance is by global PI rather than landmarks (Piéron, 1907; Wehner and Srinivasan, 1981). In

honeybees, global PI use is also seen in the waggle dance, by which a forager communicates the direction and distance of a food site to other foragers (for reviews, see von Frisch, 1967; Dyer, 2002).

Insects can have long-term memories of global PI information. A desert ant taken while foraging at a permanent feeder and held in darkness for 24 h appears to retain some memory of a home vector (Ziegler and Wehner, 1997). That honeybees have long-lasting PI memories can be deduced from the occasional spontaneous dances that bees performed in the middle of the night, signalling feeder sites that they had visited the previous day (Lindauer, 1960). There is reason to believe that honeybee global PI memories may be cumulative, by which we mean that through visiting a site over many occasions, a long-term PI memory may be gradually refined or reinforced. The best evidence comes from an intriguing ‘catch-up’ phenomenon (Lindauer, 1963; von Frisch, 1967; Gould, 1984; Dyer, 1987). If bees are trained to a feeder along a route marked by prominent landmarks, and then the feeder and

landmarks are shifted to make an angle of 30° with the initial route, the waggle dances indicating the feeder do not shift suddenly. Instead, at first the dances continue to signal the initial feeder position, and then over a period of 40 min the direction signalled by the dance shifts gradually to indicate the displaced feeder position. This gradual catch-up has been interpreted to reflect a running average of the global PI values at the feeder position over the previous 40 min period (Lindauer, 1963; von Frisch, 1967; Gould, 1984), although other interpretations of the data are possible. Such gradual updating would suggest a cumulative global PI memory of the feeder position. The present work addresses whether a cumulative global PI memory might exist in desert ants and, if so, whether such a cumulative global PI memory is associated with landmark memories and can be recalled when the associated landmarks are viewed. Our experiments were designed to test whether such a putatively recalled cumulative memory is used to reset the global PI system to its accustomed state at a recognised location.

When considering PI memories, it is important to distinguish between global and local PI vectors. Both ants and bees store views of landmarks in the immediate neighbourhood of a feeding site (Anderson, 1977; Cartwright and Collett, 1983; Wolf and Wehner, 2000). On a familiar route, these insects can link the memory of a landmark to a memory of the direction and/or distance of the subsequent path segment (Collett et al., 1993; Srinivasan et al., 1997). A 'local vector', reflecting a short path segment, can be triggered by a landmark at the beginning of the segment (Collett et al., 1993, 1996, 1998, Srinivasan et al., 1997), or by the completion of the previous path segment (Collett et al., 1993). Guidance of local vectors is likely to involve PI (Srinivasan et al., 1997), and appears to use the same environmental cues as global PI, both for the directional (Collett et al., 1998) and distance (Srinivasan et al., 1997) components. Unlike the global vectors that are observed when foragers are displaced to unfamiliar territory, local vectors seem only to be expressed within the appropriate panoramic context of the route segment (Collett et al., 2002). In the appropriate context, recognition of a familiar landmark may trigger a cumulative PI memory (Chittka et al., 1995), but current data suggest that it would be a local PI vector of the next path segment, not the global PI vector that is recalled (Collett et al., 1998).

A number of studies have already investigated whether a desert ant that experiences familiar views along a habitual route segment will recall a cumulative global PI memory and use the recalled memory to reset its global PI system to the habitual state at the recognised location (Sassi and Wehner, 1997; Collett et al., 1998; ?. Bisch-Knaden and R. Wehner, manuscript submitted). In these studies, ants were trained along a route marked by fixed landmarks, so that the recognition of a specific landmark could be associated with a particular state of the ant's global PI system. For tests, the trajectory was altered, so on reaching a familiar landmark on the homeward route an ant would have an unaccustomed global PI state. The question asked was whether the act of recognising a familiar

landmark would cause the global PI system to be reset to its accustomed state on encountering the landmark. The mismatch between landmark position and accustomed global PI state at the landmark was achieved in three ways. In one, the foodward route was altered (Sassi and Wehner, 1997). In a second, the foodward route was normal and the homeward route was altered (Collett et al., 1998). In a third, the ants were made to repeat the homeward trajectory after being captured near the nest at the end of a normal homeward trajectory (Collett et al., 1998). In both the last two conditions the landmarks elicited the performance of local vectors, so it was clear that the ants recognized the landmarks. Nevertheless, none of these studies found any evidence that the global PI system had been reset by the landmarks.

