

# How do insects use path integration for their navigation?

Matthew Collett<sup>1</sup>, Thomas S. Collett<sup>2</sup>

<sup>1</sup> Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

<sup>2</sup> Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1, 9QG, UK

Received: 6 June 1999 / Accepted in revised form: 20 March 2000

**Abstract.** We combine experimental findings on ants and bees, and build on earlier models, to give an account of how these insects navigate using path integration, and how path integration interacts with other modes of navigation. At the core of path integration is an accumulator. This is set to an initial state at the nest and is updated as the insect moves so that it always reports the insect's current position relative to the nest. Navigation that uses path integration requires, in addition, a way of storing states of the accumulator at significant places for subsequent recall as goals, and a means of computing the direction to such goals. We discuss three models of how path integration might be used for this process, which we call vector navigation. Vector navigation is the principal means of navigating over unfamiliar terrain, or when landmarks are unavailable. Under other conditions, insects often navigate by landmarks, and ignore the output of the vector navigation system. Landmark navigation does not interfere with the updating of the accumulator. There is an interesting symmetry in the use of landmarks and path integration. In the short term, vector navigation can be independent of landmarks, and landmark navigation needs no assistance from path integration. In the longer term, visual landmarks help keep path vector navigation calibrated, and the learning of visual landmarks is guided by path integration.

---

## 1 Introduction

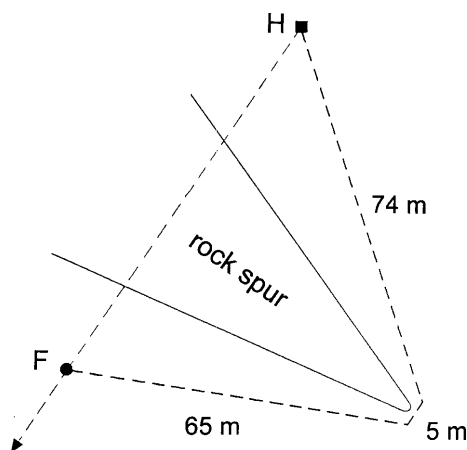
For centuries, until the age of global positioning technology, mariners relied on landmarks and dead reckoning for reliable navigation between goals. Mariners used a compass, a length of knotted rope and a clock to measure velocity. When following a steady course, they could monitor the net distance and direction travelled. To keep track of their routes, and

to communicate routes to others, sailors have produced maps recording their travels. The earliest maps were effectively one dimensional, recording a sequence of landmarks along a coastline or river. Dead reckoning allowed navigation across open seas, and the construction of two-dimensional charts to provide a record of the directions and distances between landmarks and goals. With charts, a sailor could either follow a sequence of landmarks or use dead reckoning, but often the two were combined: the eventual sighting of landmarks after a period in open sea was used to correct the calculated position of the ship. The two navigational techniques could also be combined to improve the accuracy of the charts themselves.

Like the ancient sailors, animals use both landmarks and dead reckoning for navigation. In animal navigation, dead reckoning has come to be known as 'path integration' (Mittelstaedt 1983). It is particularly useful on bare or unfamiliar terrain, when there are no visual landmarks or scent marks to provide guidance cues. Path integration is thus of particular importance to cataglyphid ants that inhabit largely featureless desert areas (Wehner and Srinivasan 1981; Wehner and Wehner 1990), and these ants feature prominently in our discussion. Path integration has an additional function for honeybees, which use it in communicating the location of a food source (von Frisch 1967). In both these insects, path integration is particularly well studied, and few fundamental differences in its functioning have been observed. We bring together recent results from desert ants with work on honeybees, and try to provide an overall framework within which we can discuss what behavioural experiments can reveal about how path integration is employed in navigation.

## 2 Three demonstrations of path integration

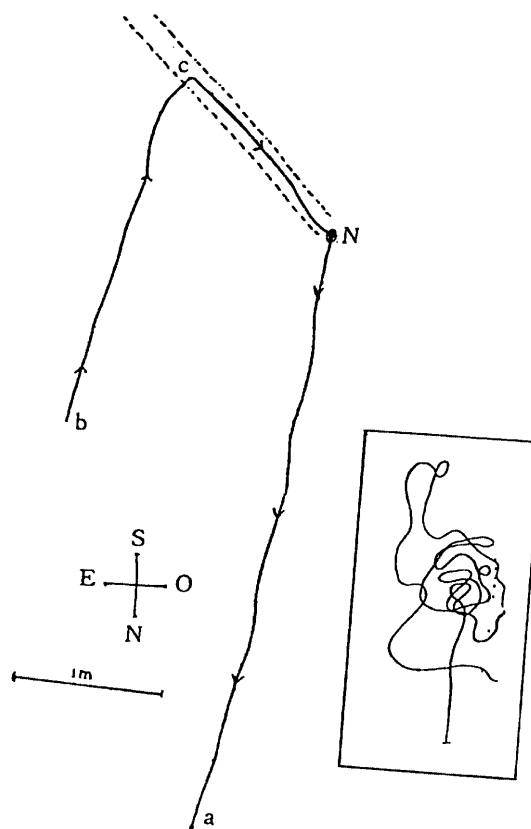
Honeybee foragers communicate the position of a food source through their waggle dance, using information that can only be acquired through path integration (reviews: von Frisch 1967; Gould 1976). The dance signals the location of the food in terms of its direction



**Fig. 1.** Detour experiment in honeybees. Honeybees are trained to fly around a tall spur of rock from their hive, *H*, to a feeder, *F*. The direction that the bees signal on the surface of a horizontal comb corresponds precisely to the direction of the straight line between *H* and *F*. Mean direction of 20 dances is shown by the arrowhead (adapted from von Frisch 1967)

and distance from the hive. Direction is defined in terms of the horizontal angle made by the feeder, the hive, and the azimuthal position of the sun. On the dark, vertical comb inside the hive, this angle is signalled by the angle of the bee's long axis with respect to gravity during the waggle phase of the dance, and the distance of the food is encoded by the number of waggles per circuit. Recruits can use the information of the dance to reach the approximate location of the feeder. Bees detouring round a large rock or building between their hive and feeder signal the direction of the straight line between the two, although they have never flown the direct path (Fig. 1). The recruited bees do not follow the initial foragers, but try to fly the direction indicated by the dance. So to both human and bee observers, the dance provides the results of path integration with no information about landmarks or detours.

At the beginning of this century, Piéron (1904) reported the first experiment to reveal that ants perform path integration. He displaced a foraging ant that was returning home, and found that whether the ant was released on unfamiliar, or familiar, ground it continued on its path as though it had not been moved, and started searching at the point where its trajectory would have reached the nest had the ant not been displaced. The ant's accurate knowledge of its home direction from its point of capture is evident in the direction of its trajectory after displacement, while its knowledge of distance is expressed by an action that the ant performs when it thinks it is in the vicinity of its nest. As Santschi (1913) wrote a few years later: "In the displacement tests of Piéron, when the ant has completed a trajectory that she considers sufficient to have brought her near to the nest, she performs 'un tournoiement de Turner', [now called searching behaviour (Wehner and Srinivasan 1981)] ... which is totally independent of visual or odour cues." We illustrate this early finding by a drawing of Santschi (Fig. 2). It shows an example of dead reckoning after



**Fig. 2.** Early displacement experiment on a foraging ant (*Messor barbarus sancta*). *N* Nest, *a* capture site on outward trip, *b* release site. The line shows the ant's track. After displacement, the ant walks parallel to its outward path until it meets a familiar path at *c* along which it returns to its nest. Boxed inset shows 'tournoiement de Turner' from another displacement experiment (from Santschi 1913)

displacement in which both outward and homeward routes are straight. The ant (*Messor barbarus sancta*) was caught at *a* with a bait of a stick of vermicelli and transported two metres NE to *b* where it ran back parallel to its outward path until it encountered a familiar path at *c*, which it then took to regain its nest. In modern displacement tests, foragers are removed to a distant test field where no familiar landmarks are available (e.g. Wehner and Srinivasan 1981). The inset of Fig. 2 shows an example of the searching behaviour occurring where path integration indicates the nest should be.

The third example is an experiment to test whether ants, like honeybees, can use path integration to head towards a previously visited feeder. Observations that desert ants direct their path across open ground from their nest to a site where they have previously found food (Wehner et al. 1983; Schmid-Hempel 1984; Wehner 1987) provide circumstantial evidence that ants use vector navigation to reach the food site. Proof from displacement experiments, however, is difficult because foraging ants when disturbed tend to return to their nest rather than to continue foraging. An alternative approach to removing the ants from a familiar landscape for testing is to remove the landscape from the ants during training (Collett et al. 1999). A nest of

