

The learning and maintenance of local vectors in desert ant navigation

Matthew Collett^{1,*} and Thomas S. Collett²

¹Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK and ²School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

*Author for correspondence (e-mail: matthew.collett@zoo.ox.ac.uk)

Accepted 16 December 2008

SUMMARY

The desert ant *Cataglyphis fortis* has at least three types of navigational strategy that can guide it between its nest and a familiar food site. The initial strategy after first finding a food site is based on a path integration memory of the position of the food site with respect to the nest. A second strategy is based on visual snapshot memories of features viewed from near or on the way to the food site. A third strategy uses local vector memories of the direction and length of habitual route segments. We show here that while such local vectors encode sufficient information to guide an individual along both the direction and distance of a route segment, its acquisition and long-term maintenance requires support from the other two strategies. We trained ants along an L-shaped route, designed to show that ants can learn local vectors on the way to a food site. The sharp turn appears to present particular difficulties for the ants. When low bushes 20–30 m from the route were removed, local vectors were briefly unaffected, but then deteriorated. The vectors improved again once the missing bushes were replaced by artificial landmarks. The fragility of local vector memories may permit an ant the flexibility to adapt its route to fluctuations in the distribution of its resources.

Key words: cognition, insects, navigation, spatial.

INTRODUCTION

Insects such as desert ants and honeybees acquire a variety of memories that help them return to a profitable food source. The process of path integration, by which a forager keeps track of its movement using directional cues from the sun (Rossel, 1989; Santschi, 1913; von Frisch, 1967; Wehner and Müller, 2006) and a step-based odometer (Ronacher et al., 2000; Wittlinger et al., 2006) can provide a memory of the position of a food site with respect to the nest (Collett et al., 1999; Wehner et al., 1983; Wolf and Wehner, 2000). Learning behaviour on leaving the food site provides a forager with snapshot memories of the features surrounding the food site (Collett and Lehrer, 1993; Lehrer, 1991; Nicholson et al., 1999; Tinbergen, 1932; Zeil, 1993). In addition, as a forager returns to a food site on later trips, it acquires procedural memories of the path it follows (Collett et al., 2002; Collett et al., 1996; Knaden et al., 2006; Lehrer and Collett, 1994; Srinivasan et al., 1997). Here we focused on one of these: a ‘local vector memory’ of a straight segment of a route (Collett et al., 1998) to show that it may encode the direction and length of a segment towards a habitual food site, and to examine some of the interactions that occur between it and the other navigational memories.

Our initial aim was to show definitively that the desert ant *Cataglyphis fortis* does use local vectors on their food-ward route. The various potential cues available to a desert ant on a route permit a variety of associated navigational strategies to be active, making it difficult to identify the use of a local vector unambiguously. An ant could reach the location at which a snapshot memory was acquired, for instance, if it moved so as to match the retinal position of features in a scene to the snapshot memory (Cartwright and Collett, 1983; Collett and Land, 1975; Junger, 1991; Wehner et al., 1996; Wehner and Rüber, 1979; Åkesson and Wehner, 2002). Or it could calculate a direct path to the food site by taking the difference between the remembered path integration (PI) state at the food site

and its PI state at its current location. The ‘PI output vector’ produced by this comparison encodes a direct path to the goal (Collett and Collett, 2000). To identify a local vector, an ant’s trajectory must therefore be performed in an environment where visual cues could not provide matches for snapshot memories, and manipulations must also control for the possible involvement of a PI output vector.

Several papers have described memories of visually impoverished routes acquired by ants and bees that are likely to have involved local vectors (Bisch-Knaden and Wehner, 2003; Collett et al., 2002; Collett et al., 1996; Srinivasan et al., 1997). In one study using desert ants, the existence of a local vector on a homeward route could be shown unambiguously because the local vector could also be expressed on a test ground without any familiar landmarks and could be seen to be different from a PI output vector (Collett et al., 1998). In another unambiguous study of a two-legged homeward route, carried out in a channel in order to control visual cues, trajectories in a test-channel reflected directions and distances corresponding to a local vector of the first segment rather than to a PI output vector (Knaden et al., 2006). The experiments in the present paper were designed to establish whether a desert ant could learn both the direction and distance of a route segment towards a food source. In order to control for the possible use of a PI output vector, we had to manipulate an ant’s PI state before it reached the route segment of interest. But because food-ward motivation is more fragile than homeward motivation – ants tend to return home when disturbed – the experiments were performed on terrain near the nest. To control for the possible use of snapshot-based memories, the terrain was cleared of two low bushes 20–30 m away, inadvertently revealing their importance in the long-term maintenance of local vectors.

