Bi-directional route learning in wood ants

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Summary

Some ants and bees readily learn visually guided routes between their nests and feeding sites. They can learn the appearance of visual landmarks for the food-bound or homeward segment of the route when these landmarks are only present during that particular segment of their round trip. We show here that wood ants can also acquire landmark information for guiding their homeward path while running their food-bound path, and that this information may be picked up, when ants briefly reverse direction and retrace their steps for a short distance. These short periods of looking back tend to occur early in route acquisition and are more frequent on homeward than on food-bound segments.

Key words: wood ant, *Formica rufa*, view-based navigation, route learning, visual landmarks.

Introduction

A number of species of ants are known to learn and follow visually guided routes when foraging. Part of the evidence for learnt, visually guided routes comes from the findings that over several trips an individual ant will follow much the same route through a visually cluttered environment, and that different individuals from the same nest travelling to the same destination will follow their own idiosyncratic routes through the same surroundings (Collett et al., 1992; Kohler and Wehner, 2005; Macquart et al., 2005; Wehner et al., 1996). Furthermore, ants will follow the same route irrespective of the state of their path integration system (Andel and Wehner, 2003; Kohler and Wehner, 2005; Wehner et al., 1996). When displaced from the feeder or nest to a point midway along the route, they immediately join the route and continue it to its end (Kohler and Wehner, 2005). A different kind of evidence for visual route guidance comes from observing how an acquired route depends on the distribution of visual features within an ant's environment (Graham et al., 2003) and how displacing, changing or removing visual landmarks after a route has been acquired influences an individual's path (Collett et al., 1998; Collett et al., 1992; Collett et al., 2001; Graham and Collett, 2002; Macquart et al., 2005).

Visually guided food-bound and homeward routes can be very similar (Santschi, 1913), but they can also differ (Kohler and Wehner, 2005; Macquart et al., 2005; Wehner et al., 1983); [also see fig. 7B,C in (Wehner, 2003)]. In either case, ants travelling in the two directions, between their nest and food or their food and nest, encounter and learn different sequence of views and associate different actions with those views. When there is a distinct spatial separation between food-bound and homeward routes (Wehner et al., 2006), visual information pertaining to the food-bound or homeward route must be acquired while performing that route. When the two routes are similar, the question arises as to whether ants might acquire landmark information to guide their homeward route on their food-bound route and *vice versa*. Such cross-route learning would help make food-bound and homeward routes more similar, which would be useful in some environments, and might speed up route learning. It would also enhance the opportunity for communication between ants travelling in opposite directions. One might expect cross-route learning to be particularly prevalent in ant species that are guided along trails by a combination of chemical and visual cues and so may tend to follow the same path in both directions.

In the first part of this paper we examine whether information for guiding a wood ant's homeward route can be acquired on the ant's outward route. The basic experimental design was to give ants ample experience of a food-bound route, but to prevent any experience of a homeward route. We then examined whether these ants, which were only accustomed to travelling towards the food, could nonetheless perform elements of a homeward route.

In the second part of the paper, we examine the way that food-bound and homeward routes develop by recording the successive food-bound and homeward trips performed by individual ants. Is there a close similarity in the evolution and final form of an individual's food-bound and homeward routes? To test whether running a homeward route facilitates acquisition of a food-bound route, we compared the developing food-bound routes of ants that were and were not allowed to run their homeward routes.

Navigational learning in insects is to a large degree anticipatory in the sense that insects learning a visually guided route are programmed to acquire relevant visual information at particular points along the route. The best understood behavioural routines aiding acquisition are the elaborately structured learning flights that bees (Lehrer, 1993) and wasps (Collett and Lehrer, 1993; Tinbergen, 1932; Zeil, 1993) perform when they first leave a significant place to which they will return, such as their nest or a newly discovered feeding site. The probable function of these localised flights is to allow an insect to pick up appropriate information that can guide its later return to the place. A failure to execute a learning flight can lead to difficulties when the insect tries to find that goal on its return (Lehrer, 1993; Wagner, 1907). Wood ants, too, have been found to look back and approach nearby landmarks after they have found a new source of food (Judd and Collett, 1998; Nicholson et al., 1999; Rosengren, 1971). Desert ants behave similarly when first leaving their nest (Wehner et al., 2004). But little is known about whether and where ants turn and look backwards along a route.

In the third section of the paper, we analyse the wood ant's food-bound and homeward routes to identify where information for guiding the opposite paths might be acquired. Because the landscape will generally look different in the two directions, ants are likely to learn landscape features for guiding their path in the reverse direction at times when they have turned around and are retracing their steps. If such potential points of acquisition do occur, how are they distributed along the ants' paths? Large landmarks act as beacons and seem to form intermediate goals that sub-divide a route [for bees (von Frisch, 1967); wood ants (Graham et al., 2003)], so that an interesting possibility is that turn-backs are particularly common close to a landmark that serves as an intermediate goal. A second question to be examined is whether turn-backs occur mostly in early routes, when ants are still inexperienced.

Materials and methods
The ants

Colonies of wood ants (*Formica rufa*, L.) were maintained in the laboratory using methods already described (Graham et al., 2003). To select ants for training, a group of potential foragers was taken from the nest and placed at the start of the route. The first 20 or so ants to reach the food site through random search were caught and then marked individually with two dots of enamel paint (Humbrol, UK). These ants constituted an experimental group. Usually, about two-thirds of the group foraged consistently and could be trained.