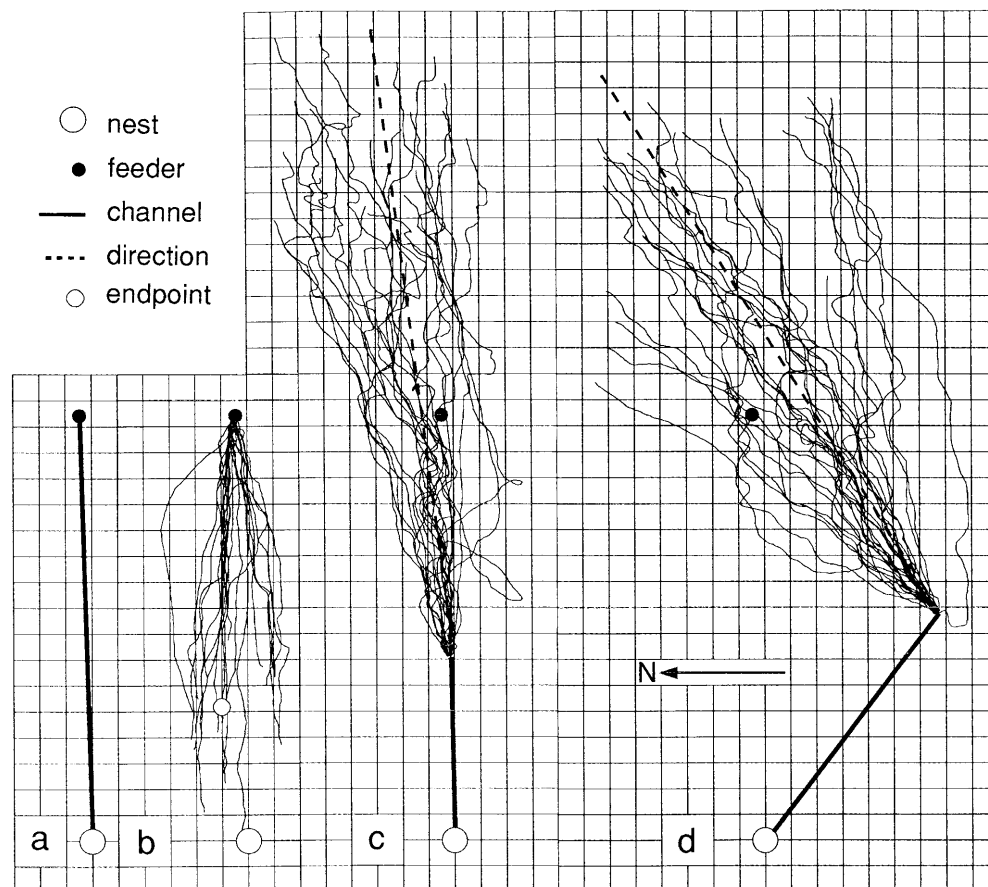
*Cataglyphis fortis* was enclosed and a single exit led to a 15-m channel along which ants were trained to a feeder (Fig. 3a). Foragers were confined to this channel for the whole foraging trip so that, although they could see the sky, and determine their direction of travel, the surrounding landscape was always hidden from view. Ants were released singly from the enclosure into a shortened channel that either pointed in the same direction (Fig. 3c) as in training or was rotated through 38° (Fig. 3d). After leaving the channel, ants ran over unfamiliar open ground in the approximate direction of the food site. Their ability to approach this unfamiliar site from two different directions indicates that they had recorded its co-ordinates relative to the nest and that they navigated by path integration to reach it. In this case, ants do not perform searching behaviour (cf. Schmid-Hempel 1984), perhaps because the position of food is less predictable than that of the nest and so requires additional familiar cues to initiate this behaviour.

The three demonstrations of path integration are similar. In each case, after reaching a food source, the foragers are able to reproduce, symbolically in the case of the waggle dance, both the direction and the distance that they have travelled. And they do this in a new context in which none of the original landmarks are present. Performing path integration while heading towards a goal makes it possible to recover from an imposed detour. A forager that has been forced away from

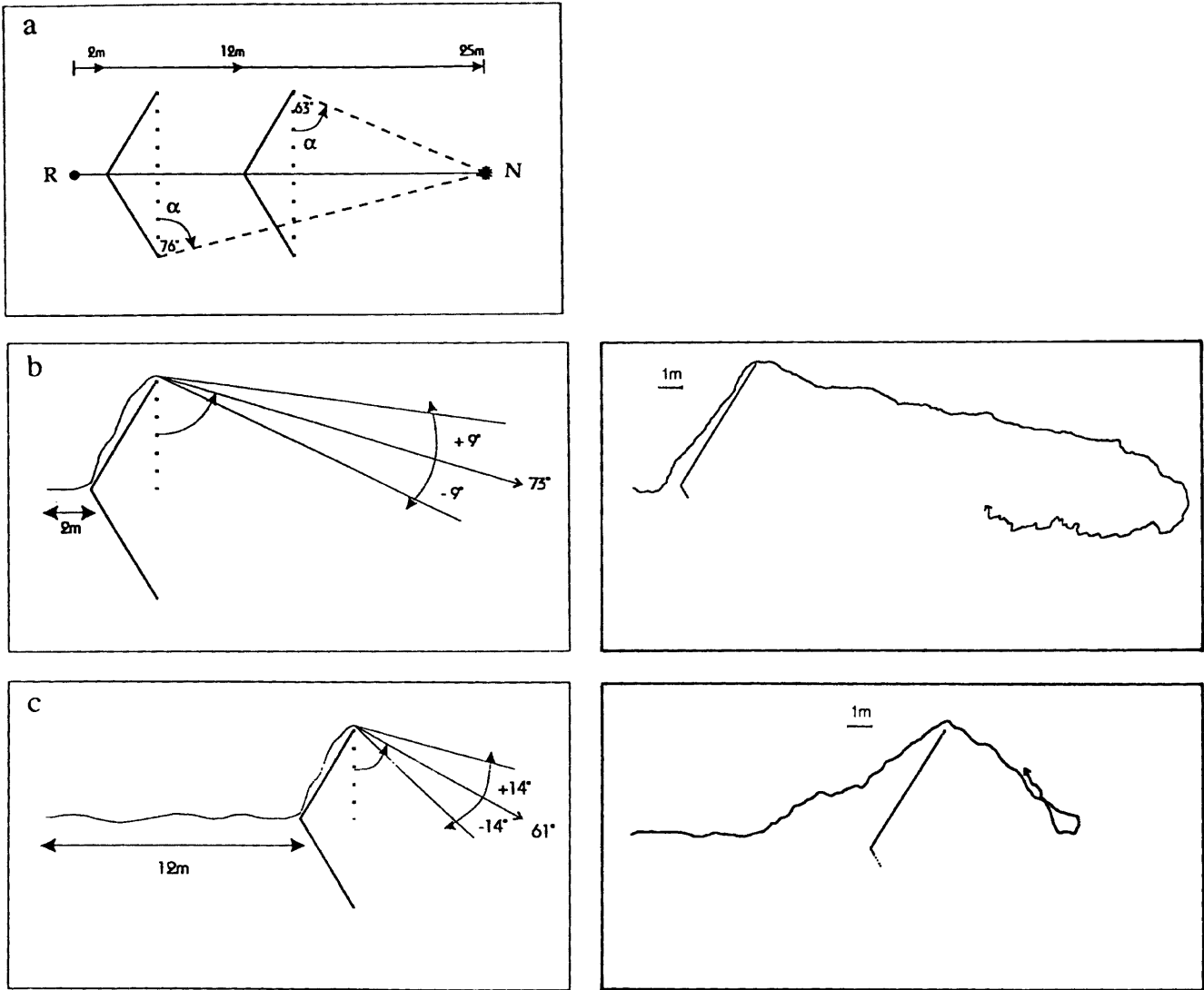
its direct route reorients towards the goal as soon as its path is unconstrained whether the goal is a feeder (Fig. 3) or the nest (Fig. 4).

### 3 Vector navigation

To perform path integration, a forager must be able to monitor changes in its position by updating some kind of accumulator (e.g. Mittelstaedt 1983). A mechanical analogue of an accumulator is the traverse board used by navigators for dead reckoning (Fig. 5). For a forager simply to return to the nest, an accumulator alone could be sufficient. The accumulator would have a special 'zero' state at the nest, and the subsequent states of the accumulator would specify the position of the forager with respect to the nest. The direct route to the nest would be given by the current accumulator state. The ability to navigate to a specific food source, however, requires two additional features: a way of recording the accumulator state at a food source (Mittelstaedt 1983), and a comparator which effectively subtracts the current accumulator state from the recorded state (see below and Collett et al. 1999). We find it useful to use the term 'vector navigation' to describe the ensemble of processes of updating an accumulator, recording an accumulator state, and combining the current and recorded accumulator states in order to direct movement towards that goal.

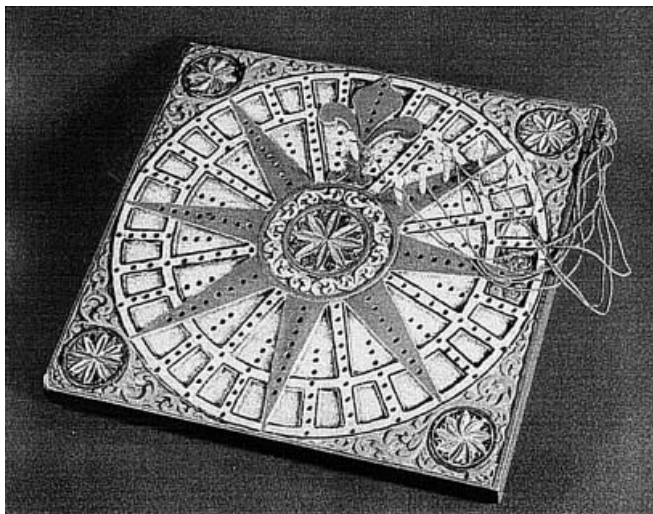


**Fig. 3.** Vector navigation to a feeder in *Cataglyphis fortis*. *a* Training route. Ants travel 15 m from their nest along an eastward pointing channel to a feeder. *b* Homing trajectories of ants taken from the feeder and released in a test area. *Large open circle* shows position of fictive nest. *Small circle* indicates mean endpoint at 11.1 m from the nest. *c* Individual foraging trajectories of ants on open ground after they have left a shortened channel connected to the nest. *Filled circle* marks the usual position of food which is absent in these tests. Mean direction  $83.95^\circ$ ,  $SD \pm 6.53^\circ$ ,  $n = 21$ . *d* Individual foraging trajectories of ants after leaving a channel pointing  $38^\circ$  to the east of the training channel. Mean direction  $(58.28^\circ)$ ,  $SD \pm 12.15^\circ$ ,  $n = 28$  is significantly ( $P < 0.01$ ) to the east of the direct path from the end of the channel to the feeder. Grid lines are spaced at 1 m (from Collett et al. 1999)



**Fig. 4a-c.** Vector navigation to the nest after an enforced detour. Ants (*C. fortis*) were trained to a feeder 25 m from the nest. They were taken from the feeder to a test area where a 10 cm high, V-shaped barrier was placed in the direct path of their homeward trajectory. On leaving the barrier, the ants turned immediately towards the virtual

nest. **a** Predicted directions (*dashed lines*) when released 2 m or 12 m from barrier. *R* Release site, *N* Virtual nest. **b, c** Means and standard deviations of the direction of the ants trajectories immediately after leaving the barrier. *Right column:* individual examples of complete trajectories (from Schmidt et al. 1992)



The operation of the vector navigation system can be formulated in the following way. Let  $\mathbf{x}$  be the current state of the accumulator and  $\mathbf{g}$  the state of the accumulator a forager expects to have on reaching the goal. The output of the vector navigation system is given by  $\mathbf{v}$ , where

$$\mathbf{v}(\mathbf{x}, \mathbf{g}) = \mathbf{g} - \mathbf{x} \quad (1)$$

This rule produces straight trajectories to the point where  $\mathbf{v}(\mathbf{x}, \mathbf{g}) = \mathbf{0}$ , i.e. where  $\mathbf{x} = \mathbf{g}$ . At this point, an ant



**Fig. 5.** Early nineteenth century replica of a traverse board used for dead reckoning. During a voyage, navigators insert pegs into the radially arranged holes at equidistant intervals to mark the direction travelled during that interval. The ship's net distance and direction from the starting point can be obtained by performing vector addition on the lines of filled holes

returning to its nest will start its search behaviour. We see that there are four pieces of information to be encoded: the accumulator state, the remembered position of a goal, the output of a comparator, and the output of the vector navigation system. It might be sufficient for the output to provide only directional information, but otherwise all four pieces of information must specify both length and direction. We use bold script to emphasise that  $\mathbf{v}$ ,  $\mathbf{x}$ ,  $\mathbf{g}$ , and  $\mathbf{0}$  must therefore effectively be vectors, and that the comparison,  $-$ , must be a vector computation. In insects, nothing is known of the neural circuitry involved, or how the information might be encoded.