MATERIALS AND METHODS

We worked with *Cataglyphis fortis* (Forel 1902) foragers from a single nest on a landmark-poor coastal region of Djerba, Tunisia,

during June 2007. The area is flooded during winter or spring high tides, leaving the ground flat and smooth. The nest was chosen because the ground around it was particularly flat, undisturbed and distant from vegetation that could be used as landmarks. To the north of the route, and west beyond the feeder, there were no prominent landmarks for at least 100 m. Two low clumps of bushes, approximately 2–3 m wide and 0.5 m high, located 20–30 m to the south of the route (Fig. 1) turned out to play a significant role.

Foragers were trained to follow an L-shaped route from the nest to a feeder. The nest was enclosed by a plastic barrier with a single gate through which the outward passage of foragers could be controlled. The inside of the barrier was coated with Fluon™ to prevent the ants escaping, while a sloping sand ramp built around the outside allowed foragers to return freely to the nest. The exit point from the nest led through a small tray and into a 10 m channel. The tray could be picked up and carried with an ant inside to manipulate the ant's travel along the channel. The channel was sunk into the ground so as to be invisible to an ant on open ground. During training, a ramp by which the ants exited onto open ground was placed 6 m along the channel. The channel was lined on one side by Fluon™-coated plastic that prevented ants from climbing out to head towards the feeder prematurely.

A feeder containing watermelon, and occasionally biscuit crumbs to increase motivation when numbers were low, was placed 6 m perpendicular to the channel so that, to follow the most direct route, ants would have to make a 90 deg. turn on leaving the channel. The feeder itself was also sunk into the ground so as to be invisible, but was marked by a small cylindrical landmark (10 cm by 10 cm) to help guide the ants' final approach. The prevailing north-easterly direction of the wind meant that the ants' approach trajectories did not usually pass through the odour plume from the feeder.

To train foragers from the channel to the final feeder position, over a 4 h period the feeder was gradually moved away from the ramp. After ants had become familiar with the route, occasional tests were given in which the ants and the route were manipulated in a variety of ways that are described in the Results. Testing began after the feeder had been in the final position for 3 days. In order to identify trained ants, ants that reached the training feeder were marked with an individual colour code painted on the abdomen and thorax. The trajectories in Figs 2 and 4 were collected while ants were allowed to travel freely to the feeder. During a test in which the ant or the route was manipulated, the nest entrance was closed

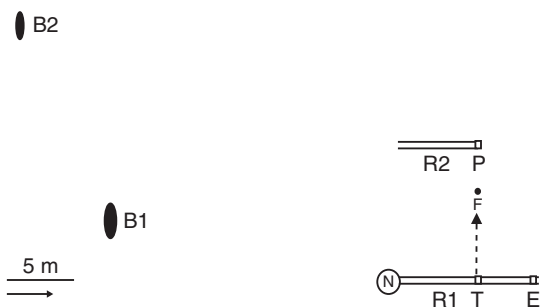


Fig. 1. Plan of the experimental area. The training route leads from the nest (N), 6 m along an open channel to the exit ramp (T), and then 6 m over open ground to a feeder (F) marked by a small cylinder (circle). There are two bushes (B1 and B2) 20–30 m to the left of the route. Initial test conditions used a release site 4 m along the channel (R1), with the exit ramp placed 10 m along the extended channel (E). Final test conditions used a parallel test channel with release site (R2) and exit (P). Scale and arrow indicating north are shown in the lower left corner.

off so that each ant was free to enter the tray only after the previous ant's trajectory had been recorded and the ant had been captured. A test continued until no more ants were willing to enter the tray. The trajectories in Fig. 3 were collected over three test periods, with the ants split approximately equally between the two manipulations within each test period. Some of the ants were therefore tested twice in the same conditions, but not within the same day. The trajectories in Fig. 5 were each collected within a single test session. To minimize any possible learning during test conditions, an individual experienced altered conditions for no more than one trip per day.

A grid of 1 m squares made from fine string was laid out on the ground beyond the barrier to permit the ants' trajectories to be recorded onto squared paper. This grid appears to have little if any effect on the ant's trajectories. For the analysis of distances, digitized trajectories were truncated at the point where it was judged that they indicated the beginning of search. It is difficult to come up with a satisfactory universal criterion to automate the identification, so these points were judged by eye. The judgments were made blind to the distance that the ant had been carried along the barrier. Trajectories that showed no clear transition point were discarded from the analysis of distances. The directions of the trajectories were measured as the angle, clockwise from the direct line from the barrier to the feeder, to the first point at which the ant was 2 m distant from the end of the barrier.