The results of the previous studies suggest that familiar landmarks on the way home do not trigger or reset a homeward global vector. They still leave open the question of whether landmarks on the foodward route, or arrival at a familiar food site, might be used to reset the global PI system or trigger the recall of a homeward global vector. The aim of the present experiments was to answer this question. Ants were trained to a feeder along channels in an L-shaped route. The second half of the route was conspicuously marked with landmarks. After extensive training along this route, ants were given an altered route with the same conspicuous landmarks in the second half, but with the first half lengthened or shortened to change the overall length of the route. The ants' homeward trajectories were then recorded on an open test field to see whether the trajectories reflected the trained or the altered route. If a forager resets its global PI system using a cumulative PI memory associated with the familiar food site, then the homeward global vector would reflect the trained rather than the altered route. If the homeward vectors instead reflect the altered routes, it would indicate that a cumulative global PI memory is not used for the homeward trajectory.

### Materials and methods

We studied foragers from three nests of the desert ant *Cataglyphis fortis* Forel on flat, sandy ground near Mahares, Tunisia, in July and August 2001. Ants were trained from the nest to a feeder along routes in which all landmark and panoramic context information could be controlled. A plastic barrier surrounded each nest restricting the ants' exit so that almost all the active foragers followed the experimentally defined route. The ants travelled along an L-shaped route to a feeder (Fig. 1), through channels that hid the surrounding natural environment. The second half of the route was marked with prominent landmarks, to promote familiarity during the approach to the feeder. The effects of recognising landmarks on the possible recall of a cumulative global PI memory was tested by altering the length of the first half of the route to the feeder, and then testing the homeward vectors of experienced ants captured at the feeder. Ants were marked on their first day at the feeder and were trained for a minimum of 4 days before being tested on an altered route.

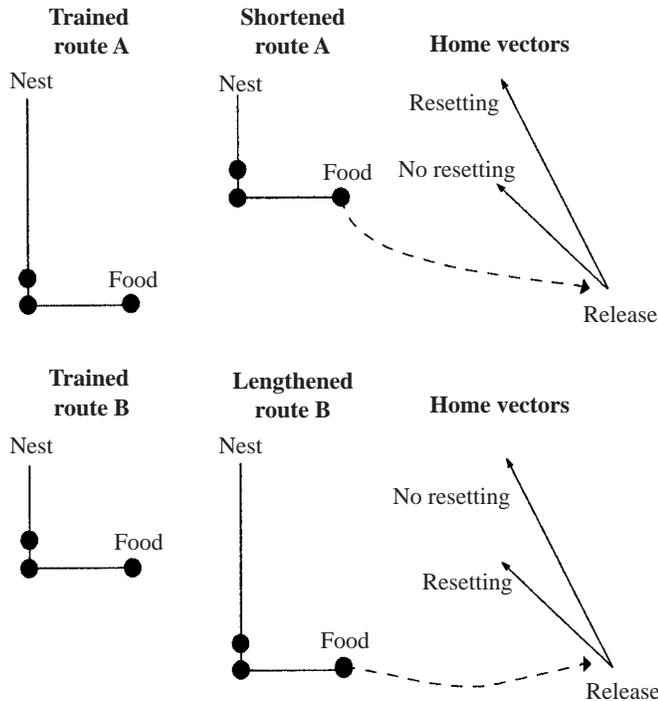


Fig. 1. Experimental design. Left: Ants were trained to a feeding site in channels along one of two L-shaped routes (A or B) with conspicuous landmarks attached to the channels (positions marked by filled circles). Centre and right: The home vectors of experienced ants are tested after a single foodward trip in which the first part of the route was shortened (A) or lengthened (B). Dashed lines indicate that ants were carried from the feeder to the test field. The 'no resetting' arrows show the expected home vectors were the ants' paths to reflect the immediately preceding trip. The 'resetting' arrows show the expected home vectors were the ants' paths to reflect the training parameters, indicating the recall of a cumulative global PI memory established in previous trips.