#### 4 Using the accumulator

Like sailors, bees and ants have instruments to monitor the path along which they move. They use a sun and polarised light compass for measuring direction (reviews: von Frisch 1967; Wehner and Rossel 1985; Dyer and Dickinson 1996; Lambrinos et al. 1997). It has recently been established that flying bees measure the distance that they travel by recording optic flow (Esch and Burns 1996; Srinivasan et al. 1996, 1997). The situation is less clear in ants (Ronacher and Wehner 1995) or in walking bees (Schöne 1996) and ‘step counting’ or proprioceptive information is likely to be more important. The direction and distance information must then be used to update an accumulator. There has been extensive modelling of path integration itself, that is the process by which the accumulator is updated (Jander 1957; Mittelstaedt and Mittelstaedt 1973; Mittelstaedt 1983; Müller and Wehner 1988; Gallistel 1990; Benhamou and Séguinot 1995; Hartmann and Wehner 1995; Maurer and Séguinot 1995; Wittman and Schwegler 1995; Maurer 1998). In this review we side-step this issue, to focus on how an accumulator may be used during navigation.

There are two broadly different possibilities. First, the accumulator may be updated continuously, so that on returning to the nest the accumulator state is the same as that on leaving (Mittelstaedt 1983). Alternatively, the updating process may be interrupted during the journey: the accumulator reset at the nest and at the turning point, and the polarity of the compass inverted. The state of the accumulator on returning to the nest is then the same as its state at the turning point (Collett et al. 1999). In the latter ‘discontinuous’ use of path integration, a forager’s accumulator state at a site would differ between the outward and return journeys.

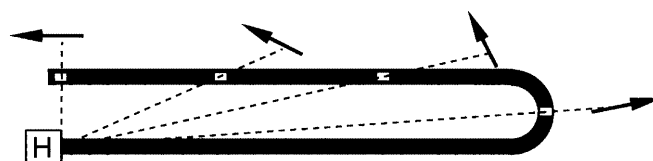
To understand how different models of vector navigation work, it is important to be able to describe how the accumulator state is related to the forager’s position. Intuitively, we can think of a Cartesian co-ordinate system with the origin at the nest. We define a site’s ‘co-ordinates’ to be the accumulator state that defines the position of a site with respect to the nest. This rather pedantic definition allows us to write a forager’s co-ordinates,  $\mathbf{c}(\mathbf{x}, \mathbf{f})$ , in terms of its current accumulator

state,  $\mathbf{x}$ , and the co-ordinates of the food site which is its present or most recent goal,  $\mathbf{f}$ . As we shall see, the relationship depends on the model, and whether a forager is outbound or nestbound.

With a continuous model of the updating process, there is a fixed relationship between the co-ordinates of a forager and the state of its accumulator [ $\mathbf{c}(\mathbf{x}, \mathbf{f}) = \mathbf{x}$ ]. On finding food, the forager records its accumulator state ( $\mathbf{f} = \mathbf{x}$ ), and subsequent trips to this food site are guided by using the comparator to bring the accumulator to this recorded state ( $\mathbf{g} = \mathbf{f}$ ). So that information about food sites can survive occasions when the forager returns to the nest with the accumulator not in its initial state, the accumulator must be set to a ‘zero’ state before leaving the nest. The accumulator states are then all in relation to this zero state. The return to the nest is guided by bringing the accumulator state back to the zero state ( $\mathbf{g} = \mathbf{0}$ ). In order to do this, the accumulator must perform the, perhaps difficult, feat of exactly compensating for the outward path; ‘emptying’ and ‘filling’ the accumulator would need to be exact inverse operations.

Two experimental results cast doubt that it is the continuous model which is implemented in ants and bees. The first comes from a study on honeybees, which suggests that an accumulator would not return to its initial state by retracing a path towards the nest. Bees were made to walk from the nest to a feeder along a long U-shaped channel (Bisetzky 1957). Although the site of the feeder was close to the hive, the dances indicated an accumulator state at the feeder quite different from the initial state (Fig. 6). If bees were to integrate accurately their path from the hive through the U to the feeder, they should perform a round dance indicating the proximity of the feeder to the hive. The second result, which suggests a discontinuity in the use of the accumulator, is the relationship between the outward and homeward trajectories of ants whose vector navigation system is transformed by training (Collett et al. 1999). We discuss this in Sect. 6.

Discontinuous models incorporating a single accumulator used for vector navigation require that the accumulator be reset at both the nest and the point at which a forager turns back to the nest, and that at both these points the polarity of the compass is inverted. From the perspective of the accumulator, vector



**Fig. 6.** Direction of waggle dance performed by honeybees after walking to and from a feeder that was positioned within a U-shaped glass-roofed tunnel (thick black line). The tunnel was connected to the hive ( $H$ ), with the hairpin bend 425 cm from the hive. In four separate experiments, the feeder (white rectangle) was placed at different locations along the tunnel. Dashed lines show predicted direction of waggle dance on the assumption that bees assess correctly the distance and direction to the feeder. Solid arrows show the mean direction that the bees actually signalled (after Bisetzky 1957)

navigation from a food site to the nest replicates the vector navigation from the nest to the food site. The specifications of the accumulator can be less stringent than for the continuous model: the updating processes in opposite directions need not exactly cancel each other out. An important difference from continuous models is that in discontinuous models, the relationship between a forager's accumulator state and its co-ordinates (relative to the nest) depends on the forager's goal.

There are at least two distinct types of discontinuous model. The first is the same as the continuous model on the outward journey ( $\mathbf{g} = \mathbf{f}$ ), but differs on the return to the nest. On deciding to return, a forager sets its goal as the co-ordinates of its current position ( $\mathbf{g} = \mathbf{x}$ ), resets its accumulator to the zero state ( $\mathbf{x} = \mathbf{0}$ ) and inverts the polarity of the sun compass. Vector navigation then repeats the process of the outward trajectory. As a consequence of the discontinuity, it is only on the outward path that accumulator states correspond to the co-ordinates [ $\mathbf{c}(\mathbf{x}, \mathbf{f}) = \mathbf{x}$ ]. On the return path, the co-ordinates correspond to the output of the comparator [ $\mathbf{c}(\mathbf{x}, \mathbf{f}) = \mathbf{v}(\mathbf{x}, \mathbf{g}) = \mathbf{f} - \mathbf{x}$ ].

The role of the comparator is different in the second discontinuous model. Instead of being used to guide the ant during its journey, the comparator is used to determine the accumulator state at the beginning of the journey. As with the other models, an inexperienced forager on its first foraging trip would start with its goal co-ordinates,  $\mathbf{f}$ , undetermined and the accumulator at zero,  $\mathbf{x} = \mathbf{0}$ . On finding food, it records the co-ordinates ( $\mathbf{f} = \mathbf{x}$ ) and returns home, moving until the accumulator returns to the zero state. On leaving the nest the next time, however, it sets its accumulator to the recorded state ( $\mathbf{x} = \mathbf{f}$ ), and navigates to the point where the accumulator is zero ( $\mathbf{g} = \mathbf{0}$ ). If food is not found, the forager continues to explore. On finding food, it records the co-ordinates of the new food site,  $\mathbf{f}'$ . The co-ordinates are given by the output of the comparator which subtracts the accumulator state from the co-ordinates of the old food site [ $\mathbf{f}' = \mathbf{c}(\mathbf{x}, \mathbf{f}) = \mathbf{f} - \mathbf{x}$ ]. To return to the nest, the accumulator is set to the co-ordinates [ $\mathbf{x}' = \mathbf{c}(\mathbf{x}, \mathbf{f})$ ], and again the ant returns to the point where the accumulator state is zero. If reset in this way, the accumulator state itself incorporates sufficient information to guide a forager to its goal.

## 5 Storing the co-ordinates of a food site

Both bees (Fig. 2) and ants (Fig. 3) can store the co-ordinates of a food site. To be able to do that, a forager must store either an accumulator state itself, or information extracted from it. With a continuous accumulator, the co-ordinates of a food site are, of course, only available at the site itself. The same is true of the second discontinuous model, but with the first discontinuous model there is an alternative possibility. The accumulator state on returning to the nest is the same as the state where the forager decided to return (provided path integration is accurate). The co-ordinates of a food site could thus be given by the accumulator state either at

the food site itself, or on arrival at the nest, or conceivably a combination of the two states. Since the return journey is usually more direct, positional errors might be smaller if the position of the feeder were recorded on reaching home than on the outward journey. On the other hand, if a visual scene is to be associated with the co-ordinates of the food site, we would expect the two to be learnt simultaneously at the feeder itself.