RESULTS

A habitual route across the feature-poor 6 m stretch between the channel and the feeder offered a good opportunity for demonstrating a local vector (Fig. 2A). The trajectories (Fig. 2B) exhibit an approximately straight segment from the channel with length 4.8 ± 1.1 m (mean \pm s.d., $N=42$). This segment was generally not directed exactly towards the feeder, but after 2 m had under-turned by 12.4 ± 12.2 deg. The trajectories then ended with a curve towards the feeder-landmark configuration. To provide evidence that the straight segment was produced by a local vector memory, our experimental challenge was to find a manipulation that could produce results consistent with the use of a local vector, but could not be explained by a combination between guidance simply from snapshots and PI.

Is travel from the end of the barrier guided by a route memory?

If the feeder and feeder landmark are removed (Fig. 2C), the straight segment is followed by a tortuous movement similar to that associated with search at the end of a home vector (Wehner and Srinivasan, 1981). The curved final section of the trajectories during training is therefore probably guided by beaconing to the feeder landmark. The direction of the straight segment itself, 15 ± 14 deg. ($N=46$), is little changed in the absence of the feeder and feeder landmark (Watson-Williams F -test: $P=0.31$, $F=1.07$, d.f.=1,86). Moreover, search occurs at 4.9 ± 2 m from the channel, which is similar to the distance at which ants turn towards the feeder landmark during training (Mann-Whitney U -test: $P=0.68$).

To test whether the straight segment was guided by a route memory or a global PI output vector calculated from the difference between the remembered coordinates of the feeder and the current global coordinates, we manipulated the positions at which experienced ants both entered and exited the channel (Fig. 3A). The tray between the enclosure and the channel had doors at each end that could be closed to trap an ant briefly. The tray could then be picked up and displaced a short distance along the channel without disturbing the ant's food-ward motivation, allowing us to control

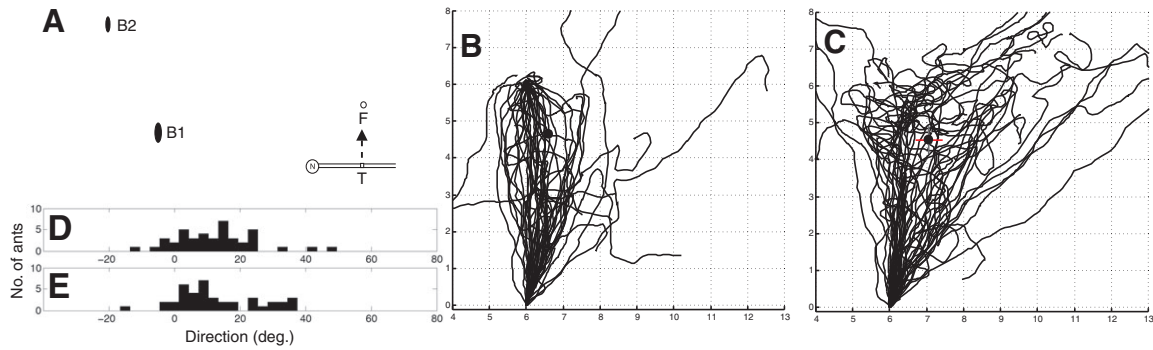


Fig. 2. Trajectories from the training 6 m channel position. (A) Configuration during training. Feeder landmark shown in outline indicates that it was removed in the test condition. (B) The forager trajectories along the trained route after 3 days of training. (C) The trajectories with the feeder landmark removed. Grid lines are spaced at 1 m. Circles show the mean endpoints of the straight segments, and crosses show the standard errors. (D) Histogram of directions over the first 2 m of trajectories in B. (E) Directions over the first 2 m of trajectories in C. Direction was measured in degrees clockwise from the direct path from channel exit to feeder.

where the ants entered the channel. By moving the ramp along the channel, we also controlled where the ants left the channel. During tests, we placed the ramp 4 m beyond its position during training, so that the ants emerged into an area well beyond their habitual trained route from the channel to the feeder. With the ramp in this test-position, ants walking all the way from the nest experienced a channel extended to 10 m, but an ant carried 4 m walked only 6 m along the channel, and thus had the same PI experience on leaving the ramp as during training. We could thus manipulate independently both an ant's PI state and its view of the surrounding features as it exited the channel to start the straight segment over open ground.

If the direction of the straight segment from the channel was guided by snapshots of the constellation of surrounding landmarks that defined the goal or points along the route, then one would expect trajectories from the extended channel position to exhibit larger turns so as to be directed towards the usual position of the feeder. But the straight segment obtained from ants that walked 6 m along the extended channel (Fig. 3B) was directed 19 ± 22 deg. ($N=32$) after 2 m, which is not significantly different from the 15 deg. that ants take across the habitual area (Watson–Williams F -test: $P=0.10$, $F=2.69$, d.f.=94) – note that the trend is in the opposite direction. These directions are therefore not towards the locations of snapshots taken along the route.