To promote recognition we used both a right-angle change in direction, and a sequence of landmarks consisting of open buckets that joined sections of channelling. Two openings were cut at the bottom of the wall of each bucket into which the ends of two lengths of channel were inserted. Ants were able to view the outside of a bucket while approaching it along the channel, and then see the inside walls on entering the bucket. The bottom of each bucket was packed with sand giving an additional tactile difference between the plastic floor of the channel and the sandy floor of the bucket. The use of channels and artificial landmarks made it possible to shorten or lengthen the first leg of the route, but still give ants exactly the same visual and tactile experience when they walked along the second part of the route.

To make it easy to collect ants for testing, the channel was connected to the feeder *via* a one-way system. The channel ended in a plastic box from which ants could enter a tube leading to a feeder bucket. The tube protruded through a hole in the side of the feeder bucket, about 10 cm above the bottom, so that ants had to drop into the bucket to reach a piece of ripe

watermelon. The sides of the bucket were coated with flouon, so that the ants could not climb up again to the entrance hole. Instead, to leave, there was an exit tube at the bottom of the bucket that returned them to the plastic box. The separate entrance and exit tubes meant that, in tests, the exit tube could be blocked and ants trapped within the feeding bucket.

#### Routes A and B

For two nests, polyethylene tubes connected the enclosed nest to the plastic channels. These channels were flat-bottomed with sloping sides and had a lip at the top to prevent escape. From the middle of the channel, ants had a 90° view of the sky. The routes started with a length of channel leading into the first bucket. For nest A the length of this channel was 7 m and for nest B it was 3 m. Thereafter the routes were the same for the two nests. A further 1 m of channel from this bucket led in the same direction to a corner bucket. The first leg of the L was thus 8 m for route A and 4 m for route B. The second leg of the route from the corner bucket comprised 4 m of channel at right angles to the first.

While a route was being rearranged in order to put the ants into a test state, the exit tube from the nest was briefly blocked. The first section of channel was shortened from 7 m to 3 m for nest A and lengthened from 3 m to 7 m for nest B. The rest of the route was moved and reconnected to the shortened or lengthened channel (Fig. 1). The test route for nest A was thus equivalent to the training route of nest B, and *vice versa*. The exit from the nest was then opened and the exit from the feeder blocked.

#### Route C

To allow a faster changeover between training and testing, the arrangement used for the third nest differed from the previous routes. In this arrangement the first segment of the route from the nest comprised 5 m of channel made from wooden walls embedded into the sand, with a rectangular cross-section 20 cm wide and walls 8.5 cm high. Tubing connected a further 1 m of plastic channel continuing in the same direction as the wooden channel and leading into a corner bucket. The first leg of the route was thus a total of 6 m. The second leg of the route was another 2 m of the plastic channel leading at right angles from the corner bucket to the feeder bucket with the same one-way arrangement as in routes A and B.

To facilitate testing, we had a parallel test channel adjacent to the training channel, and removable doors in the nest closure so that ants could be funnelled into the appropriate channel. Instead of 5 m of the wooden sided channel, the test channel had 11 m of wooden channel before the configuration of buckets and plastic channels (1 m + 2 m). At first one channel was used for training and the other only for testing. Subsequently, the test channel was also shortened during training, so that the ants could then be switched between the two adjacent short (6 m + 2 m) channels every 2 h. The test channel was then lengthened before each test. The two methods gave similar results that have been pooled.

*Recording and analysing home vectors*

Ants taken at the feeders of all nests were tested in the same way. Each ant was carried in a darkened vial from the feeder to the test area 100–400 m away (depending on the nest). The test area was flat and featureless with a grid of 1 m squares painted on to it. Each ant was released individually onto the sand where there was a small sprinkling of biscuit crumbs, and the ant's path over this grid was recorded on squared paper. Since ants perform more reliable home vectors when carrying food, the ant's path was only recorded if it picked up a crumb. To avoid interference from directional errors that ants trained in channels tend to make in the middle of the day (Müller, 1989), home vectors were recorded either before 11:00 h or after 14:30 h. Ants were tested no more than once a day and tests with the lengthened or shortened routes were only every 2–3 days. Ants were trained for a minimum of 4 days before being tested on an altered route.