The arena

Two experiments were conducted within low-walled rectangular arenas (see Fig. 1A) the floors of which were covered with large (A0) sheets of white paper that were changed regularly to eliminate scent cues. The arena for the first experiment was 168 cm×94 cm, and the arena for the second experiment was 200 cm×124 cm. These arenas were placed at the centre of a larger curtained area (280 cm×380 cm) illuminated by banks of high frequency fluorescent lights concealed above a translucent plastic ceiling. The floor-to-ceiling curtains were white on three sides and were decorated with large black shapes on the fourth side (Fig. 1A). Ants followed a two-legged outward route from one end of the arena (S) to a food site (F) at the other end of the arena. The first leg of the route was along an open-topped narrow channel, 10 cm wide, with 10 cm high solid white-finished walls. A black cylinder (47 cm high and 15 cm diameter) straddled the channel at the end of the first leg of the route. The channel prevented ants from seeing the overall position of the cylinder in the room until they had passed the cylinder. The second leg of the route extended from the channel exit across the open arena to the food site. A concealed tracking camera mounted in the ceiling recorded the paths of individual ants (Fry et al., 2000; Graham and Collett, 2002).

Experimental procedures

In the first experiment we asked whether ants learn elements of homeward routes on their food-bound paths. Ants were not allowed to make their own way home from the food site. Instead, they were carried from the food-site back to the nest, so limiting their visual experience to the outward route. To ensure that ants could not see the cylinder or the room from the food site, the feeder – a microscope slide on which was squirted a drop of sucrose solution, was placed at the bottom of an ant trap (8 cm diameter and 1.5 cm deep) that was set below floor level to limit the ant's view of the arena and its surroundings (Fig. 1A). To further impede its view of the arena, the trap was surrounded by a 2 cm high black barrier with gaps through which the ants could pass. Ants dropped into the trap, fed on the sucrose, and remained in the trap until they were collected and returned to the nest. Some ants were trained with the channel and cylinder on the left of the direct food-bound path, on the same side as the patterned curtain, and some with the channel on the opposite side.

After about 20 outward trips, each ant was given the opportunity to perform a homeward route. To avoid any possible bias due to path integration, the ant did not make its own way to the feeder. It was taken from the nest and placed adjacent to a drop of sucrose on a microscope slide that was located at floor level in the usual position of the feeder. Ants were not disturbed by this unexpected procedure and mostly began feeding straight away. Two identical cylinders were placed in the arena. One cylinder was in the training position and the other in a mirror symmetric position on the other side of the direct path between start and feeder (Figs 1 and 2). Graham et al. showed that wood ants, during route learning, memorise both the appearance of a local landmark and the surroundings in which the landmark is set (Graham et al., 2003). They tend to ignore familiar looking landmarks placed in an inappropriate context. Therefore the extra landmark, whilst balancing out any innate landmark attraction, should not disrupt any manifestation of a learnt homeward route. The arena floor was covered with fresh paper to eliminate guidance by chemical trails and the channel was removed so that the arena configuration was symmetrical.

The second experiment investigated the development of food-bound and homeward routes using the same arrangement of channel and cylinder, but in the larger arena. We recorded how routes developed in two groups of ants. The first group performed both food-bound and homeward routes, and we monitored the paths of individual ants over 30–40 round trips. For these ants, the feeder was at floor level with a small landmark close by. Ants in the second group did not make their own way home, and we just recorded each of their food-bound trips. After each ant had fed, it was carried back to the nest. To prevent ants from returning home, the feeder for this group was put at the bottom of another slightly larger ant trap (10 cm diameter and 3 cm deep) with a cylindrical landmark in its centre. To improve tracking reliability, a short narrow cardboard corridor was attached to the end of the channel. The corridor enabled tracking to start further from the large landmark and so reduced the danger of the tracking camera becoming locked onto the landmark.

Route analysis

The bias of each individual trajectory to one or other side of the arena was assessed by calculating the mean position on the horizontal (x) axis – with the feeder at $x=0$. Trajectories were said to be biased to the left if the mean x position was <0 and to the right if the mean x position was >0.

To obtain an overall measure of how routes change with experience, we computed two global characteristics of each ant's path, first its straightness and second its consistency with respect to the preceding path of the same ant. In order to measure straightness, the recorded path was divided into multiple sections of equal duration (2 s) and the heading of each section was calculated. The straightness of the trajectory is then given by the coherence of these headings (Batschelet, 1981). A value of one indicates a straight path and a value of zero indicates a path with no overall direction (e.g. a circle).

The consistency between pairs of consecutive trajectories was estimated by a procedure in which we first calculated the area enclosed by the two trajectories by counting the number of 1 cm grid squares that were enclosed by the paths or through which the paths passed. This value was then normalised by dividing it by the combined length of the paths. This procedure gives a minimum value of 0.5 when the paired trajectories are identical.

To assess the statistical significance of any changes in consistency and straightness, runs were grouped into three successive blocks of 10, and the mean straightness and consistency of the runs were computed for each individual over each block and the scores analysed with a repeated-measures ANOVA.

Results
Return routes after food-bound training

To find out whether ants had acquired information from food-bound trips that might help guide a homeward trip, we recorded each ant's behaviour after it had made about 20 food-bound trips and no homeward ones. After a further 7–10 training runs ants were tested a second time.