The food-ward trajectories of ants that had walked the extended 10 m before leaving the ramp (Fig. 3C) had a mean initial direction

of 11 ± 13 deg. ($N=39$). The slight difference from those that had walked 6 m along the channel leaves open the possibility that the PI state may play some role in determining the trajectories. But the difference is small and statistically not significant either from the trajectories of ants carried over the first 4 m (Watson–Williams F -test: $P=0.059$, $F=3.7$, d.f.=69), or from the trajectories from the training exit (Watson–Williams F -test: $P=0.52$, $F=0.41$, d.f.=77). The ants were therefore not primarily following a global PI output vector calculated from their current global PI coordinates at the turn. The trajectories must therefore be guided mostly by a direction-based route memory associated with the end of the barrier.

The long-term involvement of direct visual guidance

Even though the initial directions were not set by local landmark cues, it would still have been possible that surrounding landmarks such as the two bushes 20–30 m south of the route control the endpoints of the straight segments. To discover whether the endpoint of the straight segment was indeed triggered by an internal cue such as monitoring the distance travelled, or instead by visual landmark cues, we removed the bush closest to the feeder (Fig. 4A). Trajectories collected about an hour afterwards (Fig. 4B) had a mean initial direction of 7 ± 18 deg. ($N=11$), which does not differ greatly from the directions before the removal of the bushes (c.f. Fig. 2C). But by the next day, the number of ants at the feeder was much reduced, and remained

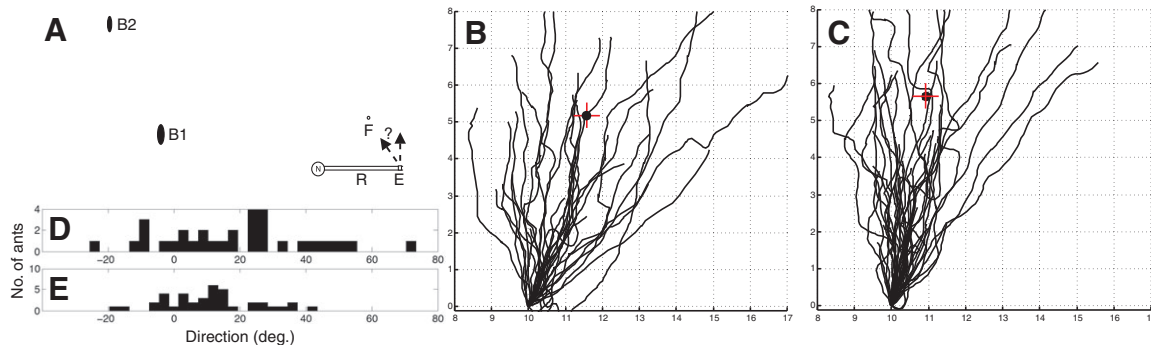


Fig. 3. Trajectories from the extended 10 m channel. (A) Configuration during tests. Do ants follow a route-based memory, or do they travel back towards the location of the feeder? (B) Trajectories after foragers are carried 4 m so that their PI state on leaving the channel is as in training. Truncated at the beginning of search. (C) Trajectories after the foragers have walked the entire 10 m along the channel. Truncated at the beginning of search. Grid lines are spaced at 1 m. (D) Directions over the first 2 m of trajectories in B. (E) Directions over the first 2 m of trajectories in C.

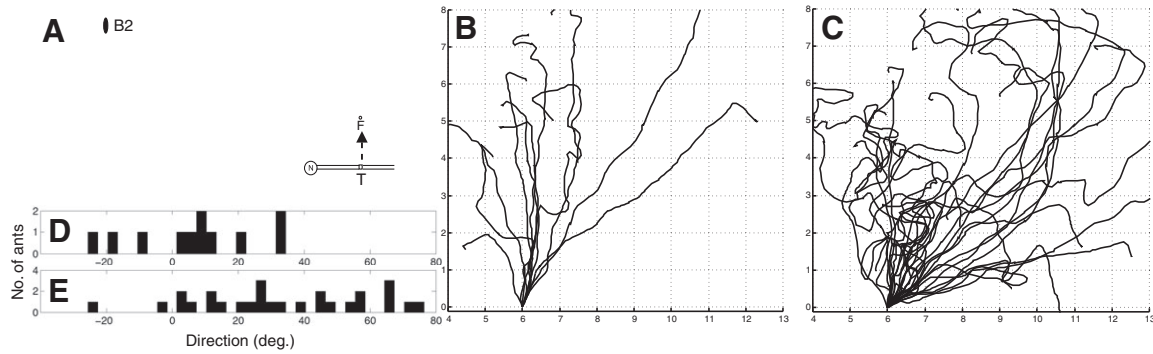


Fig. 4. Trajectories in the training configuration after the closer bush had been removed. The feeder landmark was temporarily removed during the tests. (A) Configuration during tests. (B) Trajectories within an hour of the removal of the bushes. (C) Trajectories 3 days after the bushes were removed. Grid lines are spaced at 1 m. (D) Directions over the first 2 m of trajectories in B. (E) Directions over the first 2 m of trajectories in C.

