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Bi-directional route learning in wood ants

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Abstract

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.

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., 1992a; 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) and when displaced 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., 2001; Collett et al., 1992b; Graham and Collett, 2002; Macquart et al., 2005).

Visually guided food-ward 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); see Fig 7 B and 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-ward and homeward routes (e.g. Wehner et al., in press), visual information pertaining to the food-ward 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-ward route and vice-versa. Such cross-route learning would help make food-ward 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 by a combination of chemical and visual cues and so may tend to follow the same path in both directions.

In this paper we ask whether information for guiding a wood ant's homeward route can be acquired on the ant's outward route. We test first whether wood ants do learn a part of their homeward route while running a food-bound 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 that were only used to travelling in one direction could perform elements of a homeward route with no help from path integration.

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 (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 such information is acquired 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 twenty or so ants to reach the food site were caught and then marked individually

with two dots of enamel paint. These ants comprised 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 (e.g. Fig. 1a) the floors of which were covered with large (A0) sheets of white paper that were changed regularly to eliminate scent cues. The arenas were placed in the centre of a larger curtained area (280 cm by 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 to a food site at the other end of the arena. The first leg of the route was along an open-topped narrow channel, 10 cm wide, bordered by 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 (Fig. 1a). 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. For this test, the channel was removed, the floor covered with fresh paper to eliminate guidance by chemical trails, and a second cylinder placed as shown in Figure 1b & c. This test was repeated after a further 7-10 outward journeys.

The second experiment investigated the development of food-bound and homeward routes using the same arrangement of channel and cylinder, but in a slightly larger arena (200 cm by 124 cm). We recorded how routes developed in two groups of ants. In order to increase the number of successfully tracked food-bound runs, we attached a short narrow cardboard corridor to the end of the channel and started tracking when the ants emerged from the corridor. The first group performed both food-bound and

homeward routes, and we monitored the paths of individual ants over 30 to 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. 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.

Route analysis

To obtain some 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 the straightness, the path was divided into 2s sections and the heading of each section 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.

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 ants' behaviour after it had made about twenty food-bound trips and no homeward ones. The ant was taken singly from the nest, placed close to a drop of sucrose at the usual feeding site (see Methods), and its path tracked after it had finished feeding (Fig. 2A). After a further 7-10 training runs ants were tested a second time.

The channel was absent in the tests and 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 (Fig. 1 & 2). Graham et al. (2003) showed that wood ants, during route learning, memorise both the appearance of a local landmark and the surroundings in which the landmark is set. They tend to ignore familiar looking landmarks placed in an inappropriate context. Therefore the extra landmark, whilst balancing out any innate attraction to a landmark, will not disrupt any manifestation of a learnt homeward route.

There was no significant difference between the route characteristics of ants' first test runs and their seconds test runs (Sinuosity (mean ± st. dev.), first runs: 0.30±0.27; second runs: 0.27± 0.24; $t(49)=???$, $p=0.65$; Maximum distance reached, first runs: 63±30cm; second runs: 61±28cm; $t(49)=???$, $p=0.76$)

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. The test trajectories for each of these training conditions are shown superimposed as separate density plots in Figure 1b & 1c. Both plots are biased significantly towards the side where the channel and landmark had been during outbound runs. The bias of an individual trajectory was assessed by calculating its mean position on the horizontal (x) axis - with the feeder at x=0. 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 (mean position <0). Whereas most (21/28; sign test, p=0.006) trajectories from ants trained with the channel to the left were biased to the right (mean position > 0).

The individual test trajectories are shown in Figure. 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 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 to 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 Figure. 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 (Fig. 3). The food-bound routes of those ants that performed homeward routes did not differ quantitatively in straightness or consistency from those of ants that were carried home (Fig. 4).

The ants' homeward paths were considerably more variable at the start than were the food bound paths and it took more trials for the routes to stabilise. The first few returns were no more than roughly concentrated in the correct half of the arena. The paths slowly became more direct, but they did not form a tight cluster until returns 25 to 30, even then the paths were curved. Only the final group of paths (returns 31-36) were straight.