We measured and compared the straightness and distance of the ants'
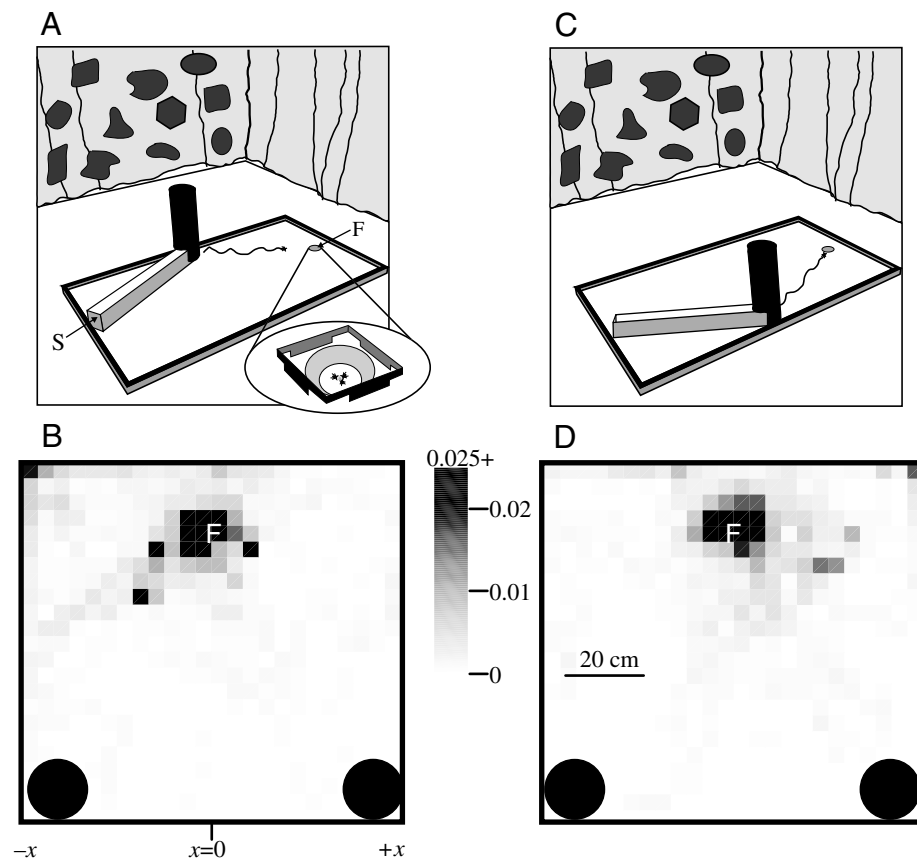

Fig. 1. The experimental arena. (A,C) Experimental arena and training layout. Ants travelled along an open-topped, narrow channel and under a large cylinder before heading over an open arena to the feeder. The feeder was at the bottom of a small pit (shown enlarged in A) and for the first experiment, a small barrier was placed around the pit to prevent the ants from viewing the landmark and its surroundings from the pit (B,D). In tests ants were taken directly from the nest and placed on a feeder (indicated by F). Two landmarks (large black circles) were positioned symmetrically in the arena. Cumulative density distributions of all return trajectories from ants trained with the channel on the left or right, respectively. Dark areas represent areas where ants spent the most time. Values are given as proportion of the total time spent in the arena. Because of the large amount of time spent at or near the feeder, all values above 2.5% are represented as black squares.

paths for each run and found no significant differences between the first and second test runs (Sinuosity; mean ± s.d.: first runs, 0.30±0.27; second runs, 0.27±0.24; Student's *t*-test; *P*=0.65, *t*=0.46, d.f.=49: Maximum distance reached; mean ± s.d.: first runs, 63±30 cm; second runs, 61±28 cm; Student's *t*-test; *P*=0.76, *t*=0.30, d.f.=49).

Half of the ants were trained with the channel and cylinder to the left of the direct line from the start to the feeder, for the other half the channel and cylinder were to the right of that line (Fig. 1A,C). The superimposed test trajectories for each of these training conditions are shown as separate density plots in Fig. 1B,D. Both plots are biased significantly towards the side where the channel and landmark had been during outbound runs. The return journeys of ants from both training conditions were biased significantly toward the position of the channel in training. Most (17/23; sign test, *P*=0.017) trajectories from ants trained with the channel to the right of the direct line to the feeder were biased to the left. Whereas most (21/28; sign test, *P*=0.006) trajectories from ants trained with the channel to the left were biased to the right.

The individual test trajectories are shown in Fig. 2A, with the paths of the right-trained ants mirrored to make them compatible with those of the left-trained ants. For clarity, a solid-circle marks the end-points of each recorded track. The end-positions are not behaviourally significant, as the tracks often stopped when the 6 min recording time was over, or before, if the tracking camera became locked onto the cylinder or the sidewall of the arena. Ants rarely took a direct path to the cylinder. Usually, they just moved somewhat erratically on the correct side but 'above' the channel exit, as they often did in early foraging trips when allowed to return home normally

(Fig. 3). The ants' erratic movements can also be seen in Fig. 2B–D, which shows with a dot where each trajectory crossed circles of 20, 40 and 60 cm radius centred on the feeder.

The development of food-bound and homeward routes

The path of each ant between the end of the channel and the feeder was recorded individually for the first 30–40 successive foraging trips. Some ants performed both out and return journeys; other ants were only allowed to perform outward journeys and were carried home. The way that the paths change with experience is shown in the different panels of Fig. 3. The food-bound paths are at first a little erratic, but straighten out rapidly, and there is little improvement in straightness from path 19 onwards (Figs 3 and 4). The food-bound routes of those ants that performed homeward routes did not differ quantitatively in straightness or consistency (see legend to Fig. 4 for details) from those of ants that were carried home.