low over the subsequent days. The trajectories recorded 3 days later (Fig. 4C) had a mean direction of 33 ± 26 deg. ($N=27$). At least 23 out of the 27 trajectories were from ants that had been marked before the bushes were removed. The trajectories were significantly more scattered (Fisher F -test: $F=3.13$, $P<0.0005$) and showed a significantly greater amount of under-turning (Watson–Williams F -test: $F=15.02$, $P<0.0003$, $d.f.=1,71$) than trajectories without the feeder landmark before the removal of the bush. The bush must therefore have been used in some way that aided or reinforced the memory of direct routes on leaving the channel.

After 4 days without the bush, we installed an artificial landmark of similar size and location to the removed bush. Within a few hours, the number of ants at the feeder recovered considerably, although it remained below the previous level. Moreover, after 2 days experience with the replacement bush, the ants' trajectories were better directed. Removal of the second bush, followed a day later by its replacement with a second artificial landmark, produced a similar decrease and subsequent partial recovery in trajectory numbers and accuracy (not shown). In almost identical experiments with L-shaped routes on two previous years, the number of foragers arriving at the feeder dropped permanently soon after nearby bushes were removed. At the time, unfortunately, we did not realize the significance and did not try replacing the missing bushes with artificial ones.

Local vectors and the encoding of distance

The trajectories after 2 days experience with both artificial bushes were reasonably well directed. Trajectories recorded during a brief temporary removal of the artificial bushes (Fig. 5A,B) had a mean initial direction of 18 ± 13 deg. ($N=18$) and lengths of 5.4 ± 2.2 m. Their similarity to the earlier trajectories with the original bushes in place (means 15 deg. and 4.9 m; see Fig. 2C) strongly suggested that the straight segment could be performed in the absence of snapshot guidance from surrounding landmarks. To be certain, we made a separate test channel, oriented parallel to the training channel, but positioned 10 m to the west so that the exit to the channel was 4 m beyond the feeder. During the test, we removed the artificial bushes.

Even though we released ants only 4 m from the exit of this parallel test channel, many ants were unwilling to travel the entire distance, possibly because they encountered odour blown from the training feeder. The straight segments of the trajectories of those individuals that did leave the test channel at the exit (Fig. 5C) had length 5.8 ± 1.6 m ($N=10$) and initial direction 19 ± 7.4 deg. The direction (Watson–Williams F -test: $F=0.005$, $P=0.94$, $d.f.=25$) and length (Mann–Whitney U -test: $P=0.12$) were similar to those from the training channel (Fig. 5A). As the two sets of trajectories were approximately co-linear, no conceivable landmark cues could specify the endpoints of both the training and test trajectories. We can therefore be confident that the length derives from a forager's

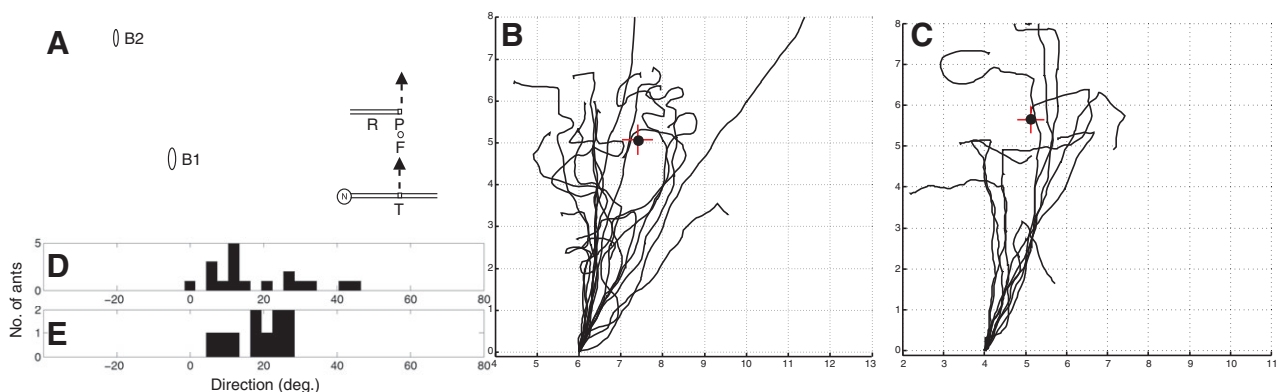


Fig. 5. Trajectories after training with the replacement bushes. (A) Configuration during tests. The bushes and the feeder landmark were removed during testing. (B) Trajectories from the 6 m training position. (C) Trajectories after ants walked 4 m along the parallel test channel. Grid lines are spaced at 1 m. (D) Directions over the first 2 m of trajectories in B. (E) Directions over the first 2 m of trajectories in C.

odometry, monitoring the distance it has travelled across the open ground. Moreover, the trajectories do not rotate as would be expected if a PI output vector was calculated at the end of the channel after only 4 m rather than 6 m. Both the direction and distance of the trajectories therefore seem to be encoded in a local vector memory of the route segment.