The recorded trajectories from the release point to where the ant started its search pattern (Wehner and Srinivasan, 1981) were digitised. The best-fitting line to a trajectory was computed by the method of principal axes (see Sokal and Rolf, 1995, p. 586). Circular statistics were used as prescribed by Batschelet (1981). The directions that are given in the text are in terms of the absolute acute angle between the compass direction of the segment of the L closest to the feeder and that of the trajectory. Trajectory lengths were taken as the distance between the start of the trajectory and the beginning of search behaviour (Wehner and Srinivasan, 1981). 95 or 99% confidence intervals (c.i.), gauged from fig. 5.2.2 in Batschelet (1981), were used to determine whether the directions of mean trajectories differed significantly from predictions.

To compare the trajectories of ants that were tested in different conditions, the endpoint of each trajectory was transformed into cartesian coordinates and a bivariate test (Hotellings  $T^2$ ) was used to decide whether the different conditions produced significantly different trajectories from the controls.

**Results***Home vectors from the trained routes A and B*

The home vectors of ants taken from the feeder after training along route A (8 m + 4 m) are shown in Fig. 2A. The directions of the home vectors ( $59.82 \pm 11.90^\circ$ , mean  $\pm$  s.d.,  $N=41$ ) are in the direction of the nest ( $62.5^\circ$ ), but their length ( $6.59 \pm 1.73$  m, 99% c.i.  $\pm 0.698$  m,  $N=41$ ) is shorter ( $P < 0.01$ ) than the real distance between feeder and nest (9.6 m). There is a similar pattern in the corresponding data for the shorter route, B (4 m + 4 m), shown in Fig. 2B. The direction of the nest ( $45^\circ$ ) falls within the 95% c.i. of the mean direction of the home vectors (mean  $49.15 \pm 12.55^\circ$ ,  $N=25$ ), but again the length ( $4.08 \pm 1.35$  m, 99% c.i.  $\pm 0.696$  m,  $N=25$ ) is too short ( $P < 0.01$ , 6.4 m). It is possible that the difference in surface between the channels and sand result in the short trajectories. These home vectors serve as controls for the lengthened and shortened tests.

*Home vectors from the shortened route A*

Home vectors recorded when the first leg of route A was shortened from 8 m to 4 m (mean direction  $40.58 \pm 10.71^\circ$ ,  $N=20$ ; mean length  $3.95 \pm 1.30$  m,  $N=20$ ) reflect the parameters of the outward trip that the ants have just taken and not the training parameters (Fig. 2A). The endpoints of shortened route A differed significantly from those of normal route A ( $T^2=58.87$ ;  $F=28.939$ ; d.f. 2,58;  $P < 0.001$ ), but the shortened endpoints did not differ from those of normal route B ( $T^2=4.26$ ;  $F=2.082$ ; d.f. 2,42;  $P=0.137$ ). These data provide no evidence that ants recall a familiar home vector when in a familiar location.