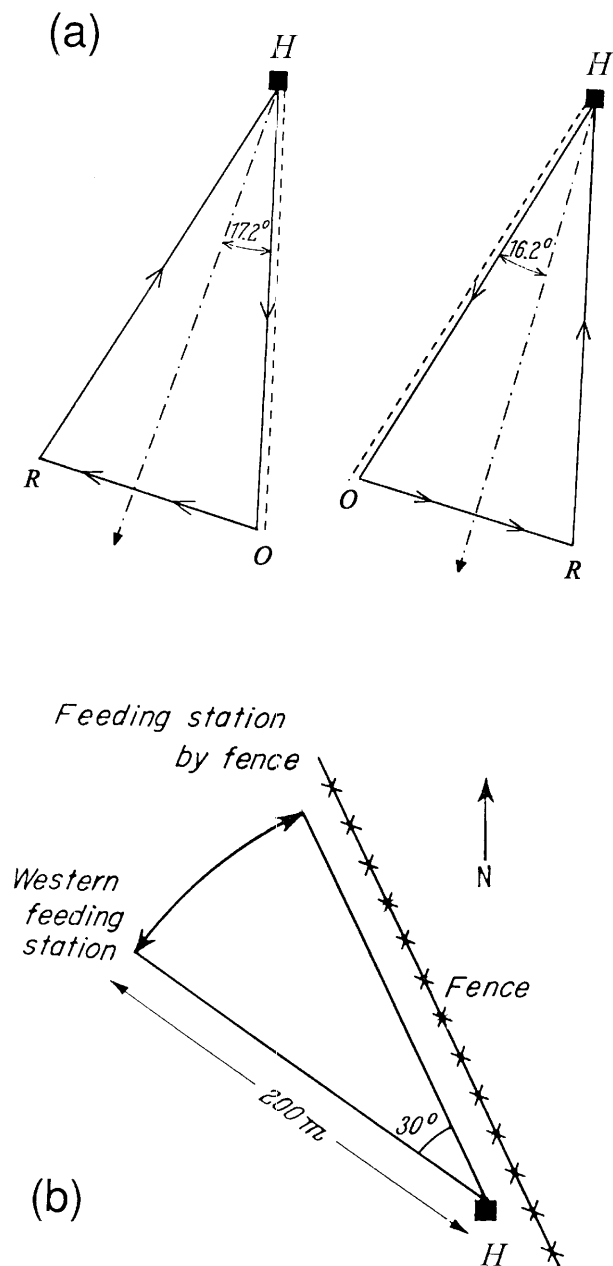
To see where the co-ordinates of a food source are learnt, one must look at situations in which the outward and return routes differ. Lindauer (1963) caught honeybees which had been newly recruited to a feeder and carried them to a second feeder, from where the bees returned to the hive. He asked where was the next destination of these foragers and, if the bees performed a waggle dance after the single foraging trip, what the signalled direction was. When the two feeders were in the same direction from the hive and foragers were displaced from the closer to the further feeder, they returned to the more distant departure feeder, even when the two feeders were more than a kilometre apart. When the feeders were in different directions and less than 150 m from the hive, the next foraging flight was to the departure feeder. Because no waggle dances were observed in any of these cases, the behaviour could be examples of landmark use rather than vector navigation. More useful from our point of view are occasions when the new recruits were induced to perform waggle dances. Waggle dances are not usually performed after a single trip, and were reported only when the two feeders were in different directions and placed 150 m from the hive (von Frisch 1967). In this case, both the waggle dance and the next foraging trip were to the arrival feeder. These are the only relevant results we know which must be the product of vector navigation, and they suggest that the co-ordinates of a food site are learnt from the state of the accumulator at the site itself.

## 6 Calibrating vector navigation

Experiments with bees (Otto 1959) and ants (Collett et al. 1999) show that in familiar terrain, the information gathered by the vector navigation system has a function additional to its immediate role in navigation and in recording co-ordinates. We suggest that the information is also used by the vector navigation system to calibrate itself.

Lindauer's result, that the waggle dance is uninfluenced by the homeward trip, comes from observations made after a single foraging trip to a new site. If bees are trained around a one-way circuit for several days, however, the homeward path does have an effect on the direction of the waggle dances (Otto 1959). Bees first flew from the hive to a feeder, from which they were carried to a site at a similar distance from the hive, where they were released to fly home. Otto used angles of 30, 60, 90 and 120° between the outward and homeward routes. In each case, the dance signalled a direction along the bisector of the angle between the two paths

(Fig. 7a). Analogous dance behaviour was found when bees were trained to feed at one distance and transported to a release site along the same direction, either further or closer to the hive. The distance signalled by the dance was intermediate between the capture and release sites.



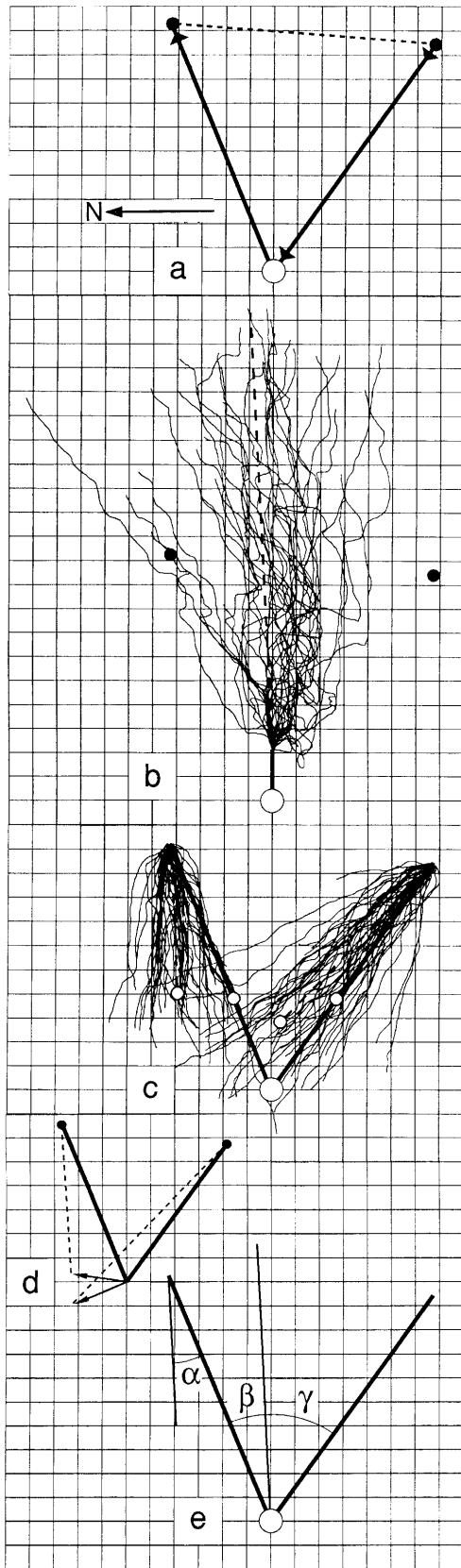
**Fig. 7a,b.** Recalibration of vector navigation in honeybees. Foragers were trained from the hive, *H*, around a one-way circuit in which outward and return routes differ by  $30^\circ$ . **a** Bees are taken from a feeder at *O* and carried to *R*, where they are released to make their way home. Dashed arrows show mean direction signalled by waggle dance after this training. Bees signal a direction between the outward and return paths. Dashed line parallel to *HO* shows direction of waggle dance of bees that fed at *O*, but were not displaced. **b** Training as in **a** except that either the outward or the return path was adjacent to a high fence. In contrast to **a**, dancing bees signal the direction parallel to the fence; they do this whether the outward or the homeward journey lay along it (Otto 1959, adapted by von Frisch 1967)

Perhaps, thinking in terms of the first discontinuous model, Otto's interpretation of these results was, in effect, that the learnt position of the feeder is a combination of the recorded states of the accumulator at the feeder and at the nest. The following experiment with ants suggests that training affects the homeward as well as the outward trajectories, and leads us to reinterpret Otto's findings. We preserve Lindauer's and von Frisch's basic conclusion that the co-ordinates of the feeder are recorded on the outward trip, and suggest that the information accumulated on the homeward path is used to calibrate the vector navigation system.

In a similar way to Otto's bees, foraging *Cataglyphis fortis* were trained, for several days, from an enclosed nest along a channel to a feeder (as in Fig. 3) and were then transported to the end of a second channel to return in a different direction to the nest (Collett et al. 1999). To ensure that ants travelled in only one direction around the circuit, there were several points at which ants had to jump down and could not return (Fig. 8a). Corresponding to Otto's observations of the waggle dance, the outward trajectories of ants over open ground (as in Fig. 8b) were intermediate between the direction of the two channels.

What had not been predicted by Otto's observations and hypothesis was that the homeward trajectories of ants taken from the feeder to a test ground were not parallel to the outward channel, but were also intermediate in direction between the two channels (Fig. 8c, left-hand side). An alternate hypothesis which can explain the directions of both types of trajectories is that the co-ordinates of the feeder are learnt from the outward journey, but that the vector navigation system is recalibrated to reduce the difference between the route it sets and the enforced route along the return channel to the nest. The difference between the trajectories and the training channels cannot be explained by a change in the accumulator, but can be explained by the calibration of a later stage in the vector navigation process. Two possibilities are the processes of storing accumulator states in memory, or of comparing the memory and the present state to give the direction of desired movement.

The 'untransformed' homeward trajectories of normal ants after a straight outward path along a straight channel are in the same direction as the channel (Müller and Wehner 1988), but their length is shortened. By comparing the 'transformed' homeward trajectories of recalibrated ants from more points, and comparing these with untransformed trajectories, it is possible to elucidate the form of the transformation induced by training around the circuit. To obtain homeward trajectories from a second point, training was briefly interrupted to allow ants to travel outwards to a 'test' feeder at the same distance, but along the direction of what was normally the return channel. In this case too, the homeward trajectories (Fig. 8c, right-hand side) were rotated with respect to the outward path, but were longer than those from the 'training' feeder. The differences between the untransformed and transformed homeward trajectories from the two feeders were similar,



so that the transformation can be described approximately as a shift of the endpoint of the homeward trajectories by a 'correction' vector (Fig. 8d).