DISCUSSION

A single experience can be enough for an insect to learn cues for snapshot-based guidance to a place (Tinbergen, 1932) and probably to acquire its PI coordinates (Wehner et al., 2004). When these guidance cues produce a stable route between the nest and a food source, they provide a framework for acquiring local vectors (Collett and Collett, 2002). We could infer the existence and use of a local vector in the present case because the trajectories of well-trained ants were little influenced by either the PI state or the location at which the ants emerged from the channel. With experience, as in the present case, the local vector appears to take control over guidance (Collett et al., 1998). But the loss of route stability with the removal of the bushes suggests that even well-established local vectors may require a persistent underlying framework provided here by guidance from visual snapshots and the PI output vector. The effects that changes in the visual cues have on the trajectories raise a number of questions about the interactions between navigational strategies.

The use of PI and snapshot-based guidance along an L-shaped route

Our results suggest that an L-shaped route may pose particular problems for desert ants. Even with the bushes in place, almost all trajectories turned too little on leaving the channel. The under-turning into the straight segment is a robust finding for ants trained to an L-shaped food-ward route in a landmark-poor area (Collett et al., 1999) (and several unpublished studies; M.C. and T.S.C.), or after a large unexpected detour on the way to the food (Collett et al., 1999). Possibly similar under-turning has also been reported in the human use of PI (Foo et al., 2005). The error on the food-ward route may reflect a propensity against large turns, or possibly a systematic error in calculating the PI output vector for a 90 deg. turn. The food-ward errors may be related to the systematic errors in the global PI home vector that follow an L-shaped food-ward route (Müller and Wehner, 1988). The directions of both food-ward and homeward errors are consistent with over-estimating the size of a sharp turn.

After the end of the straight segment encoded by the local vector, the final stretch to the feeder was only well directed if the feeder landmark was present (Fig. 2B), implying that the last stretch is guided by the feeder landmark. But might the use of the feeder landmark need additional support from cues provided by the two bushes to the side of the route? The reduction in forager numbers visiting the feeder after the bushes were removed, even though the feeder landmark and cues from PI remained, suggests that the feeder landmark may become less useful without the bushes. An insect's use of visual landmarks seems often to be associated with a consistent viewing direction (Collett, 1995; Collett and Baron, 1994). But along the most oblique trajectories from the channel, the compass bearing of the landmark relative to the ant can shift anti-clockwise considerably as an ant approaches the end of the local vector. Moreover, the feeder landmark was short and sand coloured, and, with a width of approximately 10 cm, from 2 m away it subtended only about 3 deg. horizontally – less than the angle between the lines of sight of neighbouring ommatidia (Zollikofer et al., 1995) – and may barely have risen above the horizon. Robust

recognition or use of the small isolated landmark at the end of an oblique local vector may well therefore need support from a distinctive panoramic context provided by the bushes.

Encoding of distance and the use of panoramic context

Although this study only examined route segments of one distance, the most likely explanation for our results is that the *Cataglyphis* foragers have formed local vector memories that encode the length, as well as direction, of the route segment over open ground. In earlier studies where honeybees learnt to travel the length of a habitual route segment from an *en route* landmark to a feeder (Collett et al., 2002; Collett et al., 1996; Srinivasan et al., 1997), visual features marking the start of the segment could conceivably have provided snapshot cues to define the endpoints. But our results here, with their more complete controls for the use of snapshots, suggest that these previous examples were also examples of local vectors. A study using *C. fortis* along a U-shaped homeward route also provides compelling evidence for the encoding of distance along a route segment (Knaden et al., 2006).

A honeybee appears to require an appropriate panoramic context to express a local vector (Collett et al., 2002). Such a dependence may also explain why in a previous study, where desert ants performed local vectors on a test ground, the vectors averaged less than 3 m in length for an 8 m long habitual route segment (Collett et al., 1998). The landscape on the test ground in that case may have been sufficiently different from the panorama during training that the local vectors were not fully expressed. In the present study, as in previous ones (Bisch-Knaden and Wehner, 2001; Knaden et al., 2006), the test and training conditions also shared very similar panoramic contexts, and the local vectors appeared to be of more appropriate lengths.

