

INSECT NAVIGATION *EN ROUTE* TO THE GOAL: MULTIPLE STRATEGIES FOR THE USE OF LANDMARKS

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Summary

There are at least four distinct ways in which familiar landmarks aid an insect on its trips between nest and foraging site. *Recognising scenes*: when bees are displaced unexpectedly from their hive to one of several familiar locations, they are able to head in the direction of home as though they had previously linked an appropriate directional vector to a view of the scene at the release site. *Biased detours*: ants recognise familiar landmarks *en route* and will correct their path by steering consistently to the left or to the right around them. *Aiming at beacons*: bees and ants also guide their path by approaching familiar landmarks lying on or close to the direct line between start and finish. Simulations suggest that such mechanisms acting together may suffice to account for the routes taken by desert ants through a landmark-strewn environment: the stereotyped trajectories of individual ants can be modelled by a weighted combination of dead reckoning, biased detours and beacon-aiming. These mechanisms guide an insect sufficiently close to an inconspicuous goal for *image matching* to be successfully employed to locate it. Insects then move until their current retinal image matches

a stored view of the surrounding panorama seen from a vantage point close to the goal.

Bees and wasps perform learning flights on their first departure from a site to which they will return. These flights seem to be designed to pick up the information needed for several navigational strategies. Thus, a large portion of the learning flight of a bee leaving a feeder tends to be spent close to the feeder so aiding the acquisition of a view from that vantage point, as is needed for image matching. Bees and social wasps also tend to inspect their surroundings while facing along preferred directions and to adopt similar bearings before landing, thereby making it easy to employ retinotopically stored patterns in image matching. Aiming at beacons, in contrast, requires a landmark to be familiar to the frontal retina. Objects tend to be viewed frontally while the insect circles through arcs centred on the goal. This procedure may help insects to pick out those objects close to the goal that are best suited for guiding later returns.

Key words: Hymenoptera, landmarks, dead reckoning, navigation, visual learning.

Introduction

This brief review emphasises that hymenopterous insects exploit familiar landmarks in several distinct ways in order to navigate over long distances between nest and foraging site. It is suggested that these separate mechanisms of landmark guidance may have arisen by an opportunistic grafting of visual pattern learning onto pre-existing navigational and visuo-motor control mechanisms.

The start of the journey – recognising scenes and recalling vectors

A bee or an ant leaving its nest or a food site travels in the correct direction towards its goal. Many biologists, starting with Piéron (1904), have displaced insects from their starting position and released them at a new one. The insect's direction and distance of travel are often unchanged as though it were unaware of the displacement to which it had been subjected. This behaviour implies that the insect's path is dictated by internal instructions, termed here a goal-vector, which

incorporate the direction and distance of the goal. Dead-reckoning of this kind is probably the most significant item in an insect's navigational toolkit (Wehner, 1992).

Dead-reckoning can work in unfamiliar surroundings when the goal-vector is computed by monitoring the net distance and direction covered on the previous journey from the current goal to the current starting point (path-integration). But sometimes the vector is recalled from longer-term storage, as on a bee's first trip of the day to a familiar foraging site. Long-term storage of goal vectors provides an opportunity to embed vector navigation within a particular familiar environment. For instance, a bee might associate a vector directed to the nest with its memory of the scene around a feeder (Cartwright and Collett, 1987), thereby helping the recall of the home-vector on leaving the feeder. Linkages of this kind are particularly valuable when insects learn complex foraging routes (Janzen, 1971) and must execute a sequence of vectors in the correct order.

Recent studies indicate that such links may indeed be forged.

For example, Wehner *et al.* (1990) trained bees to forage at two sites 210 m apart and 175 m from the hive. After bees had become well acquainted with both sites, they were caught at the hive entrance at the end of their home journey. They were then taken to one of the two foraging sites and released. The bees' vanishing bearings were in most cases appropriate for reaching home from that release site. Bees probably recognised from which site they had been released and then recalled the associated goal-vector. It is unlikely that the bees were attracted directly by a view of the hive or by landmarks near to it because on release at a site midway between the two familiar release sites the bees' bearings were undirected. However, it cannot be excluded that the insects saw different route landmarks from the two familiar sites and aimed at these.