The ants' initial homeward paths were considerably more variable than were the food-bound paths and it took more trials for the homeward routes to stabilise (Fig. 3C). The first few returns were no more than roughly concentrated in the correct half of the arena. Paths slowly became more direct, but they did not form a tight cluster until returns 25–30. It took a long time for the paths to straighten, and even the paths in the final group were a little curved (Fig. 4C). The curvature to the right was consistent for most ants, suggesting that it may be caused by visual features, which the ants gradually come to ignore as routes straighten.

Looking back along food-bound and homeward routes

Ants on the food-bound or homeward leg of their foraging route can give themselves an opportunity of acquiring views for guiding travel in the reverse direction by turning around and retracing their steps for a short segment. We scanned the recorded routes for reversals of this kind to discover when and where reversals occurred and how long they were. We
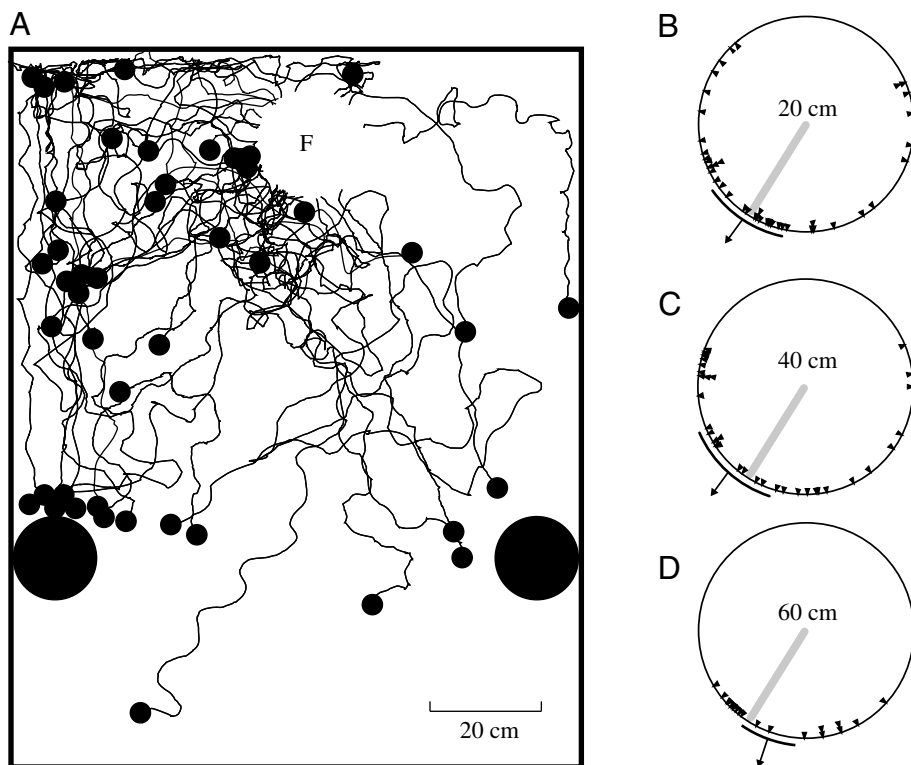
A

B

20 cm

C

40 cm

D

60 cm

20 cm

Fig. 2. The ants' first and second trips home after many food-bound runs. (A) Trajectories of ants after leaving the feeder (F). Trajectories ended after 6 min or before if the camera 'lost' the ant. Trajectories are shown from when the ant has reached at least 10 cm from the feeder and end-points are marked by small black circles; large black circles indicate the landmarks. Trajectories from ants trained with the channel on the right hand side of the direct route to the food have been mirrored. (B,C,D) Circumferential positions of ants at 20 cm, 40 cm and 60 cm from the feeder. Grey lines represent the direct trajectory to the normal position of the cylinder. Arrow and range represent the mean heading and 95% confidence interval.

looked for path segments in which the ants turned around and faced within ±20° of the cylinder at the end of the channel on food-bound routes or within ±20° of the feeder on homeward routes.

Reversals on the food-bound path

Occasionally, when ants were already some distance away from the channel exit, they reversed direction, returned to the channel exit and re-entered the channel. They then usually re-emerged to walk to the feeder. Loops at the start of food-bound routes occurred on about 25% of early runs and became rarer as ants became experienced with the route. None occurred after run 12.

More frequently, ants turned back, retraced their path for a short segment and then continued with the food-bound segment. Twenty-seven out of 29 trained ants reversed direction at least once. Reversals were usually marked by the ant looping or making a U-bend (e.g. Fig. 5A). Most reversals were less than 3 cm long (25th, 50th and 75th percentile of the distribution were 0.966, 2.450 and 8.387 cm, respectively, *N*=92). Reversals occurred more often in early than in later runs (Fig. 5B) and were distributed evenly along the path (Fig. 5C). The occurrence of brief U-bends and loops on relatively straight segments is consistent with the suggestion that the reversals are performed to acquire landmark information and that they are not just a by-product of the ant's erratic path on early trials.

Reversals on the homeward path

Short reversals are also seen on successful homeward paths. The distribution of the length of reversals is single peaked with a tail that is shorter than reversals on the food-bound trip (25th, 50th and 75th percentile of the distribution were 0.775, 2.753 and 4.202 cm respectively, *N*=87). Reversals occurred most frequently on early trials (Fig. 5E). Homeward reversals differed from the food-bound reversals in two major respects. First, all ants generated more reversals on their homeward than on their food bound paths, with a ratio of roughly two to one. Second, reversals were not evenly distributed along the route, but had a clear peak close to the food-site (Fig. 5F). This peak suggests that the reversals may be more for learning the location of the site than the route to it.