◀  
**Fig. 8a–e.** Recalibration of vector navigation in ants (*C. fortis*). **a** Training arrangement. Foragers travel from nest along the outward NE channel (solid line) to a feeder at the end. They were carried (dotted line) to the end of the return NW channel from where they returned home. Arrows show position and direction of 'one-way valves' that prevented ants from back tracking through the circuit. Gridlines are at 1 m intervals. **b** Outward trajectories after training around route. Mean direction is shown by dashed line. Solid circles indicate normal positions of the ends of the two channels. **c** Homeward trajectories of ants taken from the training or test feeder to an empty test ground are shown as though originating from the feeders where the ants were collected. Small open circles show the mean lengths and directions of the trajectories relative to the feeder. The directions of mean trajectories differ significantly from that of the associated outward channel. Open circles on solid lines give mean lengths of homing trajectories obtained in separate experiments after travelling along 10 m channels to a feeder. **d** Correction vectors (arrows) as given by the vector difference between mean transformed trajectories (dashed lines) and normal, untransformed homeward trajectories (solid lines) **e** The relationship between outward and homeward trajectories in terms of the angles between the mean trajectories (see b, c) and the two training channels (from Collett et al. 1999)

Using the idea of a correction vector **d** arising from calibration, the output of the vector navigation system during the homeward trajectories is given by

$$v(\mathbf{x}, \mathbf{g}) = \mathbf{g} - \mathbf{x} + \mathbf{d} . \quad (2)$$

This rule produces straight homeward trajectories to the point where  $\mathbf{x} = \mathbf{g} + \mathbf{d}$ . If Eq. (1) holds also for outward journeys, it is possible to make predictions about how calibration affects the relationship between the outward and homeward trajectories. Because the predictions differ for the continuous and discontinuous models, and because they also depend on when ants record the location of food, observed outward trajectories in conjunction with homeward trajectories can help resolve these issues.

If the accumulator is used in a continuous way, the transformation given by the equation would mean that the endpoint of vector navigation would be shifted by **d** with respect to the co-ordinates of the goal. Since in this case the goal must be derived from the accumulator state at the feeder, the outward trajectories would lie to the left of the outward channel ( $\beta < 0$  in Fig. 8e). This does not correspond to observations, so we must discard either the continuous model, or the use of the equation for the outward trajectory. Because of the reversal of the compass polarity, predictions from the discontinuous models fit the observations better. If the co-ordinates of the feeder are derived from the outward journey then **g** is the same for both the outward and the homeward trajectories ( $\mathbf{g} = \mathbf{f}$  or  $\mathbf{g} = \mathbf{0}$  depending on the model), and so the directions of the trajectories should be  $180^\circ$  apart ( $\alpha = \beta$ ). This is approximately what is observed, and should be tested further. If the co-ordinates of the feeder were derived from the return journey, the equation would predict outward trajectories to the right of the return channel ( $\gamma < 0$ ). The transformed trajectories therefore support a discontinuous model with co-ordinates learnt on the outward journey.



Using Eq. (2) to describe navigation with a discontinuous accumulator, it is possible to describe how a gradual process of calibration at both points would result in the unconstrained trajectories intermediate in direction between the two channels. Calibration at a goal adjusts  $\mathbf{d}$  to reduce the difference between  $\mathbf{g} + \mathbf{d}$  and the accumulator state  $\mathbf{x}$  at that goal. If the goal coordinates derive from the outward route, then at the feeder  $\mathbf{x} = \mathbf{g}$  ( $\mathbf{g} = \mathbf{0}$  or  $\mathbf{g} = \mathbf{f}$  depending on which discontinuous model is used), and the difference is  $\mathbf{d}$ . After being carried over a section equivalent to the co-ordinates  $\mathbf{l}$ , the accumulator state on returning to the nest is  $\mathbf{x} = \mathbf{g} + \mathbf{l}$  (correcting the sign error in Collett et al. 1999), and then the difference is  $\mathbf{d} - \mathbf{l}$ . So while calibration at the nest reduces the magnitude of  $\mathbf{d} - \mathbf{l}$  by increasing  $\mathbf{d}$ , it is counteracted by calibration at the feeder which reduces  $\mathbf{d}$ . Calibration at the nest, while reducing the differences between the output of the navigation system and the constraints of the return channel, produces differences along the outward channel. Calibration at the feeder would therefore act in opposition to calibration at the nest.

Whatever process is calibrated, the calibration is likely to occur at locations that can be recognised independently of path integration, and where the process can be adjusted to bring the output towards an expectation. The conditions for calibration are most obviously met at the nest and at the feeder. Both places can be recognised by visual landmarks or odours. At these places, the current accumulator state should correspond to the memory serving as a goal, and the output of the comparison should specify a zero movement. Connections can then be adjusted to make the memory reflect the actual accumulator state, or to make these inputs to a comparator produce zero output.

Calibration at more than one site would produce the intermediate directions observed. It might be possible to test this interpretation of the intermediate trajectories by varying the position of food. If there is no constant food site that can be associated with stable landmarks, calibration at the feeder might be reduced, and so transformed trajectories would be biased towards the return channel. In bees, Otto showed that it is possible to alter the direction of the waggle dances by providing landmarks along the route. A set of white poles or a fence placed along either the outward or return route biased the direction of the dance towards the marked route (Fig. 7b). The unequal calibration must have occurred either because of additional calibration occurring at these landmarks, or because of stronger calibration at the end of the marked route. While there remain many aspects of the calibration process to be explored, it is likely that repetition and familiar landmarks play an important role.

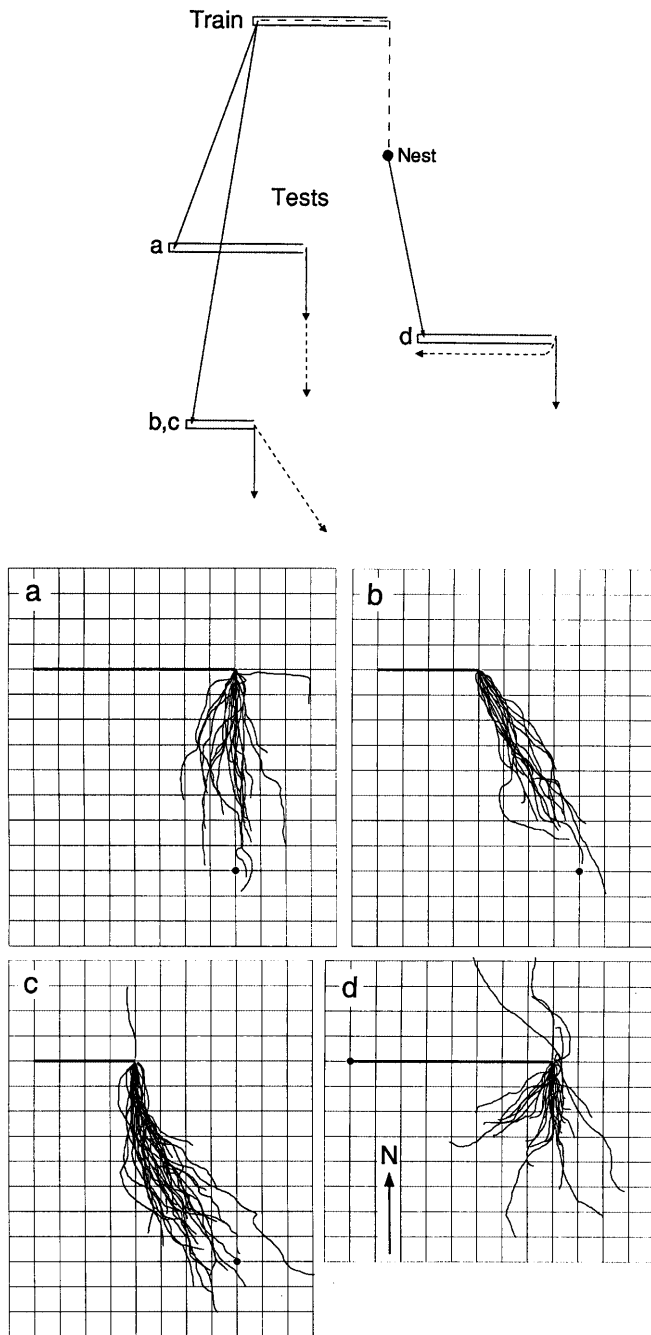
## 7 The effect of a familiar scene during vector navigation

At the nest, bees and ants can recall the co-ordinates of a food site as the goal for their next foraging trip. In a familiar landscape, do foragers also recall co-ordinates

at other points and reset the vector navigation system to those co-ordinates, much as sailors can correct their position on sighting landmarks that are indicated on a map? Such realignment would require resetting the accumulator, usually to a non-zero state. This resetting might well be difficult for an insect brain. For the discontinuous models, resetting could be easier in order to return to the nest, than to continue go a goal on the outward trip. To return to the nest, the task of resetting the system at a familiar site is similar to what, in any case, the discontinuous models require at the turning point. On the outward trip, or at any point with the continuous model, the accumulator would have to be set to a non-zero state. There is an important difference between resetting both the goal and accumulator states at the turning point in the discontinuous models and in just resetting the accumulator. In the former case, the resetting does not discard the information in the accumulator state, because this information is contained jointly in the two new states. On the other hand, resetting the accumulator on encountering a familiar landmark is a risky strategy because, in this case, the current path integration information is entirely discarded.

Desert ants employ a different strategy to resetting their vector navigation system. Foragers transiently override the output of the vector navigation system when responding to landmarks along a route, and in this way resolve any conflicts between landmark guidance and vector navigation. Suppression of the output of vector navigation was found when ants (*Cataglyphis fortis*) were trained along an L-shaped route to a feeder: 8 m N over open ground followed by 8 m W along a channel to a feeder at the end of the channel (Fig. 9, top). Both the channel and feeder were sunk into the ground so as to be invisible. When the ant emerged from the channel on its normal homeward route, it travelled S to the nest. To see how the contextual information provided by a familiar channel might be used, an identical feeder and channel were set up in a test ground. Ants were taken, either from the training feeder, before they started returning home, or when they had almost reached the nest. They were released into the test feeder and their trajectories on leaving the channel were observed. Ants taken from the training feeder went S on exiting the channel, as is to be expected of ants guided by vector navigation (Fig. 9a). When ants taken from the training feeder were released at the feeder at the W end of a shortened 4-m channel, some (35%) followed the SE trajectory expected from vector navigation (Fig. 9b). But the majority (65%) first went S for approximately 3 m before turning to follow the trajectory dictated by vector navigation (Fig. 9c), having continued with path integration all the while. The initial S directed 'local vector' must be associated with the channel and recalled in the context of leaving it.