Observations during the present studies suggest that the trigger for the expression of the local vector may be the change into the appropriate panoramic visual context. Ants performed similar local vectors whether they left the channel *via* the ramp or climbed out of the channel before reaching the exit ramp, or even were helped from the channel onto the open ground by the experimenter. Experiments by Knaden and Wehner also suggest that entering the appropriate context (both panoramic and motivational) may provide a possible trigger (Knaden et al., 2006). Together, these findings suggest that a local vector is often triggered by panoramic and behavioural contexts that identify a habitual segment (Collett et al., 2002), rather than by a landmark indicating a specific start position.

A compromise between navigational strategies

Our results suggest that the local vectors acquired before the removal of the bushes reflect a compromise between snapshot-based guidance and other guidance cues such as the PI output vector. The removal of the bushes reduced the influence of the snapshot cues, eventually causing trajectories to under-turn more on leaving the channel, or become more tortuous.

How does an ant generate trajectories that are intermediate between the commands from two navigational strategies? One possibility is that commands from different strategies combine to produce an averaged response in the ant. A second possibility is that, at any instant, an ant follows only the commands from a single strategy, but that control switches between strategies either within a trip or between trips. In this second case, a local vector developed over a number of trips would embody the compromise, encoding a route that the original strategies themselves would not generate.

The direction of the local vector might be learnt directly from the commands produced by the other navigational strategies. But

how would guidance by placing landmarks on appropriate retinal positions (Collett et al., 2001; Graham and Collett, 2002; Judd and Collett, 1998; Junger, 1991) be combined with the celestial-based cues used for a PI output vector (Wehner and Müller, 2006)? A more parsimonious solution might be to learn the compass cues experienced while following these commands. In other species, this latter mechanism would also allow individuals to learn local vectors while following pheromone trails.

Generative versus selective maintenance of the local vector

An increased degree of under-turning encoded by the local vector makes it more difficult for an ant to find the feeder. The resulting reduced success, or possibly simply an increased delay, in reaching the feeder would reduce over-all reinforcement, so that, as observed, individuals might give up on the feeder. But why might removing a bush affect the direction of a local vector?

One possibility is that, although a temporary change in the PI and landmark cues did not have an effect large enough to be statistically significant during a single test run, the local vector does not entirely suppress the other guidance cues. With visual cues weakened by the removal of the bush, the factor that produces the under-turning may have a relatively greater, or more frequent, input into generating the trajectories. Each trajectory that under-turns could then shift the local vector memory slightly.

Cues from the framework might also provide learning signals during or at the end of the straight segment, selecting which trajectories form the basis for the local vector memory. The snapshot cues would provide a less precise indication of position without the bushes, and so their reinforcement signals would be both weakened and provided over a larger area. Accurate trajectories would be reinforced by the feeder and feeder landmark, but trajectories that miss would receive reduced reinforcement from visual cues, allowing the local vector to drift. Because of the systematic error, the PI-based cues would selectively reinforce the trajectories that under-turn.

Interactions and use of local vectors

The continued interaction between local vectors and other navigational strategies gives routes the flexibility to track resources. A change in the PI output vector would gradually shift trajectories towards the newly found resources, and unsuccessful routes would be abandoned. The inter-dependence also means that route geometry is constrained by the availability of landmarks. Even with the ability to use global PI and learn local vectors, ants cannot learn or retain arbitrary routes that are unsupported by landmarks.

Local vectors are likely to be most useful to an ant, and most easily demonstrated by an experimenter, along habitual routes in uncluttered environments where snapshot memories are either unavailable or unreliable. If there are landmark features that can provide orientation cues from their position on an individual's retina, then the individual will follow these cues rather than the context-associated compass direction (Collett et al., 2001). But if the landmark cues are removed, then the panorama might be too greatly altered to trigger any local vector memory (Collett et al., 2002). In landmark-poor environments, local vectors are useful where the habitual route diverges from the PI output vector, and generally provide more accurate distance information (Srinivasan et al., 1997). Because of the continuing interaction between a local vector and its framework, a local vector provides only temporary stability to a route, and allows it to adapt to changes in the distribution of resources or landmarks.