On early runs ants often moved away from the feeder and looped back after a short excursion before eventually making a full homeward trip. These loops could be in any direction and were not biased towards the exit to the channel. As reported earlier for learning flights in wasps (Zeil, 1993) and also for similar loops in wood ants (Nicholson et al., 1999), these loops often occur on the first runs of each day, even in well-trained ants (Fig. 5G).
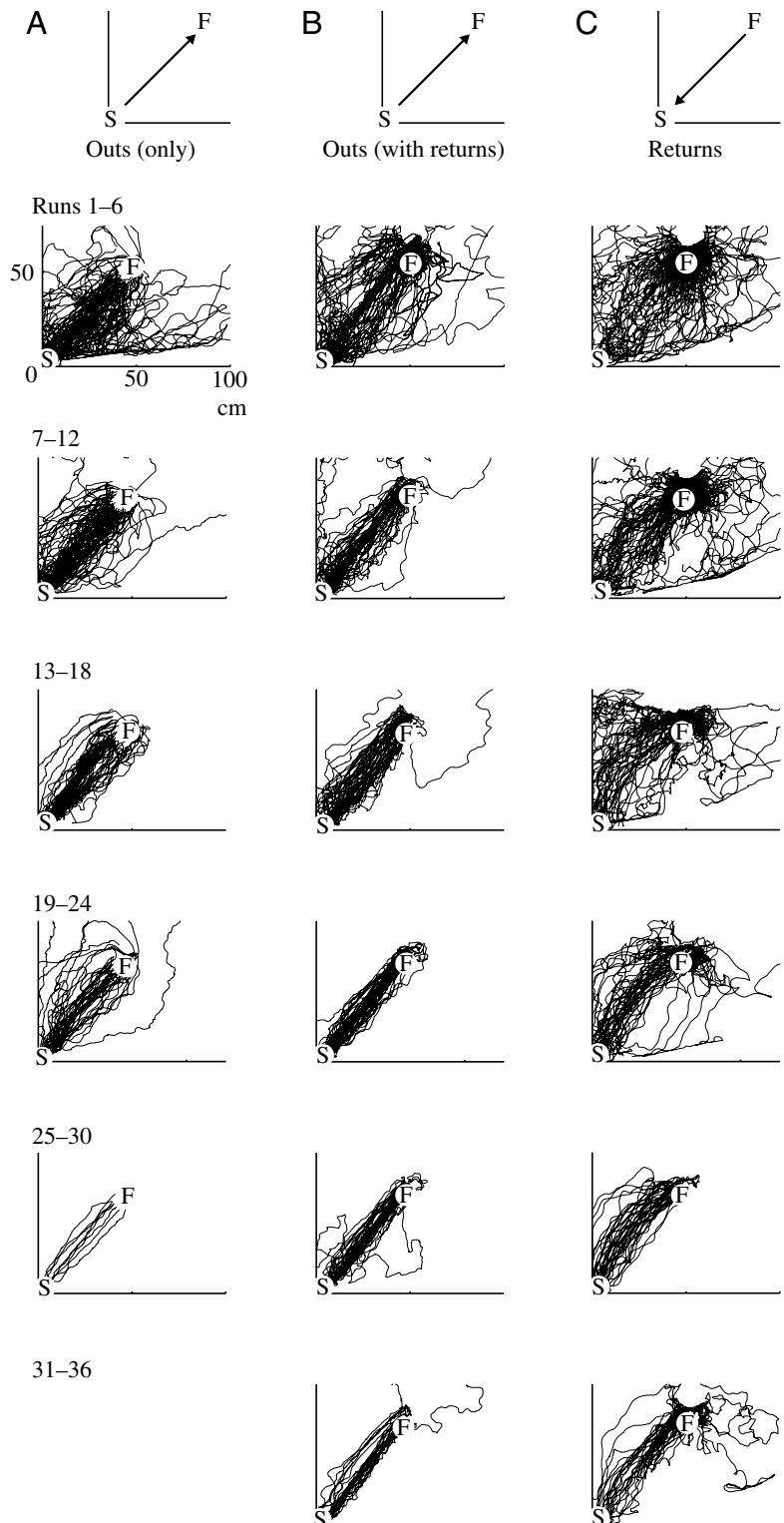