Menzel *et al.* (1995) provide firmer evidence for the linkage of goal-vectors to scenes. Bees were again trained to forage at two sites. In the morning they were fed at a location SE of and 630 m distant from the hive. In the afternoon the feeder was NE of and 790 m from the hive. Bees caught in the morning, either at the feeder or at the hive, and released at the afternoon site flew directly towards the hive. Likewise, the departure bearings of bees caught in the afternoon and released at the morning site were mostly directed at the hive. The bees' goal-vectors were thus specified by the release site rather than by the immediate results of path integration. When bees were released midway between the two sites, their vanishing bearings were also directed towards the hive, suggesting an averaging of the two vectors. This compromise vector probably occurs because the visual panorama at the midway site has features in common with the familiar views from both of the flanking sites. Thus, bees released far from both feeders adopted a time-linked goal-vector and flew NW in the morning and SE in the afternoon. And the goal-vector of bees trained to just one of the feeders did not change direction when bees were transported to the midway site.

Analogous phenomena are seen in a small-scale environment (Collett and Baron, 1995). Insects flew from compartment to compartment through a large box (Fig. 1). Entrance from one compartment to the next was through a small hole in the partition separating the two. In two of the compartments, the direction in which the bee had to fly from entrance hole to exit hole was labelled by a grating of stripes on the back wall of the compartment. Stripes of one orientation signalled that the trajectory should be to the left, while stripes of another orientation indicated a trajectory to the right. To discover whether bees had associated stripe orientation with trajectory direction, flight paths were recorded in the second compartment when the exit hole was replaced by a horizontal slit running the width of the partition that allowed bees to enter the next compartment at any point along the partition. The bees' direction through the test compartment varied with the orientation of the grating on the back wall. With the grating in the training orientation for that compartment, the bees' trajectory was to the right, as in training. When the orientation was switched through 90°, to match that of the other compartment, bees flew to the left. Intermediate orientations

evoked trajectories with intermediate directions. Bees had linked trajectory direction to stripe orientation and had formed a mapping between these sensory and motor parameters.

Path-integration is available to arthropods with and without good vision. The association of visual scenes with the stored results of path-integration brings several benefits. It may both aid the performance of complex routes and increase the flexibility of path-finding by allowing bees to interpolate from known scenes and vectors to slightly different ones, thus helping them to home correctly from new locations.

Landmarks and dead-reckoning: biased detours

Although path integration is impressively good, there are errors of direction and of distance inherent in calculating the vector during the outward path and in following it on the homeward path. These internally generated errors are compounded further by irregularities in the terrain and buffeting by side winds. One way in which insects cope with this problem is by foraging within a restricted area (for a review, see Wehner, 1992). Operating within familiar terrain allows insects to use landmarks to correct paths based upon dead-reckoning.

Cataglyphis bicolor and *C. fortis* illustrate one way of combining landmark guidance and dead-reckoning (Collett *et al.* 1992). If ants are accustomed to forage at a constant location, with the path between foraging site and nest flanked by conspicuous landmarks, individual ants come to follow a stereotyped route (e.g. Fig. 4). To see whether ants learn the appearance of individual landmarks along such routes, a copy of a landmark is placed on a test ground many metres away. An ant taken from the feeding site is released at a point on the test ground where its home-vector passes directly through the landmark. If the ant normally uses this object to correct its path and can recognise it on the test ground, it should skirt to the left or to the right of the landmark according to whether the landmark is habitually to the right or to the left of the ant on its normal journey home (Fig. 2). Ants consistently behave according to this rule, and the details of their path while skirting the landmark suggest that they associate the visual properties of a given landmark with the decision to keep the landmark consistently on one side. If the landmark is on the correct side of the goal-vector, it does not influence the ant's path. But when the landmark is on the wrong side, ants turn away from it. Simulations suggest that two factors contribute to an ant's angular velocity while turning: (i) the angular size of the landmark (the larger the apparent size, the faster the ant turns); and (ii) the goal-vector (the ant turns to reduce the difference between its current heading and the current bearing of its goal-vector). Such a strategy of landmark guidance is not effective in isolation but only as a supplement to dead-reckoning or to aiming at beacons (see below).