It is not clear why homeward routes crystallise more slowly than food-bound routes. Some possibilities 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. 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. 3. There is some asymmetry in what is acquired on outbound and homeward routes. Support for the third suggestion comes from studies on both bees and ants. Honeybees seem to learn local vectors on their outward but not on their homeward routes (Srinivasan et al., 1998), and data from a recent study on *Formica japonica* (Fukushi and Wehner, 2004) hints that outward routes may also be learnt better than homeward ones.

Looking back along food-bound and homeward routes

Ants on the food-bound or homeward leg of their foraging route could give themselves an opportunity of acquiring views for guiding travel in the reverse direction by turning around and then 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 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. These ants usually remerged to walk to the feeder. Such complete loops occurred on about 25% of early runs. Loops became rarer as ants became experienced with the route. No loops occurred after run 12.

More frequently, ants turned back, retraced their path for a short segment and then continued with the food-bound segment. 27 out of 29 trained ants reversed direction at least once. These reversals were usually marked by the ant looping or making a U-bend (e.g., Fig. 5A). Most reversals were less than 3cm 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

On early runs ants often moved away from the feeder and then looped back after a short excursion. 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).

Short reversals are also seen on paths that successfully reach the channel exit. 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 occur most frequently on early trials (Fig. 5E) Homeward reversals differ 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 are not evenly distributed along the route, but have 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.

Discussion

Evidence is presented that wood ants learn some features of their homeward route on their way out to the feeder. Ants, which had made twenty 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.

While, 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, the conclusion

from one study to examine when homeward route information is acquired (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-ward journey. Ants, in this 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 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 when they began to search at the end of their home vector. Each ant was trained over 5 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 home 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-ward trip. The barren terrain makes interference of this kind unlikely, and the more plausible account is that given by Bisch-Knaden and Wehner

(2003) that landmark induced local vectors are only learnt in the context in which they are used. In contrast, the current wood ant data suggest that visual cues to guide the homeward trip may be acquired when ants are in a food-ward 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-ward or homeward trip according to whether they are unfed or have fed (Harris et al., 2005). Similarly, a homeward bound *Melophorus* ignores its food-ward route if placed on it, but will immediately join its homeward route (Wehner et al. in press). The current data suggest that a wood ant on acquiring a view on the way to a food site tags the view as foodward or homeward according to whether the view is acquired when the ant is facing in the direction of food or home.

One worrying characteristic of our data is that it took many trials for the homeward route to straighten. This slow development of the route may result from the absence of sky compass information within the laboratory. Repetition of the experiment out of doors, where the ant's sky compass could operate normally, might both speed up route acquisition and also make it easier for an ant to determine whether a view acquired on the food-ward route should be pigeonholed as information for guiding future food-ward or homeward trips.

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). 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. *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology* **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. (1992a). Visual landmarks and route following in desert ants. *J. Comp. Physiol. A.* **170**, 435-442.

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

Collett, T. S., Dillmann, E., Giger, A. and Wehner, R. (1992b). Visual Landmarks and Route Following in Desert Ants. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology* **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. *Proceedings of the Royal Society of London Series B-Biological Sciences* **252**, 129-134.

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

Fukushi, T. and Wehner, R. (2004). Navigation in wood ants Formica japonica: context dependent use of landmarks. *Journal of Experimental Biology* **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. *Journal of Experimental Biology* **205**, 2499-2509.

Graham, P., Fauria, K. and Collett, T. S. (2003). The influence of beacon-aiming on the routes of wood ants. *Journal of Experimental Biology* **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**, 302-302.

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

Lehrer, M. (1993). Why Do Bees Turn Back and Look. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology* **172**, 549-563.