Fig. 3. The development of trajectories. Trajectories are shown grouped by run number. Ants are only included if they survived to perform at least 10 routes. The end of the channel and the food are at (0,0) and (50,50), respectively. Low barriers that were used to constrain ants within the half of the arena containing the feeder influenced the paths on initial runs. (A) Food-bound trajectories of ants (*N*=14) that were carried back to the nest after feeding without performing homeward trajectories. (B,C) The food-bound and homeward trajectories, respectively, of ants that performed round trips (*N*=12).
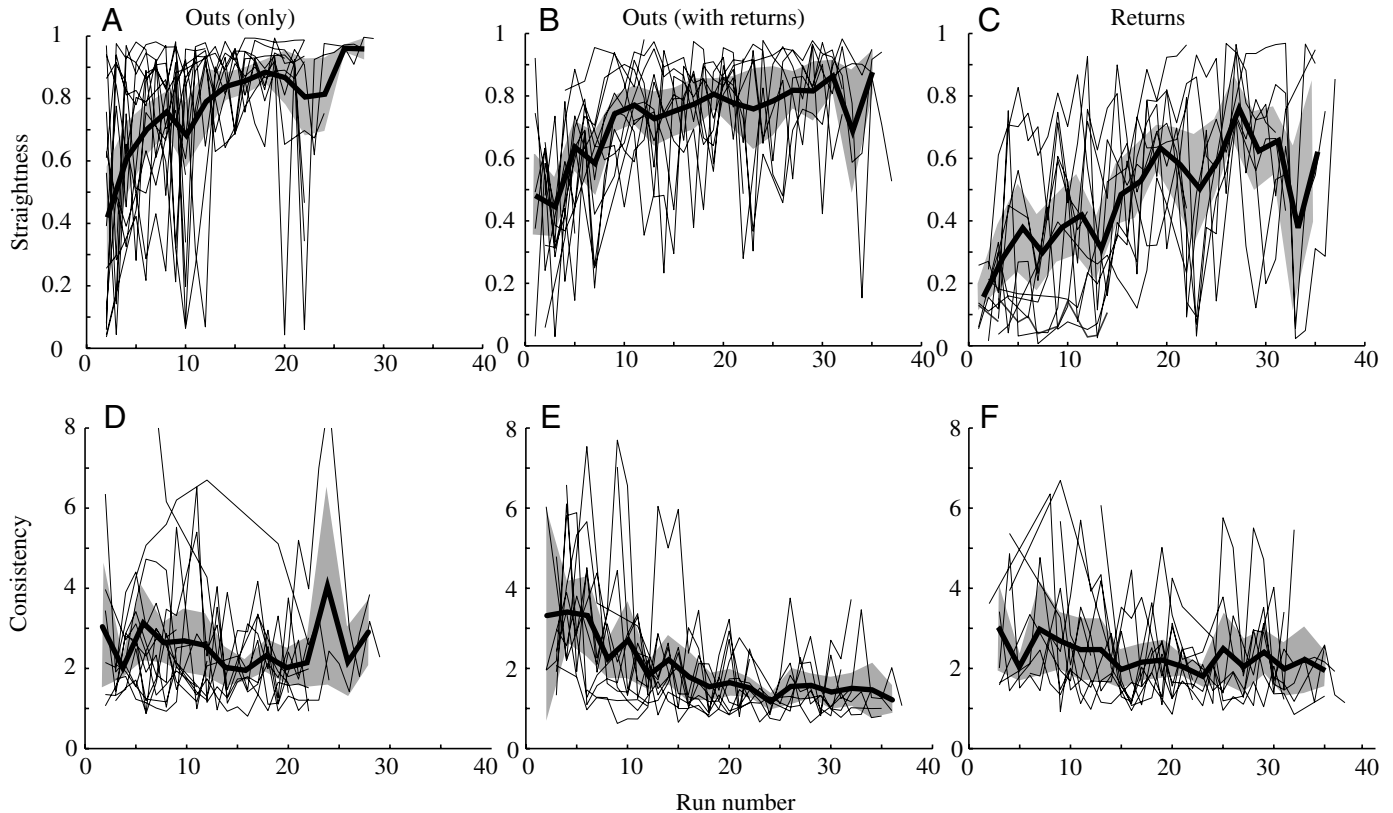
Fig. 4. The straightness and consistency of trajectories. (A–C) Measure of the straightness of food-bound and homeward trajectories plotted against run number. (A) Ants that only performed food-bound routes. (B,C) Ants that performed both food-bound and homeward routes. (D–F) Consistency of trajectories plotted against run number for ants grouped as in A–C. Thin lines plot the straightness or consistency of individual ants over time. The thick black line and the grey area show the overall mean and the 95% confidence interval, respectively. Both straightness (repeated measures ANOVA; $F=39.7$; d.f.=2,48; $P<0.005$) and consistency (repeated measures ANOVA; $F=10.2$; d.f.=2,46; $P<0.005$) improved with experience. There was a significant difference between the groups in their straightness (one-way ANOVA, $F=28.8$; d.f.=2,24; $P<0.005$), but not in their consistency (one-way ANOVA, $F=1.2$; d.f.=2,23; $P=0.313$). The two types of food-bound paths were significantly straighter than homeward paths, but were not significantly different from each other.

Discussion

Evidence is presented that wood ants learn some features of their homeward route on their way to the feeder. Ants that had made 20 or more trips to a feeder, but were always carried home after feeding, tended to move in a roughly homeward direction when they were first allowed to move freely from the food site. These initial homeward paths were biased strongly to the predicted side, but they were not straight, and they were not aimed accurately at the start of the next route segment. The same imprecise and erratic behaviour was seen in the early homeward paths of ants learning foraging routes (Fig. 3).

What did ants acquire during their previous outbound trips that might guide their homeward segments? By testing ants after they were carried to the feeder, we eliminated the possibility that ants just reversed their immediately preceding food-bound trip, either using path integration or by reversing their compass direction. It also seems unlikely that the ants stored the overall compass direction of their habitual outbound trip and then after feeding reversed that direction on their first permitted homeward trip.

We suggest that in the tests ants guide their homeward path

using views that include the rough location of the cylinder, which they have stored on earlier food-bound trips. Because ants cannot see the location of the cylinder from within the channel we suppose that the ants were guided by directional views acquired between the exit from the channel and the food site, and that these views were acquired when ants were facing roughly in the direction of the channel. The third section of the Results contains evidence that ants do reverse direction on this segment of their outward trip, particularly when they are inexperienced.