This navigational strategy may have evolved from a procedure to avoid obstacles. A plausible means of avoiding collision is to turn away from an object at a rate determined by the object's retinal size. To transform such a general reaction

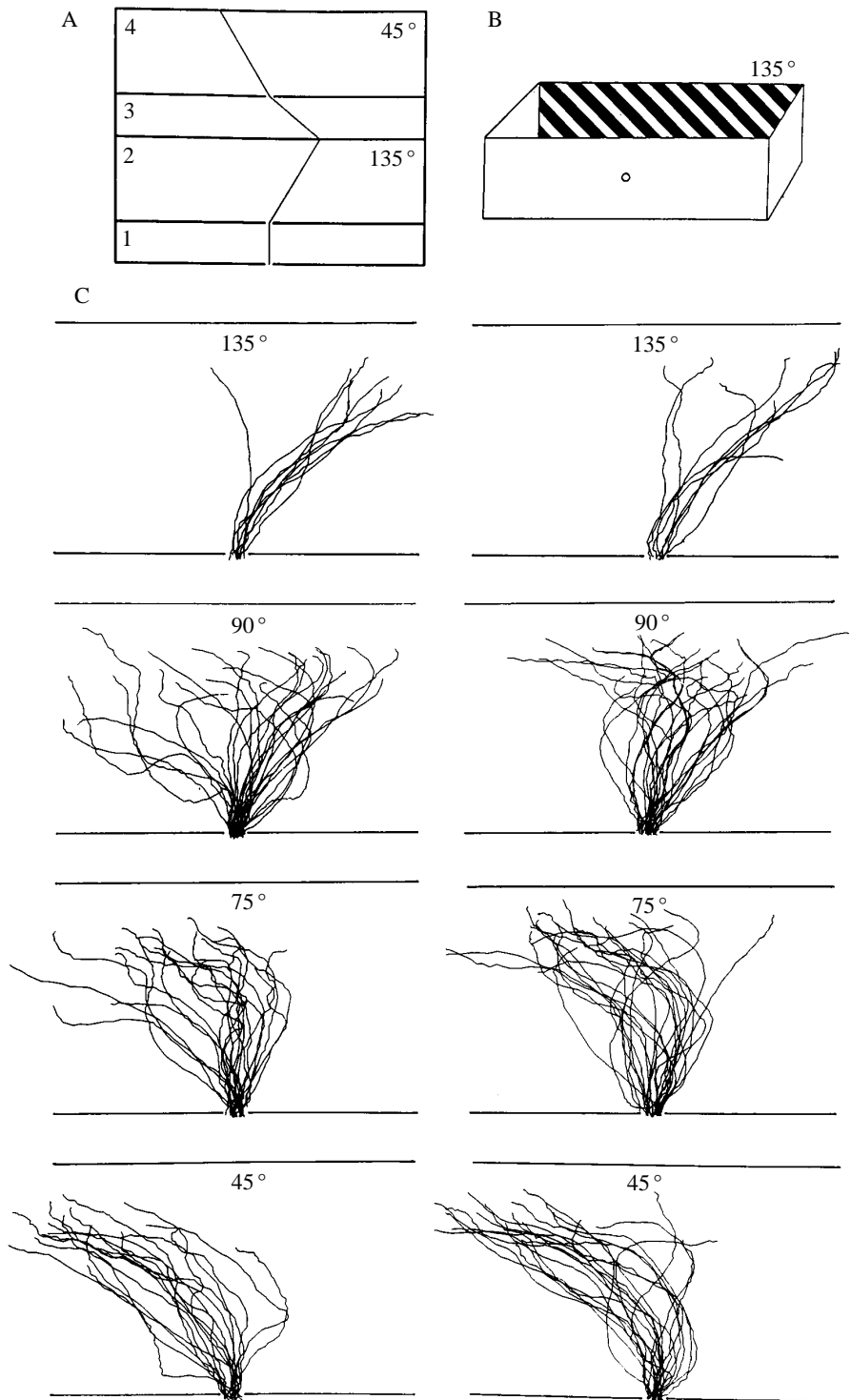


Fig. 1. Bees flying a stereotyped route through a large compartmented box learn to associate a rightward trajectory with stripes oriented at 135° in compartment 2 and a leftward trajectory with stripes oriented at 45° in compartment 4. When confronted with stripes of differing orientations, the direction of their trajectory varied with the orientation of the stripes. (A) Left: plan view of training route. The box is 220cm wide. (B) Compartment 2, in which bees were tested with stripes of differing orientations. (C) The bees' trajectories during tests with gratings of differing orientations fixed to the back wall of compartment 2. Left and right columns show trajectories from the same bees on two successive days (from Collett and Baron, 1995).

into a method of landmark guidance, deviations need only be linked to the visual properties of individual landmarks such that the ant on encountering a particular, familiar landmark detours consistently to one side. On this hypothesis, the trajectories of ants without familiar landmarks on their home route will look much like those of trained ants when an object is placed in the path of their goal-vector but with one telling difference. Whereas the detours of experienced ants are biased

to one side, the detours of naive ants would be directed equally often in either direction. If this form of landmark guidance is indeed an elaborated avoidance response, it becomes clear why ants are not drawn towards landmarks lying on the correct side.

Aiming at beacons