Macquart, D., Garnier, L., Combe, M. and Beugnon, G. (2005). Ant navigation *en route* to the goal: dignature routes facilitate way-finding of *Gigantiops destructor*. *J. Comp .Physiol. A.*

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). *Journal of Experimental Biology* **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 Lehrer, M. (1998). Honeybee navigation: odometry with monocular input. *Animal Behaviour* **56**, 1245-1259.

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 Untersuschungen an Hummeln. Stuttgart: Schweizerbartsche Verlagsbuchhandlung.

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

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

Zeil, J. (1993). Orientation Flights of Solitary Wasps (Cerceris, Sphecidae, Hymenoptera) .1. Description of Flight. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology* **172**, 189-205.

Figure 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. In tests ants were taken directly from the nest and placed on a feeder (indicated by **F**). Two landmarks were positioned symmetrically in the arena. **B, D:** Cumulative density distributions of all return trajectories from ants trained with the channel to 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.

Figure 2. **The ants' first and second trips home after many food-bound runs**. **A:** Trajectories of ants after leaving the feeder. Trajectories ended after 6 min or before if the camera 'lost' the ant. Trajectories are shown from when the ant has reached at least 10cm from the feeder and end points are marked by small black circles. Trajectories from ants trained with the channel on the right hand side of the direct route to the food have been mirrored to correspond with the training arrangement shown in Figure 1A. **B, C, D:** Circumferential positions of ants at 20cm, 40cm and 60cm 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.

Figure 3. **How trajectories change with experience.** Trajectories are shown grouped by run number. Ants are only included if they had performed 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 with out performing homeward trajectories. **B,C:** The food-bound and homeward trajectories, respectively, of ants that performed round trips (N=12).

Figure 4. **Improvements in the straightness and consistency of trajectories. A,B,C:** Measure of the straightness of food bound and homeward trajectories plotted against run number. A: ants that only performed food-bound routes. B and C, ants that performed both food-bound and homeward routes. **D,E,F:** Consistency of trajectories plotted against run number for ants grouped as in A to C. Thin lines plot the straightness or consistency of individual ants. The thick black line and the grey area show the overall mean and the 95% confidence interval respectively. To assess the statistical significance of any changes, 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. Both straightness (repeated measures ANOVA; $F = 39.662$, DF2, 48, $p < 0.005$) and consistency (repeated measures ANOVA; $F = 10.152$, DF2, 46, $p < 0.005$) improved with experience. The types of route differed significantly in their straightness (One-way ANOVA, $F = 28.825$, DF 2, 24, $P < 0.005$), but not in their consistency (One-way ANOVA, $F = 1.223$, DF 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.

Figure 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:** Closed 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 come from 12 ants performing a total of 259 homeward trajectories. The length of each X-axis indicates the maximum number of training runs on that day.