REFERENCES

- Åkesson, S. and Wehner, R. (2002). Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial system of reference? *J. Exp. Biol.* **205**, 1971-1978.
- Bisch-Knaden, S. and Wehner, R. (2001). Egocentric information helps desert ants to navigate around familiar obstacles. *J. Exp. Biol.* **204**, 4177-4184.
- Bisch-Knaden, S. and Wehner, R. (2003). Local vectors in desert ants: context-dependent landmark learning during outbound and homebound runs. *J. Comp. Physiol. A* **189**, 181-187.
- Cartwright, B. A. and Collett, T. S. (1983). Landmark learning in bees-experiments and models. *J. Comp. Physiol.* **151**, 521-543.
- 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., Bisch, S. and 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. (1995). Making learning easy: the acquisition of visual information during orientation flights of social wasps. *J. Comp. Physiol. A* **177**, 737-747.
- Collett, T. S. and Baron, J. (1994). Biological compasses and the coordinate frame of landmark memories in honeybees. *Nature* **368**, 137-140.
- Collett, T. S. and Collett, M. (2002). Memory use in insect visual navigation. *Nat. Rev. Neurosci.* **3**, 542-552.
- Collett, T. S. and Land, M. F. (1975). Visual spatial memory in a hoverfly. *J. Comp. Physiol. A* **100**, 59-84.
- Collett, T. S. and Lehrer, M. (1993). Looking and learning: a spatial pattern in the orientation flight of the wasp *Vespa Vulgaris*. *Proc. R. Soc. Lond. B Biol. Sci.* **252**, 129-134.
- 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., Collett, M. and Wehner, R. (2001). The guidance of desert ants by extended landmarks. *J. Exp. Biol.* **204**, 1635-1639.
- Foo, P., Warren, W. H., Duchon, A. and Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *J. Exp. Psychol. Learn. Mem. Cogn.* **31**, 195-215.
- Graham, P. and Collett, T. S. (2002). View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. *J. Exp. Biol.* **205**, 2499-2509.
- Judd, S. P. D. and Collett, T. S. (1998). Multiple stored views and landmark guidance in ants. *Nature* **392**, 710-714.
- Junger, W. (1991). Waterstriders (*Gerris paludum* F) compensate for drift with a discontinuously working visual position servo. *J. Comp. Physiol. A* **169**, 633-639.
- Knaden, M., Lange, C. and Wehner, R. (2006). The importance of procedural knowledge in desert-ant navigation. *Curr. Biol.* **16**, R916-R917.
- Lehrer, M. (1991). Bees which turn back and look. *Naturwissenschaften* **78**, 274-276.
- Lehrer, M. and Collett, T. S. (1994). Approaching and departing bees learn different cues to the distance of a landmark. *J. Comp. Physiol. A* **175**, 171-177.
- Müller, M. and Wehner, R. (1988). Path Integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.
- Nicholson, D. J., Judd, S. P. D., Cartwright, B. A. and Collett, T. S. (1999). Learning walks and landmark guidance in wood ants (*Formica rufa*). *J. Exp. Biol.* **202**, 1831-1838.
- Ronacher, B., Gallizzi, K., Wohlgeuth, S. and Wehner, R. (2000). Lateral optic flow does not influence distance estimation in the desert ant *Cataglyphis fortis*. *J. Exp. Biol.* **203**, 1113-1121.
- Rossel, S. (1989). Polarization sensitivity in compound eyes. In *Facets of Vision* (ed. D. G. Stavenga and R. C. Hardie), pp. 298-316. Berlin: Springer.
- Santschi, F. (1913). Comment s'orientent les fourmis. *Rev. Suisse Zool.* **21**, 347-425.
- Srinivasan, M. V., Zhang, S. W. and Bidwell, N. J. (1997). Visually mediated odometry in honeybees en route to the goal: visual flight control and odometry. *J. Exp. Biol.* **200**, 2513-2522.
- Tinbergen, N. (1932). Über die Orientierung des Bienenwolfes (*Philanthus triangulum*). *Z. Vgl. Physiol.* **16**, 305-334.
- von Frisch, K. (1967). *The Dance Language and Orientation of Bees*. London: Oxford University Press.
- Wehner, R. and Müller, M. (2006). The significance of direct sunlight and polarized skylight in the ant's celestial system of navigation. *Proc. Natl. Acad. Sci. USA* **103**, 12575-12579.
- Wehner, R. and Rüber, F. (1979). Visual spatial memory in desert ants. *Cataglyphis bicolor*. *Experientia* **35**, 1569-1571.
- Wehner, R. and Srinivasan, M. V. (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. Comp. Physiol.* **142**, 315-338.
- Wehner, R., Harkness, R. D. and Schmid-Hempel, P. (1983). Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). In *Information Processing in Animals* (ed. M. Lindauer), pp. 1-79. Stuttgart: 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., Meier, C. and Zollikofer, C. (2004). The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. *Ecol. Entomol.* **29**, 240-250.
- Wittlinger, M., Wehner, R. and Wolf, H. (2006). The ant odometer: stepping on stilts and stumps. *Science* **312**, 1965-1967.
- Wolf, H. and Wehner, R. (2000). Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. *J. Exp. Biol.* **203**, 857-868.
- Zeil, J. (1993). Orientation flights of solitary wasps (*Cerceris*, Sphecidae, Hymenoptera). 1. Description of flight. *J. Comp. Physiol. A* **172**, 189-205.
- Zollikofer, C. P. E., Wehner, R. and Fukushi, T. (1995). Optical scaling in conspecific *Cataglyphis* ants. *J. Exp. Biol.* **198**, 1637-1646.