The same S directed local vector is recalled if ants are taken on their return trip when they have nearly reached the nest and are placed in the feeder at the end of the 8-m test channel (Fig. 9d). At the nest, the accumulator is either near the zero state, or near the state of the feeder, depending on the model of vector navigation. Had the

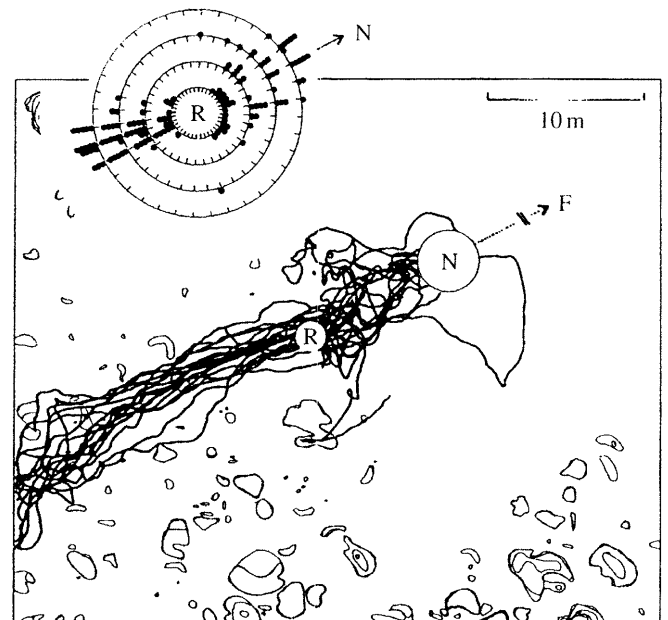


ant taken from the nest just used its vector navigation system, its trajectories would be directed back along the channel to the test feeder. Had the ant's familiarity with the channel caused the accumulator to be reset to its accustomed state on leaving the channel, then its trajectories would have been like those in Fig. 9a instead of as in Fig. 9d.

The actual strategy of following a local vector briefly over-rides vector navigation but then reverts in the absence of further familiar landmarks. When vector navigation disagrees with landmark cues which indicate a familiar route segment, ants temporarily place their bets on the landmark information and follow their associated responses (but see Fig. 10). The current information



**Fig. 9a–d.** Local vectors associated with a familiar channel. *Top* Schematic of experimental design. Ants (*C. fortis*) were trained from the nest (filled circle) to travel 8 m N over open ground and then along an 8 m channel (double line) to a feeder at its W end. They returned along the same path to the nest (dotted line). Trained ants were taken either from the training feeder or from the nest to a test field where they were placed in a test feeder at the end of an 8- or 4-m channel similar to the training channel. Trajectories were recorded when ants left the channel until they started searching. Dotted line and arrow shows the ant's predicted path on the assumption that it is guided by vector navigation. Solid line and arrow show the ant's path on the assumption that it follows a local vector associated with the channel. **a** Ants taken from the training feeder to an 8-m channel. The ants' trajectories on leaving the channel point south. Filled circles in this and panels **b–d** represent the predicted goal of vector navigation. **b,c** Ants taken from the training feeder to a 4-m test channel. The trajectories were divided into two categories. A minority of trajectories (**b**) followed vector navigation from the outset. Most trajectories (**c**) followed 'local vector' south for about 3 m and then returned to vector navigation. **d** Ants taken at the end of the return journey, when they have almost reached the nest, to the end of an 8-m test channel. On exiting the channel their trajectories are directed south following the local vector, although vector navigation would be directed towards the test feeder (from Collett et al. 1998)



**Fig. 10.** Vector navigation can suppress landmark guidance. Ants were trained to feeder (*F*) 30 m from their nest (*N*). Trained ants that are displaced from the nest, to a site (*R*) in the opposite direction, return directly to the nest, showing that landmark information is available. In contrast, ants displaced from the feeder to the same point use vector navigation. Circular histogram plots the directions of ants displaced from the nest (right-hand cluster) and from the feeder (left-hand cluster) at 2-m intervals from release site. We suspect that while the landmarks are sufficiently familiar for a forager to use image matching for guidance (review: Collett and Zeil 1998), the scene is not similar enough to a familiar route to trigger a local vector (from Wehner et al. 1996)

supplied by vector navigation is not dismissed, but is relegated to the background while the accumulator continues to be updated so that it can be used if landmarks fail. Different conclusions might have been

reached if we had not recorded the whole trajectory. If only the initial portion had been monitored, as is commonly done with vanishing bearings in honeybees (Wehner et al. 1990; Menzel et al. 1998), Fig. 9c might have led us to suppose erroneously that ants reset the vector navigation system on leaving the channel. Radar tracking of individual honeybees allows entire trajectories to be followed (Riley et al. 1996), and should help resolve the present uncertainties in interpreting honeybee displacement experiments.

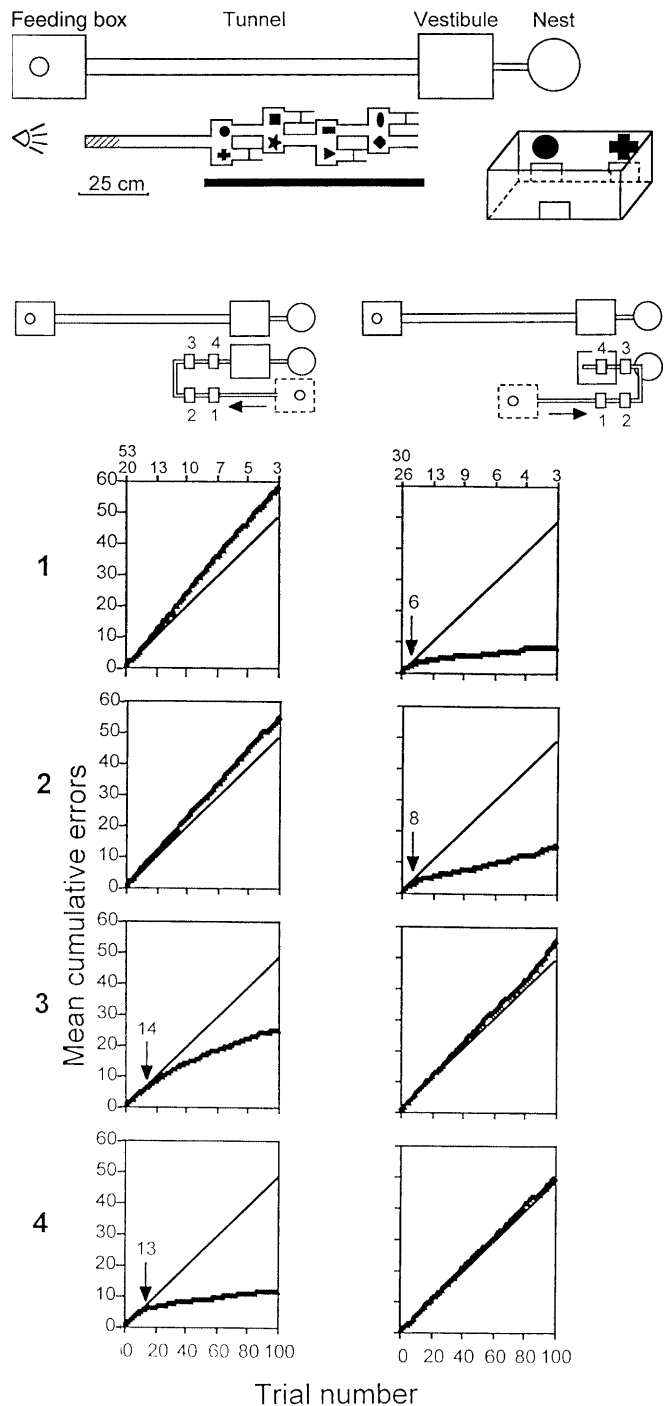
## 8 The role of vector navigation in landmark learning

In unfamiliar terrain, path integration provides the only positional information available, and vector navigation is the only possible strategy. An individual gains familiarity with an area by learning landmarks and associating them with navigational information. It appears that the vector navigation system is used to guide the learning of landmarks, so that a landmark is learnt only if the vector navigation system signals that the forager is heading towards its goal.

The role that path integration may play in landmark learning was examined by training foraging ants (*Cataglyphis cursor*) to return to their nest through a variety of mazes (Schatz et al. 1999). Ants reached a feeder through a transparent connecting tunnel. Marked individuals then had to return to the nest through a maze in which choice points were labelled by visual cues (Fig. 11). Ants successfully learnt the cues when the maze led straight in the direction from the feeder to the nest. But when the maze was formed into a U, so that the two arms pointed in opposite directions, ants only learnt the visual cues in the maze segment directed from

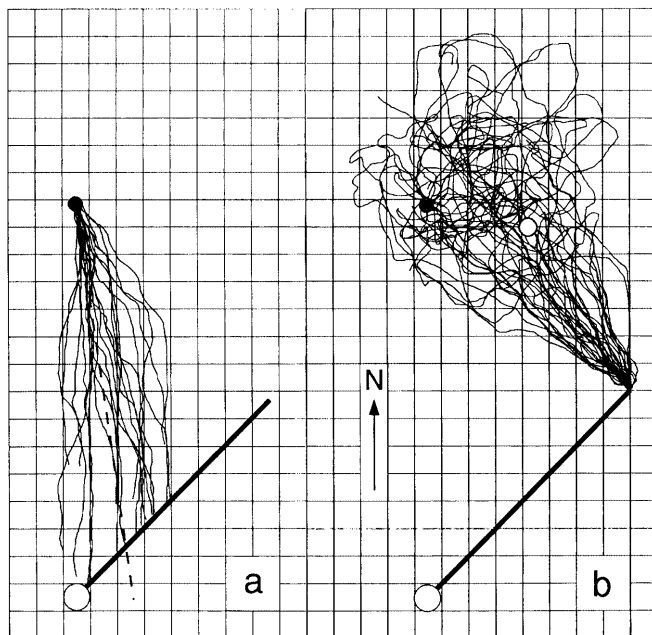
the feeder to the nest. They showed no signs of learning the cues which they met in the other arm. The acquisition of visual cues may therefore only take place when the output of the vector navigation system is decreasing. Such a learning signal aids the rapid acquisition of routes because it allows reinforcement to act along the whole route on the very first trip home.

Observations in a very different situation suggest that a foraging ant does not learn landmarks once it has gone beyond the goal specified by its vector navigation system. Ants (*C. fortis*) were trained from an enclosed nest to a feeder along a two-leg route (Collett et al. 1999).