Figure 1

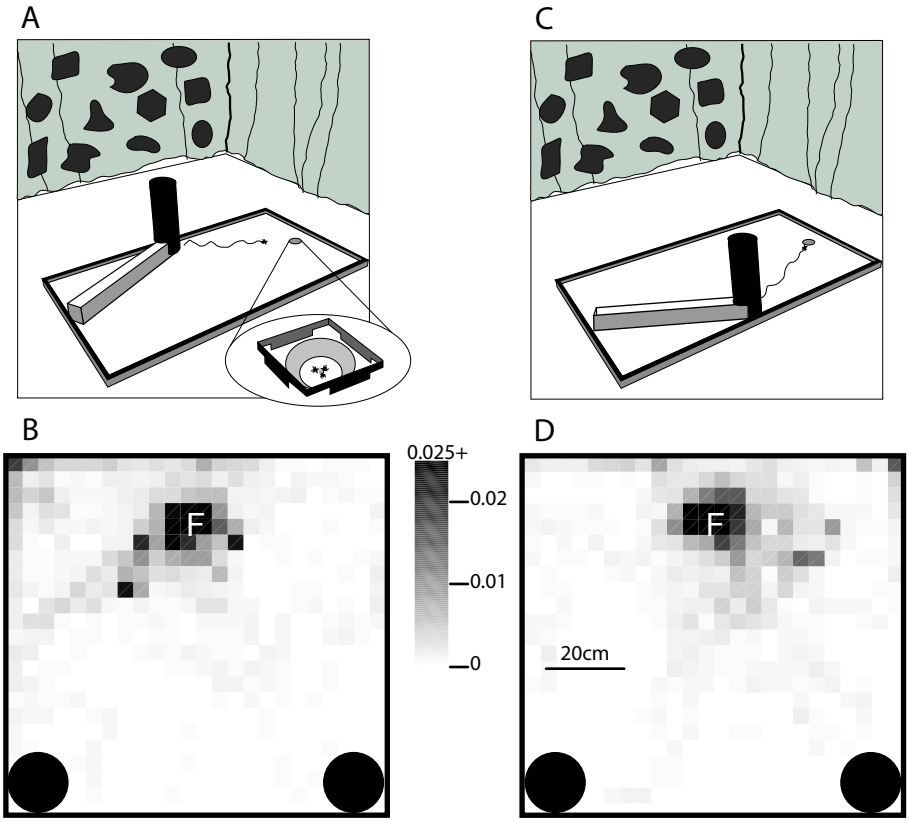


Figure 2

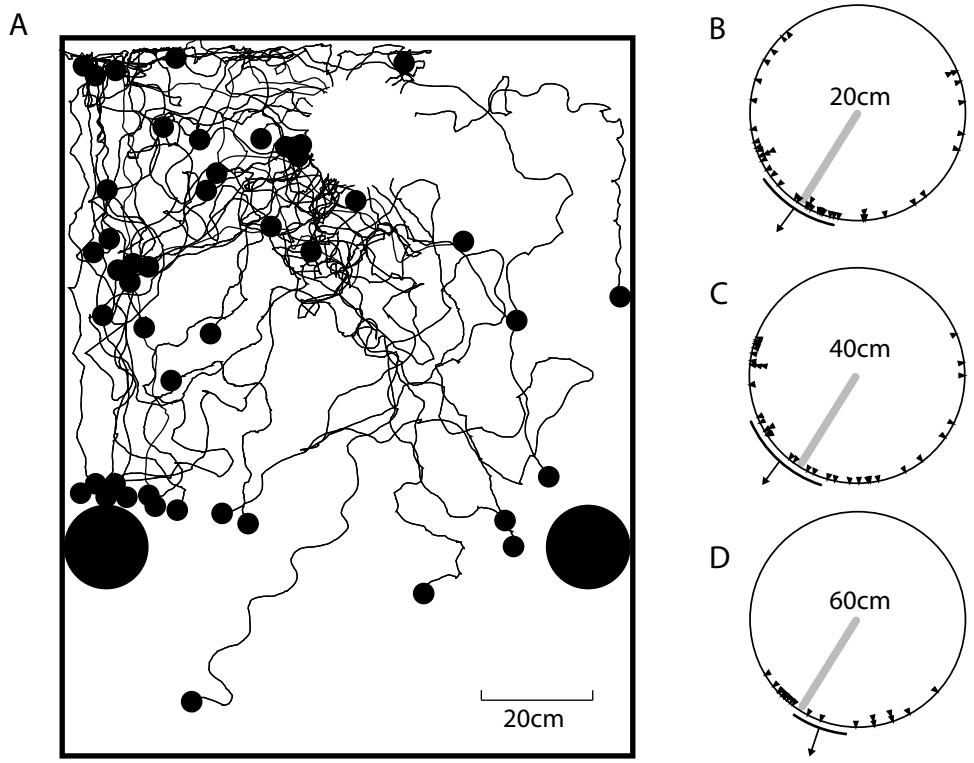


Figure 3

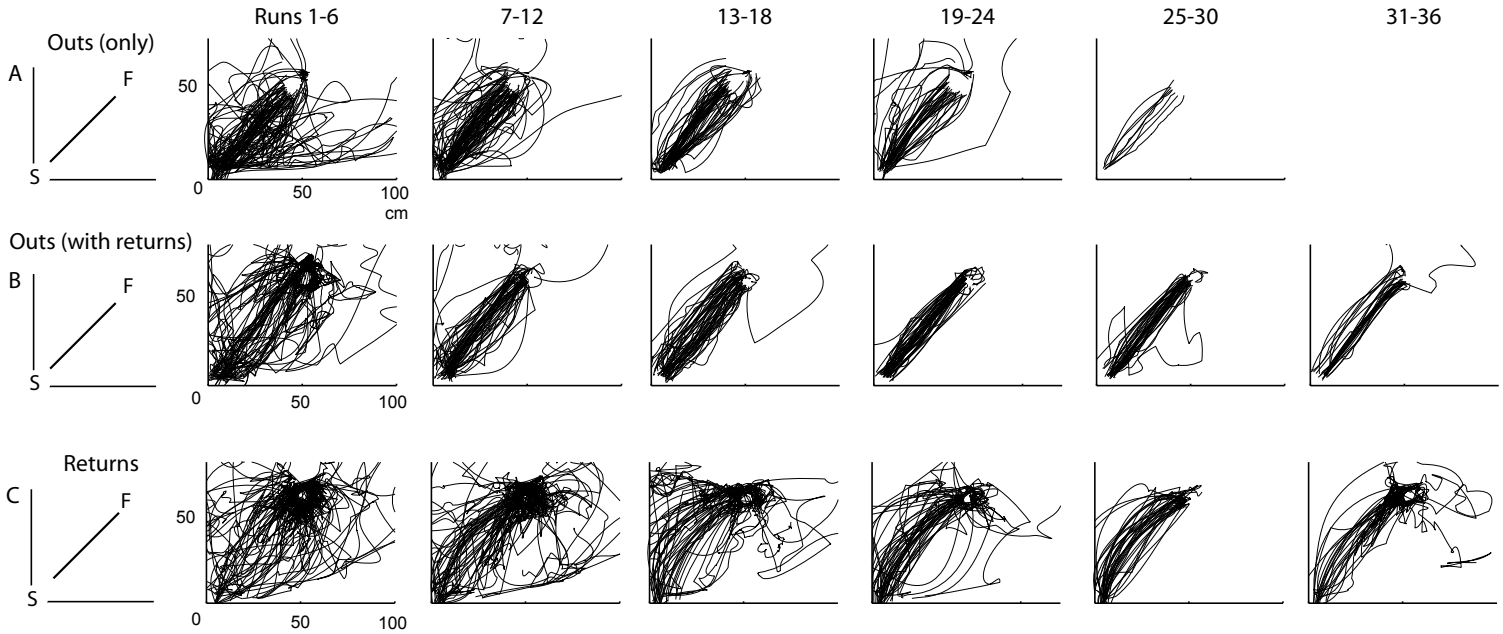

Runs 1-6
7-12
13-18
19-24
25-30
31-36
Outs (only)
A
F
S
50
0
50
100
cm
Outs (with returns)
B
F
S
50
0
50
100
Returns
C
F
S
50
0
50
100