As outlined in the Introduction, there is clear evidence that bees and wasps acquire information to guide their return to a goal when leaving it. However, the only study to examine when ants acquire homeward route information (Bisch-Knaden and Wehner, 2003) concluded that the desert ant *Cataglyphis fortis* learns homeward local vectors (Collett et al., 1998) only on the homeward journey and not on the food-bound journey. Ants, in the Bisch-Knaden and Wehner study, experienced an array of landmarks close to the feeder either when they approached the feeder from the nest or only when they left the feeder to return to the nest. To accomplish this separation, ants were
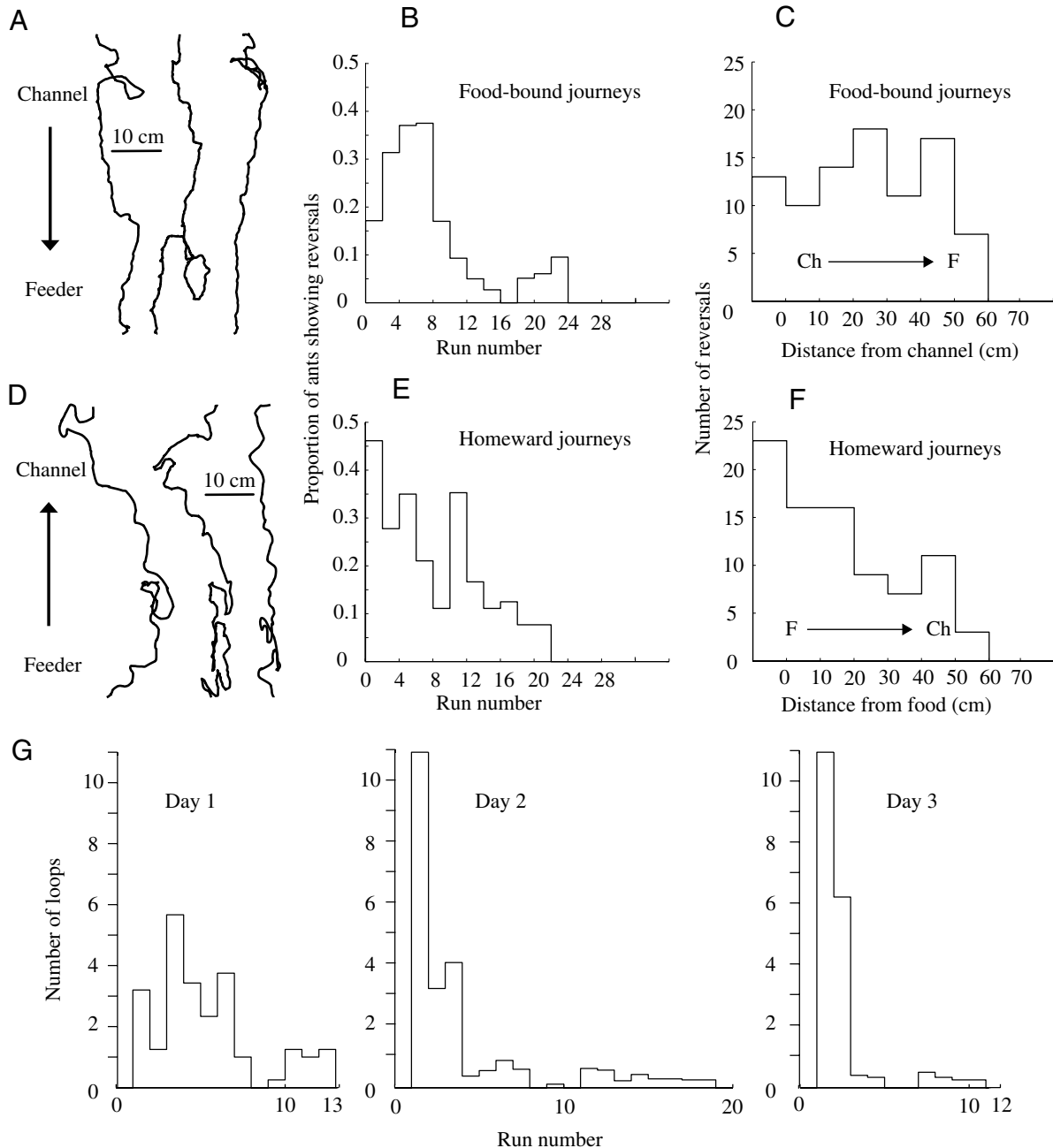
Fig. 5. Temporal and spatial distribution of reversals on food-bound and homeward routes. (A,D) Examples of reversals on food-bound (A) and homeward (D) routes. (B,E) The proportion of ants whose food-bound (B) and homeward (E) trajectories contain reversals is plotted against run number. (C,F) The distribution of reversals along the food-bound (C) and homeward (F) paths is shown relative to the end of the channel. (G) Starting loops from the feeder. The mean number of loops per trajectory is plotted against run number over three successive days. Loops are defined as round trips from, and back to, the feeder in which the ant travels at least 5 cm from the feeder. Data are from 12 ants performing a total of 259 homeward trajectories. The length of each x axis indicates the total number of training runs on that day.

caught at the feeder and carried to a distant site where they performed a homeward trip driven by their path integration home vector. They were caught and returned to the nest as soon as they began to search at the end of their home vector. Each ant was trained over five round trips of this kind before it was tested. For testing, the ant was caught at the end of the home vector and replaced at the departure point. This manipulation ensured that the ants had no global vector and would only move in a defined direction if a response were to be triggered by the landmarks. Ants accustomed to viewing landmarks on their way home exhibited a local homeward-directed vector by travelling a few metres in the direction of their nest. Ants accustomed to landmarks on the way to the feeder searched around the release point in an undirected fashion, as did ants

trained either with no landmarks or with landmarks on both routes and then tested with no landmarks.