*Home vectors from the lengthened route B*

Fig. 2B shows the home vectors for ants trained to route B (4 m + 4 m) and tested with the first leg extended from 4 m to 8 m. The data were less clearcut than they were with the previous route. When the first leg of the route was extended, the length of the home vector (mean length  $5.52 \pm 1.85$  m,  $N=23$ ) increased and the direction (mean direction  $57.80 \pm 10.09^\circ$ ,  $N=23$ ) shifted in the expected direction ( $62.5^\circ$ ) (Fig. 2B). The endpoints of the lengthened route B (8 m + 4 m) differed significantly from the endpoints of the normal route B (4 m + 4 m) ( $T^2=19.28$ ;  $F=9.431$ ; d.f. 2,45;  $P < 0.001$ ) and did not differ significantly from the endpoints of training route A (8 m + 4 m) ( $T^2=4.557$ ;  $F=2.24$ ; d.f. 2,61;  $P=0.115$ ). Nonetheless, the changes were not as great as one would have expected from the complementary data of Fig. 2A. To try to understand this result further, ants from this nest were retrained with the first leg extended to 8 m. The length of the home vector then increased slightly (mean length  $6.24 \pm 1.81$  m,  $N=29$ ), but the direction (mean direction  $56.17 \pm 9.62^\circ$ ,  $N=29$ ) was essentially unchanged. The endpoints of lengthened and retrained routes B were not significantly different ( $T^2=4.33$ ;  $F=2.123$ ; d.f. 2,49;  $P=0.130$ ) (Fig. 2B). These data also provided no evidence that ants recall a familiar home vector when in a familiar location.

*Home vectors from route C*

Because the results from route B did not appear straightforward when first obtained, we decided to increase the difference between the training and test conditions. Ants from a third nest were trained to a different L-shaped route (6 m + 2 m) (Fig. 2C). As with routes A and B, the mean direction of the global vector ( $75.07 \pm 7.82^\circ$ ,  $N=27$ ) corresponded closely to the predicted direction of the nest from the feeder ( $69.6^\circ$ ). Also like routes A and B, the mean length ( $5.3 \pm 1.66$  m, 99% c.i.  $\pm 0.822$  m,  $N=27$ ) was a little shorter ( $P < 0.01$ ) than the distance between feeder and nest (6.6 m). In tests, the first leg of the route was extended from 6 m to 12 m. In this case, the direction of the vector rotated ( $83.37 \pm 12.67^\circ$ ,  $N=31$ ) to match the direction from feeder to nest ( $80.1^\circ$ ). The home vector also increased in length ( $10.90 \pm 2.32$  m, 99% c.i.  $\pm 1.073$  m,  $N=31$ ) but was again shorter ( $P < 0.01$ ) than the distance between feeder and nest (12.4 m). The endpoints of the training and lengthened routes differed significantly ( $T^2=164.93$ ;  $F=80.996$ ;