Figure 4

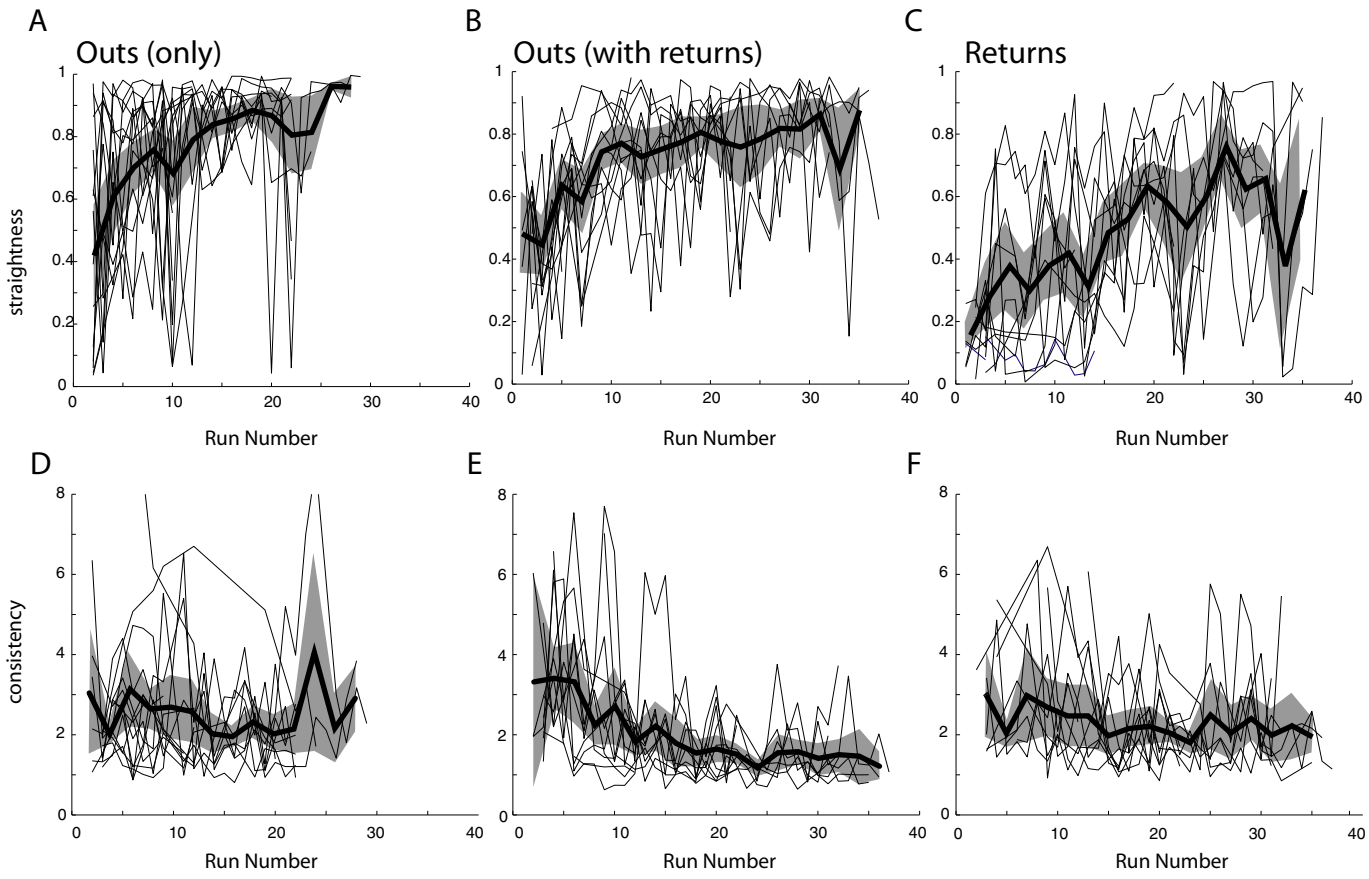
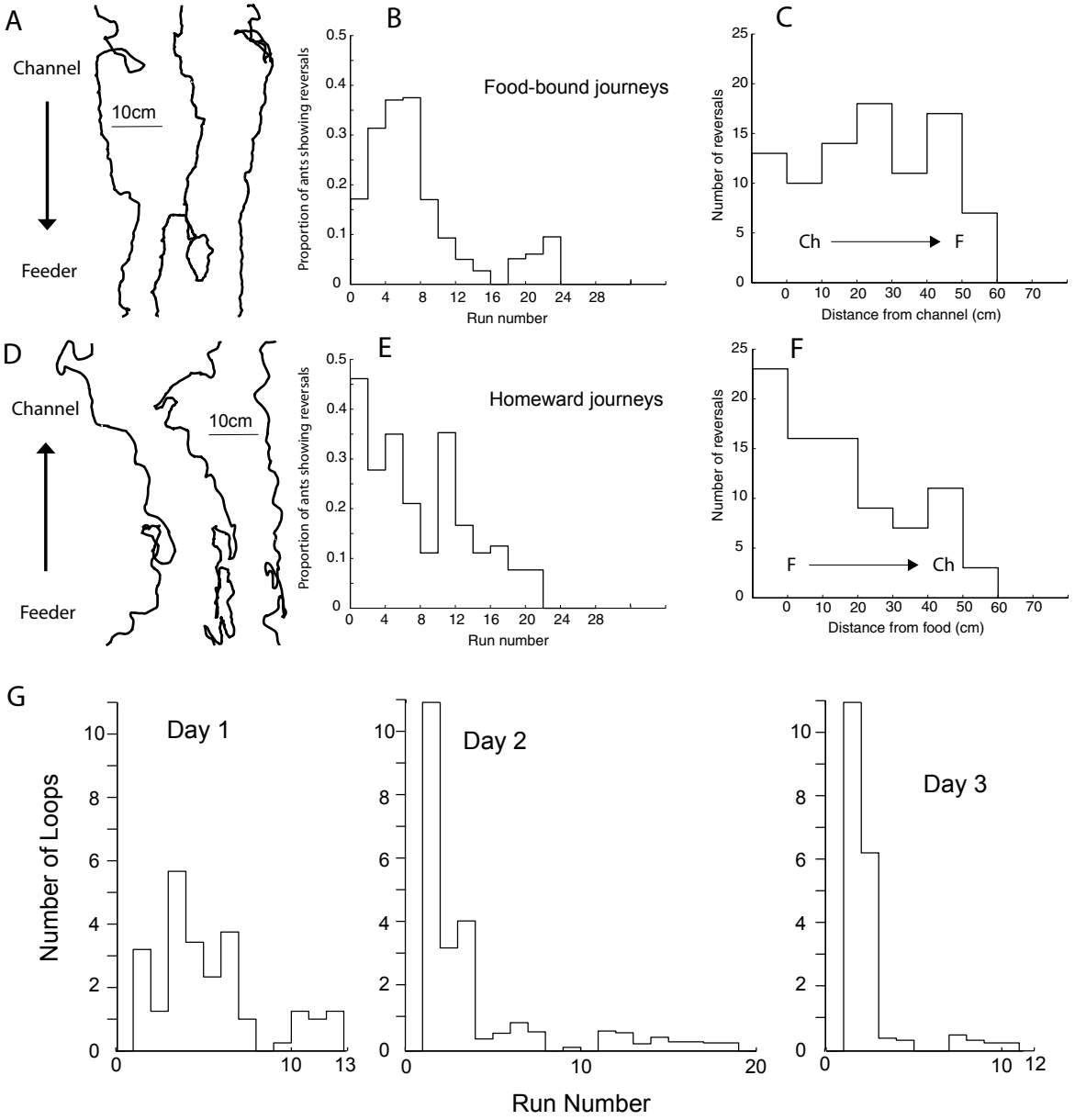

A
Outs (only)
B
Outs (with returns)
C
Returns
straightness
Run Number
D
E
F
consistency
Run Number

Figure 5


A
Channel
10cm
Feeder
B
Food-bound journeys
Proportion of ants showing reversals
Run number
C
Number of reversals
Ch
F
Distance from channel (cm)
D
Channel
10cm
Feeder
E
Homeward journeys
Proportion of ants showing reversals
Run number
F
Number of reversals
F
Ch
Distance from food (cm)
G
Day 1
Day 2
Day 3
Number of Loops
Run Number