**Fig. 11.** A possible role for vector navigation in landmark learning. *Top* Diagrams of mazes used to test visual learning. Ants approached the feeder along a linear tunnel, and returned home singly through a linear maze, which was placed directly over the tunnel. Ants could pass efficiently through the maze by choosing the exit in each compartment that was associated with the 'positive' shape. The open exit in compartment 1 was labelled by a black circle, in compartment 2 by a star, in compartment 3 by a rectangle, and in compartment 4 by a diamond. Directional cues came from a floodlight at one end of the room and a large piece of black card fixed to one wall. *Inset* Three-dimensional sketch of one compartment to show ant's view of the shapes and exits. Ants that homed through this linear maze learn to approach the positive shapes in all compartments. Another group of ants was trained to home through a U-shaped maze and had to recognise the same shapes as in the linear maze. *Bottom* Acquisition curves for two arrangements of the U-shaped maze, as drawn at the head of each column. Numbers at the top of each column give sample size; the upper number is the total at the start of the experiment. The sample size dropped during the experiment, as shown by the numbers given every 20 trials. Each row displays the error plots for one compartment (1-4). Plots are of the mean number of errors per ant accumulated over successive trials. Only the first choice made in each box on each trial is considered, giving a 50% chance of an error in each compartment. The line indicates random choice. Arrows show when the plots depart from random choices at  $P < 0.01$ . Ants learn shapes only in those compartments in which the path through the maze is in the direction of the nest (from Schatz et al. 1999)

The exit tube from the enclosure surrounding the nest led to a 10 m NE channel sunk into the ground, from the end of which ants travelled 10 m NW across open ground to the food. From the feeder, ants were free to return directly to the nest (Fig. 12). The straight outward (Fig. 12a) and homeward (Fig. 12b) trajectories to inappropriate positions (see figure legend for explanation), and the subsequent search patterns, show that up to the point where searching starts, both outward and homeward trajectories are driven by vector navigation. It was striking that even after a week of training, ants at the end of the straight portion of the trajectories would search for minutes to find the feeder or their nest only a couple of meters distant. This suggests that they had not learnt the appropriate landmarks to lead them there. In the case of the nest, such a landmark was provided in the form of a large mound surrounding the nest. The mound was clearly visible when returning over open ground, but could not be seen from the channel on leaving the nest. Extrapolating from the maze experiment, we suggest that learning failed to occur after the end of the straight trajectory because the vector navigation system indi-

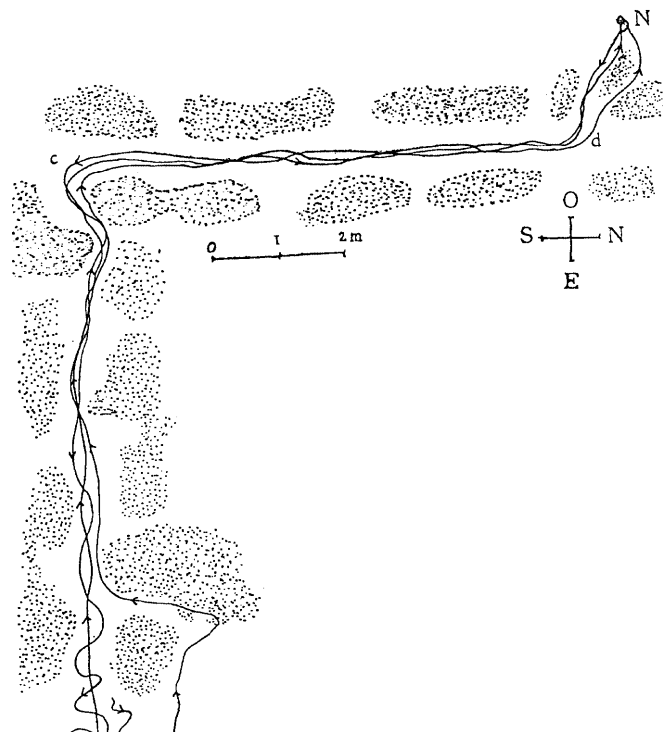


**Fig. 12a,b.** Outward and homeward trajectories of ants trained to a feeder (solid circle) along an L-shaped route. Ants left the nest via a NE pointing channel (solid line) and then proceeded over open ground. **a** Homeward trajectories recorded on training field from when ants left the feeder until they began searching or reached the channel. Mean direction  $172.40^\circ$ ,  $SD \pm 5.66^\circ$ ,  $n = 20$ . Mean trajectory is rotated significantly eastward from the direct route home ( $P < 0.01$ ). As is typical after L-shaped routes, errors in path integration result in homeward trajectories, which are not directed towards the nest. **b** Outward trajectories were followed on training field until ant reached feeder or was lost from sight. Open circle indicates mean endpoint at which ant starts its search behaviour (mean direction  $327.95^\circ$ ,  $SD \pm 13.07^\circ$ , mean length 6.90 m,  $SD 2.48$  m,  $n = 40$ ). The mean direction of the outward trajectories differs significantly from the direct path from the channel to the feeder ( $P < 0.01$ ), suggesting recalibration has occurred as in Fig. 8a (from Collett et al. 1999)

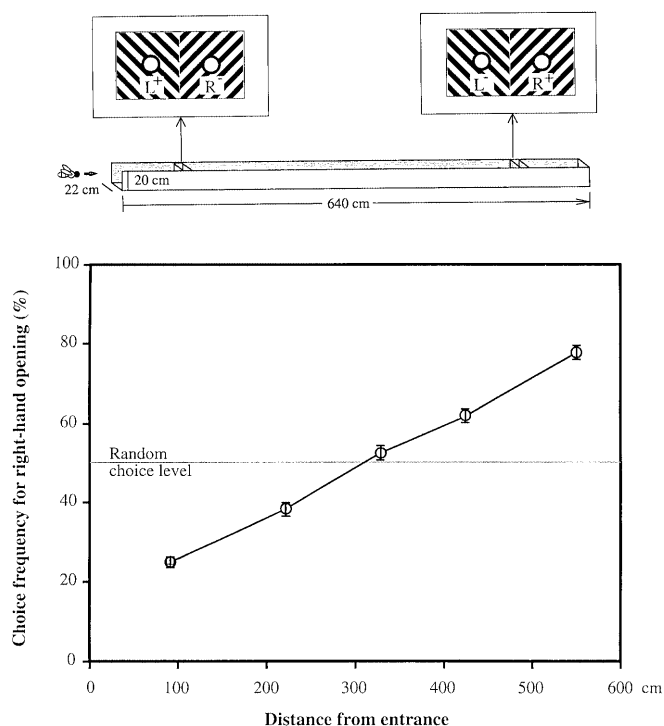
cated movement away from the goal. Taking this argument one step further, a forager, which does not find food at its goal, would discontinue landmark learning when exploring beyond the goal specified by vector navigation. Learning would begin again only when the forager finds foods and returns to its nest.

## 9 The role of path integration when navigating in familiar territory

We have seen already that recognised cues can override vector navigation. This raises the question of whether path integration has any role at all in familiar territory. Figure 13 shows an example from Santschi (1913) of a route taken by an individual *Cataglyphis bicolor*. On neither outward nor homeward trajectories does the ant follow the straight course, which would be produced by the vector navigation system, but appears to be guided by the surrounding vegetation. Strikingly, the homeward route is identical on separate occasions, suggesting that the ant follows a fixed route learnt with respect to a sequence of landmarks (see also Rosengren 1971). Even more striking is the behaviour of *C. fortis* returning home from a feeder along a well landmarked route. A returning forager that is displaced from near the nest back to the feeder will take exactly the same zig-zag course it followed before being displaced (Wehner et al.



**Fig. 13.** Foraging trips of a single *Cataglyphis bicolor* over familiar terrain. Inward and outward paths are very similar. *N* Nest; *a*, *b* departure points of the first and second returns. Principal bends are marked *c* and *d*. Stippling indicates bushes. Bushes are attractive as a source of dead insect food, but also dangerous because they harbour predators (from Santschi 1913)



**Fig. 14.** Bees can link visual scenes to distances flown. *Top* Set-up. Bees are trained to fly down a tunnel to a reward box at one of two distances. At 90 cm from the entrance they must choose the left-hand hole and at 550 cm the right-hand hole. *Bottom* After training the bee's preferences for the two opening are recorded with the box in different positions along the tunnel. Graph shows mean choice frequency of the right-hand hole ( $\pm 1$  SD) at different distances along the tunnel (from Srinivasan et al. 1999)

1996). These examples of fixed routes can be explained without recourse to vector navigation.

Fixed routes are composed of separate components that can be performed independently of the vector navigation system. Ants recognise landmarks and perform the behaviour appropriate to them irrespective of the state of accumulator (Collett et al. 1992). Similarly, honeybees flying through mazes or tunnels can associate a path segment of particular direction and length with a visual cue (Collett et al. 1993, 1996; Srinivasan et al. 1997, 1999), and can learn a sequence of such segments each linked to a different visual cue. Should the order of visual cues be changed, bees follow the sequence dictated by the visual cues (Collett et al. 1996; Srinivasan et al. 1997).

Although landmarks can be used out of context (e.g. Chittka et al. 1995a), path integration may nonetheless provide a loose structure, such that foragers that are familiar with a route expect to encounter particular landmarks at positions corresponding to particular states of the accumulator. This possibility has long been suggested, but until recently good evidence has been absent. The first hints come from an experiment that was carried out for a different reason. Srinivasan et al. (1999) trained honeybees to fly through a 22-cm-wide tunnel that was 640 cm long to reach a reward box that was placed either 90 cm or 550 cm into the tunnel. The

reward box had two holes. One on the left was marked by 135° stripes and the one on the right by 45° stripes. At the shorter distance, the reward was available through the left-hand hole and at the longer distance the reward was obtained through the right-hand hole. Bees easily learnt this task suggesting that they expected to encounter the two stripe patterns at different distances, measured with respect to either the hive or beginning of the tunnel. Well-trained bees were occasionally tested with the reward box in intermediate positions, and, when the box was midway between the two training sites, they chose the two holes with equal frequency, showing that their expectations change in a graded way with distance (Fig. 14). Thus while ants/bees can follow familiar routes with no contribution from vector navigation, they may perform routes more fluently when they can make use of both navigational strategies (see also Chittka et al. 1995b).