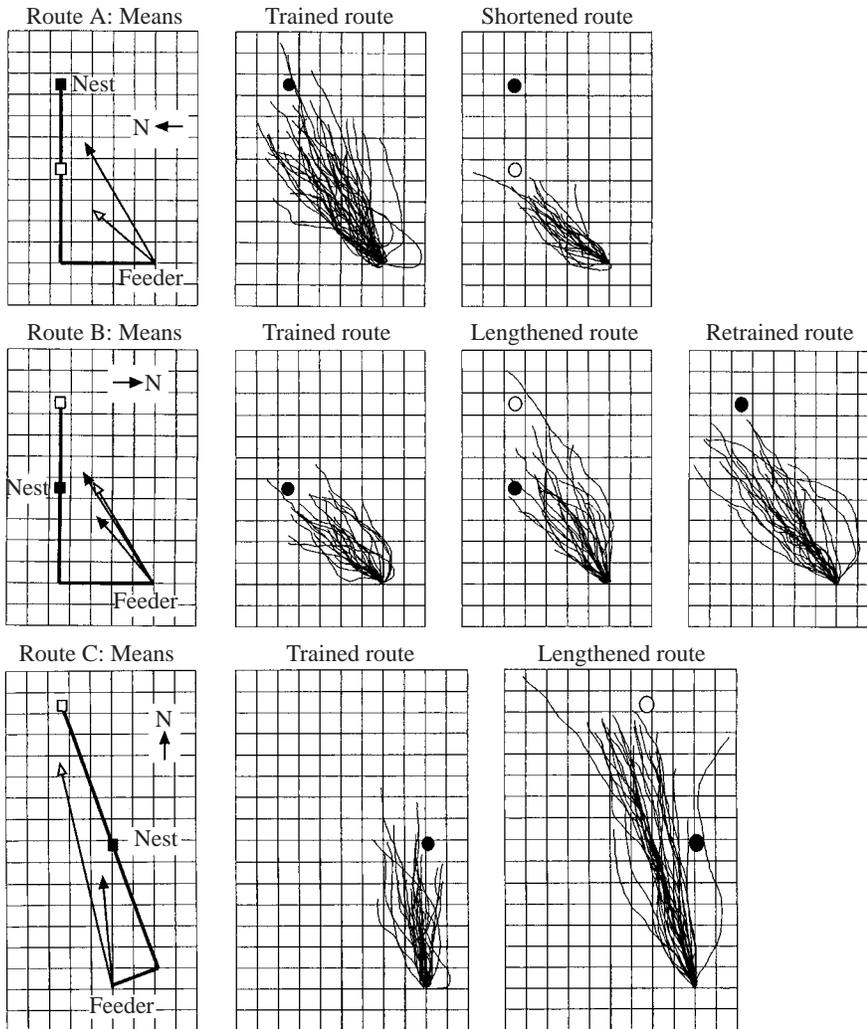


Fig. 2. Home vectors of ants taken from the feeder at the end of a trained or an altered route. The left column shows a sketch of the route, incorporating the short additional distance that the ants cover when going from the nest to the start of the channel and from the end of the channel to the feeder. The solid square shows the nest position for the trained route, and the open square shows the nest position for the altered route. The superimposed arrows show the mean home vectors of tested ants – solid arrows for the trained or retrained conditions, and open arrows for the altered routes. In the columns to the right, superimposed individually recorded home vectors are plotted from the ants' release until the start of search behaviour. The position of the nest relative to the feeder (i.e. the position of the fictive nest relative to the release site) is shown by a circle. A filled circle indicates the position for the training route, and an open circle indicates the position for an altered route. Top row, route A; middle row, route B; bottom row, route C.

d.f. 2, 55;  $P < 0.001$ ). As in the results from nests A and B, the global home vector after performing the lengthened foodward route corresponded to the parameters of the altered route rather than to those of the training route.

### Discussion

The goal of the present study was to see whether a foraging ant that reached a familiar food site, having taken a familiar route that produced an unaccustomed global PI state, would use a cumulative global PI memory for the homeward trajectory. We therefore designed a route that included, near the feeder, a stable section that was made as distinctive as possible with landmarks, and a landmark-free section that could be altered inconspicuously for testing. We saw no sign that ants tested with an extended or a contracted route were disturbed by the alteration. In particular, when the route was lengthened, ants did not hesitate at the usual position of the first landmark or corner, but continued to walk at their accustomed speed along the extra length of the landmark-less first segment. Did the landmarks in the stable section of the

route help the foragers recognise the test route as familiar? Although we have no direct evidence from this study that the landmarks were learnt, there are abundant data from previous studies that desert ants learn landmarks both along a route and around the feeder (Collett et al., 1992; Wehner et al., 1996; Wolf and Wehner, 2000), and that the recognition of familiar landmarks or route segments can elicit the recall of local vectors (Collett et al., 1998). Given our still limited understanding of how insects perceive and use landmarks, it remains possible that different landmarks might produce different results, but we believe that the ants in the present study had ample opportunity to become familiar with the landmarks and to use them to recall an associated memory.

We have shown here, then, that ants do not discard a global PI state that conflicts with their previous experiences on the way to, or at, a familiar food site. When the beginning of a well-learned route was lengthened or shortened, the ants' global homeward vector reflected the altered route rather than the habitual route. This finding complements the results of the previous studies mentioned in the Introduction, which show that also on the way back from a familiar food site, an ant does

not discard a global PI state that disagrees with its previous experiences. Taken together, these studies suggest the general conclusions that, while desert ants may suppress guidance by global PI (for instance, by following local vectors or landmarks), they do not modify a global PI state that conflicts with their previous experiences. It is still possible that ants do possess a cumulative global PI memory of a food site, but its function would have to be to provide a target for the PI navigation system during the foodward trip, reflecting long-term experience of where abundant food is to be found, rather than to give a forager its current position. It appears that the current global PI coordinates of a foraging ant are set without the aid of landmarks or of cumulative memories, and are not modified by recognising a familiar location. The use of global PI on the return trip simply allows an ant to travel home after an outward trip that may differ from previous ones.