The methodologies of the *Cataglyphis* and *Formica* experiments differ in the sense that the wood ants had no experience of a homeward route before testing, whereas the desert ants were trained without landmarks on their homeward route and so could have learnt associations that competed with any reaction to the test landmarks acquired on the food-bound trip. The barren terrain makes interference of this kind unlikely, and the more plausible account is that given by Bisch-Knaden and Wehner, that landmark-induced local vectors are only learnt in the behavioural context in which they are used (Bisch-Knaden and Wehner, 2003). By contrast, the current wood ant data suggest that visual cues to guide the homeward trip may be acquired when ants are in a food-bound motivated state.

If ants travelling their food-bound route acquire views for guiding both their food-bound route and their homeward route, how do they know which of the two sets of stored views they should apply on the way home? Ants must in some manner label memories as being appropriate either for the way out or for the way home. Wood ants, which are familiar with a visually guided route, prime visual memories for their food-bound or homeward trip according to whether they are unfed or have fed (Harris et al., 2005). Similarly, a homeward bound *Melophorus* ignores its food-bound route if placed on it, but will immediately join its homeward route (Wehner et al., 2006). The current data suggest that a wood ant, on acquiring a view on the way to a food site, tags the view as food-bound or homeward according to whether the view is acquired when the ant is facing or moving in the direction of food or home.

One puzzling feature of our data is that it took many trials for the homeward route to straighten. Two possible reasons for the slow development of homeward routes are: (1) The learning of homeward routes relies on path integration more than food-bound routes, and the necessary compass information to sustain path integration is missing in these laboratory experiments. It is worth testing if routes are acquired more rapidly outside and if sky compass cues make it easier for an ant to determine whether a view acquired on the food-bound route should be pigeonholed as information for guiding future food-bound or homeward trips. (2) Segments of routes close to the goal may be learnt faster than more distant segments. In the present experiments, the monitored part of the route consists of the last segment of the food-bound route, but the first segment of the homeward route. However, there is some evidence from bees and ants for a difference in what is acquired on outbound and homeward routes. Honeybees may learn local vectors on their outward but not on their homeward routes (Srinivasan et al., 1997), and data from a recent study on *Formica japonica* navigating out of doors (Fukushi and Wehner, 2004) hints that outward routes may be learnt better than homeward ones.

References

Andel, D. M. and Wehner, R. (2003). Path integration in desert ants, *Cataglyphis*: redirecting global vectors. In *Proceedings of the 29th Göttingen Neurobiology Conference 2003* (ed. N. Elsner), pp. 499. Stuttgart: Thieme Verlag.

Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.

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 Neuroeth. Sens. Neural Behav. Physiol.* **189**, 181-187.

Collett, M., Collett, T. S., Bisch, S. and Wehner, R. (1998). Local and global vectors in desert ant navigation. *Nature* **394**, 269-272.

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

Collett, T. S. and Lehrer, M. (1993). Looking and learning – a spatial pattern in the orientation flight of the wasp *Vespula-Vulgaris*. *Proc. R. Soc. Lond. B Biol. Sci.* **252**, 129-134.

Collett, T. S., Collett, M. and Wehner, R. (2001). The guidance of desert ants by extended landmarks. *J. Exp. Biol.* **204**, 1635-1639.

Fry, S. N., Bichsel, M., Muller, P. and Robert, D. (2000). Tracking of flying insects using pan-tilt cameras. *J. Neurosci. Methods* **101**, 59-67.

Fukushi, T. and Wehner, R. (2004). Navigation in wood ants *Formica japonica*: context dependent use of landmarks. *J. Exp. Biol.* **207**, 3431-3439.

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.

Graham, P., Fauria, K. and Collett, T. S. (2003). The influence of beacon-aiming on the routes of wood ants. *J. Exp. Biol.* **206**, 535-541.

Harris, R. A., de Ibarra, N. H., Graham, P. and Collett, T. S. (2005). Ant navigation – priming of visual route memories. *Nature* **438**, 302.

Judd, S. P. D. and Collett, T. S. (1998). Multiple stored views and landmark guidance in ants. *Nature* **392**, 710-714.

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.

Lehrer, M. (1993). Why do bees turn back and look? *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **172**, 549-563.

Macquart, D., Garnier, L., Combe, M. and Beugnon, G. (2005). Ant navigation *en route* to the goal: signature routes facilitate way-finding of *Gigantiops destructor*. *J. Comp. Physiol. A Neuroeth. Sens. Neural Behav. Physiol.* **192**, 221-234.

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.

Rosengren, R. (1971). Route fidelity, visual memory and recruitment behaviour in foraging wood ants of genus *Formica* (Hymenopterus, Formicidae). *Acta Zool. Fenn.* **133**, 1-106.

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. *J. Exp. Biol.* **200**, 2513-2522.

Tinbergen, N. (1932). Uber die orientierung des Bienenwolfes (*Philanthus triangulum* Fabr.). *Z. Vergl. Physiol.* **16**, 305-335.

von Frisch, K. (1967). *The Dance Language and Orientation of Bees*. London: Oxford University Press.

Wagner, W. (1907). *Psycho-biologische Untersuchungen an Hummeln*. Stuttgart: Schweizerbartsche Verlagsbuchhandlung.

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

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.

Wehner, R., Boyer, M., Loertscher, F., Sommer, S. and Menzi, U. (2006). Ant navigation: one-way routes rather than maps. *Curr. Biol.* **16**, 75-79.

Zeil, J. (1993). Orientation flights of solitary wasps (*Cerceris*, Sphecidae, Hymenoptera). 1. Description of flight. *J. Comp. Physiol. A* **172**, 189-205.