## 10 Conclusions

Vector navigation gives a forager the flexibility to move around in unknown territory and then to return directly to its starting point. In practise, desert ants forego the flexibility provided by vector navigation. They prefer to stick to fixed routes along which they have the benefit of being guided by landmarks, even though food is often scattered and a forager must often search extensively before finding a dead insect to take home. Both vector navigation and route following conspire so that an individual tends to head out from the nest along the same direction that it took on previous trips (Wehner et al. 1983) and return to its most recent food site (Schmid-Hempel 1984). On exploring from this site, an ant's search is often biased so that it continues along the same direction outward from the nest (Schmid-Hempel 1984). Foraging is thus structured so that individual ants remain as far as possible within familiar territory. This sector fidelity preserves the investment made in learning landmarks. It may also be advantageous for vector navigation, if accurate calibration is sector specific, or if vector navigation can be calibrated at several sites along a landmarked route. It is unknown whether honeybees are also concerned to keep to familiar territory when seeking a new source of nectar. Do bees prefer to follow dances that are roughly in the same direction as their previous foraging site?

Sector fidelity provides a forager with knowledge about familiar landmarks. At certain sites, bees and ants seem to record views of the surrounding landscape so as to provide locational information (review: Collett and Zeil 1998). Co-ordinates may be attached to a view by associating the recorded accumulator state when at the site. The combination of co-ordinates and site recognition is reminiscent of the information contained in the cartographic maps we produce for travel. The information, however, is almost certainly encoded differently in the two navigational systems and it is misleading to think of vector navigation in terms of such a map. Indeed, both the acquisition and the use of information by

insect navigators are quite different from the way in which humans navigate with the aid of a map.

Cartographers can extend the borders of a map as they explore unknown territory, and they can determine the location of distant landmarks by triangulation. Insect foragers, on the other hand, can only record the coordinates of sites that they have visited, and desert ants may only learn landmarks on route to or from a goal. There are also striking differences between the way that a human traveller can use a map and the way in which insects use stored information for navigation:

1. Systematic errors produced when ants follow detours (Müller and Wehner 1988) suggest that the coordinates of a site given by path integration will depend on the route taken to that site. The use of vector navigation to plan a new route from one site to the stored coordinates of another would thus be an error-prone process.

2. From the perspective of our current understanding, vector navigation seems limited and stereotyped, when compared with the potential flexibility of a map. *a.* Desert ants always return to the site where they most recently found food, and there is no evidence that their goal can be set otherwise. *b.* Once a forager has reached a food site by vector navigation, it seems unable to use vector navigation to redirect itself to a new food site without first returning to the nest (Wehner et al. 1990; Menzel et al. 1998). The systematic path integration errors, in any case, would not allow accurate vector navigation between foodsites which are not in the same direction from the nest. *c.* There is also no evidence that a nestbound forager returning from a food site can return to that site using vector navigation, without first returning to the nest. In the first discontinuous model, such a manoeuvre is demanding: a forager would have to reset its accumulator to  $\mathbf{x}' = \mathbf{f} - \mathbf{x}$ .

3. Unlike travellers, insects may not use landmarks to determine their present co-ordinates (e.g. by resetting an accumulator on encountering a familiar scene).

4. Travellers can rely on mathematics to calculate their path to a goal. Insects perform similar operations but by means of a comparator which is an analogue rather than a symbolic device, and needs to be calibrated.

It will be interesting to see in the coming years whether these suggested differences between insect vector navigation and human map use survive further research, and whether new differences emerge. At present, they indicate that path integration in insects should be thought of as providing information about progress to goals along circumscribed routes rather than underpinning a map that contains geometrical relations between points.

*Acknowledgements.* We thank Robert Biegler for an English translation of Lindauer's (1963) paper and Roland Maurer for a photograph of a traverse board. The paper was improved by valuable comments from Daniel Glaser, Roland Maurer, Horst Mittelstaedt and two anonymous referees and we are very grateful to them. Financial support came from the UK BBSRC and the Human Frontier Science Program.

## References

- Benhamou S, Séquinot V (1995) How to find one's way in the labyrinth of path integration models. *J Theor Biol* 174: 463–466
- Bisetzky R (1957) Die Tänze der Bienen nach einem Fussweg zum Futterplatz unter besonderer Berücksichtigung von Umwegversuchen. *Z Vergl Physiol* 40: 264–288
- Chittka L, Geiger K, Kunze J (1995a) The influence of landmarks on distance estimation of honey bees. *Anim Behav* 50: 23–31
- Chittka L, Kunze J, Shipman C, Buchmann SL (1995b) The significance of landmarks for path integration in homing honeybee foragers. *Naturwissenschaften* 82: 341–343
- Collett M, Collett TS, Bisch S, Wehner R (1998) Local and global vectors in desert ant navigation. *Nature* 394: 269–272
- Collett M, Collett TS, Wehner R (1999) Calibration of vector navigation in desert ants. *Curr Biol* 16: 1031–1034
- Collett TS, Zeil J (1998) Patterns and places: an arthropod perspective. In: Healy S (ed) *Spatial representation in animals*. Oxford University Press, Oxford, pp 18–53
- Collett TS, Dillmann E, Giger A, Wehner R (1992) Visual landmarks and route following in desert ants. *J Comp Physiol A* 170: 435–442
- Collett TS, Fry SN, Wehner R (1993) Sequence learning by honeybees. *J Comp Physiol A* 172: 693–706
- Collett TS, Baron J, Sellen K (1996) On the encoding of movement vectors by honeybees. Are distance and direction represented independently? *J Comp Physiol A* 179: 395–406
- Dyer FC, Dickinson JA (1996) Sun-compass learning in insects: representation in a simple mind. *Curr Direct Psychol* 5: 67–72
- Esch HE, Burns JE (1996) Distance estimation by foraging honeybees. *J Exp Biol* 199: 155–162
- Frisch K von (1967) *The dance language and orientation of bees*. Harvard University Press, Cambridge, Mass
- Gallistel CR (1990) *The organization of learning*. MIT Press, Cambridge, Mass
- Gould JL (1976) The dance-language controversy. *Q Rev Biol* 51: 211–244
- Hartmann G, Wehner R (1995) The ant's path integration system: a neural architecture. *Biol Cybern* 73: 483–493
- Jander R (1957) Die optische Richtungsorientierung der roten Waldameise (*Formica rufa* L.). *Z Vergl Physiol* 40: 162–238
- Lambrinos D, Maris M, Kobayashi H, Pfeifer R, Wehner R (1997) An autonomous agent navigating with a polarized light compass. *Adapt Behav* 6: 131–161
- Lindauer M (1963) Kompassorientierung. *Ergeb Biol* 26: 158–181
- Maurer R (1998) A connectionist model of path integration with and without a representation of distance to the starting point. *Psychobiology* 26: 21–35
- Maurer R, Séquinot V (1995) What is modelling for? A critical review of the models of path integration. *J Theor Biol* 175: 457–475
- Menzel R, Geiger K, Joerges J, Müller U, Chittka L (1998) Bees travel novel homeward routes by integrating separately acquired vector memories. *Anim Behav* 55: 139–152
- Mittelstaedt H (1983) The role of multimodal convergence in homing by path integration. *Fortschr Zool* 28: 197–212
- Mittelstaedt H, Mittelstaedt ML (1973) Mechanismen der Orientierung ohne richtende Aussenreize. *Fortschr Zool* 21: 46–58
- Müller M, Wehner R (1998) Path integration in desert ants, *Cataglyphis fortis*. *Proc Natl Acad Sci USA* 85: 5287–5290
- Otto F (1959) Die Bedeutung des Rückfluges für die Richtungs- und Entfernungsangabe der Bienen. *Z Vergl Physiol* 42: 303–333
- Pièron H (1904) Du rôle du sens musculaire dans l'orientation de quelques espèces de fourmis. *Bull Inst Gen Psychol Paris* 4: 168–186
- Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL, Williams IH, Carreck NL, Poppy GM (1996) Tracking bees with harmonic radar. *Nature* 379: 29–30

- Ronacher B, Wehner R (1995) Desert ants (*Cataglyphis fortis*) use self-induced optic flow to measure distances travelled. *J Comp Physiol A* 177: 21–27
- Rosengren R (1971) Route fidelity, visual memory and recruitment behaviour in foraging woodants of the genus *Formica* (Hymenoptera, Formicidae). *Acta Zool Fenn* 133: 1–10
- Santschi F (1913) Comment s'orientent les fourmis. *Rev Suisse Zool* 21: 347–425
- Schatz B, Chameron S, Beugnon G, Collett TS (1999) The use of path integration to guide route learning in ants. *Nature* 399: 769–772
- Schmid-Hempel P (1984) Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Behav Ecol Sociobiol* 14: 263–271
- Schmidt I, Collett TS, Dillier F-X, Wehner R (1992) How desert ants cope with enforced detours on their way home. *J Comp Physiol A* 171: 285–288
- Schöne H (1996) Optokinetic speed control and estimation of travel distance in walking honeybees. *J Comp Physiol A* 179: 587–592
- Srinivasan MV, Zhang SW, Lehrer M, Collett TS (1996) Honeybee navigation en route to the goal: visual flight control and odometry. *J Exp Biol* 199: 155–166
- Srinivasan MV, Zhang SW, Bidwell NJ (1997) Visually mediated odometry in honeybees navigation en route to the goal: visual flight and odometry. *J Exp Biol* 200: 2513–2522
- Srinivasan MV, Zhang SW, Berry J, Cheng K, Zhu H (1999) Honeybee navigation: linear perception of short distances travelled. *J Comp Physiol A* 185: 239–245
- Wehner R (1987) Spatial organization of foraging behaviour in individually searching desert ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namib desert). *Experimentia* [Suppl] 54: 15–42
- Wehner R, Rosell S (1985) The bee's celestial compass – a case study in behavioural neurobiology. *Fortschr Zool* 31: 11–53
- Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J Comp Physiol* 142: 315–338
- Wehner R, Wehner S (1990) Insect navigation: use of maps or Ariadne's thread? *Ethol Ecol Evol* 2: 27–48
- Wehner R, Harkness RD, Schmid-Hempel P (1983) Foraging strategies in individually searching ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Akad Wiss Lit Mainz. Information Processing in Animals* 1: 1–79
- Wehner R, Bleuler S, Nievergelt C, Shah D (1990) Bees navigate by using vectors and routes rather than maps. *Naturwissenschaften* 77: 479–482
- Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. *J Exp Biol* 199: 129–140
- Wittman T, Schwegler H (1995) Path integration – a network model. *Biol Cybern* 73: 569–579