We acknowledge financial support from the Swiss National Science Foundation, the BBSRC and the HFSP. M.C. was supported by a NIH post-doctoral NRSA fellowship.

### References

- Anderson, A. M.** (1977). A model for landmark learning in the honey-bee. *J. Comp. Physiol.* **114**, 335-355.
- Batschelet, E.** (1981). *Circular Statistics in Biology*. London: Academic Press.
- Cartwright, B. A. and Collett, T. S.** (1983). Landmark learning in bees: experiments and models. *J. Comp. Physiol.* **151**, 521-543.
- Chittka, L., Kunze, J., Shipman, C. and Buchmann, S. L.** (1995). The significance of landmarks for path integration in homing honeybee foragers. *Naturwissenschaften* **82**, 341-343.
- Collett, M. and Collett, T. S.** (2000). How do insects use path integration for their navigation? *Biol. Cybernet.* **83**, 245-259.
- Collett, M., Collett, T. S., Bisch, S., Wehner, R.** (1998). Local and global vectors in desert ant navigation. *Nature* **394**, 269-272.
- Collett, M., Collett, T. S. and Wehner, R.** (1999). Calibration of vector navigation in desert ants. *Curr. Biol.* **9**, 1031-1034.
- Collett, M., Harland, D. and Collett, T. S.** (2002). **The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees.** *J. Exp. Biol.* **205**, 807-814.
- Collett, T. S., Baron, J. and Sellen, K.** (1996). On the encoding of movement vectors by honeybees. Are distance and direction represented independently? *J. Comp. Physiol. A* **179**, 395-406.
- 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.
- Collett, T. S., Fry, S. N. and Wehner, R.** (1993). Sequence learning by honeybees. *J. Comp. Physiol. A* **172**, 693-706.
- Dyer, F. C.** (1987). Memory and sun compensation by honey bees. *J. Comp. Physiol. A* **160**, 621-633.
- Dyer, F. C.** (2002). **The biology of the dance language.** *Annu. Rev. Entomol.* **47**, 917-949.
- Gould, J. L.** (1984). Processing of sun-azimuth information by honey bees. *Anim. Behav.* **32**, 149-152.
- Lindauer, M.** (1960). Time-compensated sun orientation in bees. *Cold Spring Harbor Symp. Quant. Biol.* **25**, 371-377.
- Lindauer, M.** (1963). Kompassorientierung. *Ergebn. Biol.* **26**, 158-181.
- Müller, M.** (1989). Mechanismus der Wegintegration bei *Cataglyphis fortis* (Hymenoptera, Insecta). PhD thesis, University of Zurich.
- Müller, M. and Wehner, R.** (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.
- Piéron, H.** (1907). Du rôle sens musculaire dans l'orientation des fourmis. *Bull. Inst. Gen. Psychol.* **4**, 168-187.
- Sassi, S. and Wehner, R.** (1997). Dead reckoning in desert ants, *Cataglyphis fortis*: Can homeward vectors be reactivated by familiar landmark configurations? *Proc. Neurobot. 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.
- Sokal, R. R. and Rolf, F. J.** (1995). *Biometrics*. 3rd edition. New York: W. H. Freeman.
- Srinivasan, M. V., Zhang, S. W. and Bidwell, N. J.** (1997). Visually mediated odometry in honeybees navigation en route to the goal: visual flight control and odometry. *J. Exp. Biol.* **200**, 2513-2522.
- von Frisch, K.** (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.
- Wehner, R.** (1992). Arthropods. In *Animal Homing* (ed. F. Papi), pp. 45-144. London, New York: Chapman and Hall.
- 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. and Srinivasan, M. V.** (1981). Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol.* **142**, 315-338.
- Wehner, R. and Wehner, S.** (1986). Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. *Monit. Zool. Ital. (NS)* **20**, 309-331.
- Wolf, H. and Wehner, R.** (2000). Pinpointing food sources: Olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. *J. Exp. Biol.* **203**, 857-868.
- 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.