Aiming at familiar beacons that are distributed along an

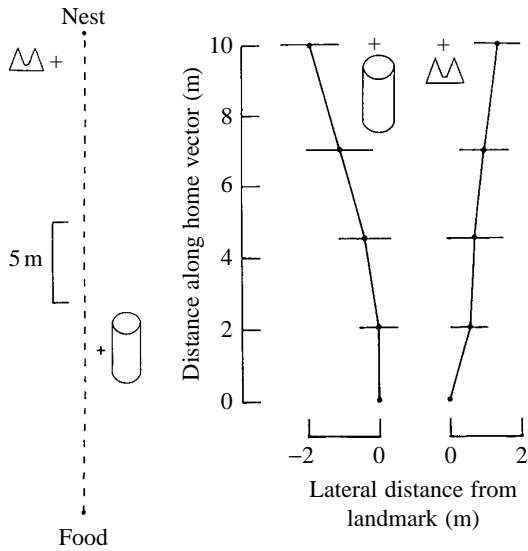


Fig. 2. Homeward trajectories of ants trained to the route shown on the left. An oil barrel is positioned on their right far from the nest and triangles are placed on their left close to the nest. Single ants are released on the testing ground with either the barrel or the triangles placed 10m from the release point in the path of the home vector. Ants detour consistently to the left of the barrel and to the right of the triangles. Filled circles give the mean position of the ants and the horizontal bars show ± 1 standard deviation of the mean ($N=28$ for barrel and $N=27$ for triangles; from Collett *et al.* 1992).

insect's habitual route is also an effective means of coping with disturbances that compromise the accuracy of goal-vectors. Its virtues were apparent to Santschi (1913), who studied the homing of a colony of ants living at the bottom of an isolated palm tree. An ant displaced from home could return by approaching the palm tree, the most prominent object in the neighbourhood. Here a single beacon guided the whole journey. More often, the way is marked by a succession of beacons. Thus, bees will fly towards a conspicuous object, such as a lone tree that lies close to their route, even if the object is

positioned a little off their direct path (von Frisch, 1967; Chittka *et al.* 1995). When the insect is near to the goal and close to the ground, small objects become prominent and can serve as beacons. For instance, if a feeder on the ground is marked by a small cylinder some centimetres away, bees and wasps typically aim for that before moving towards the feeder (Collett and Baron, 1994; Collett, 1995; Fig. 3).

The task requires an insect to pick out prominent objects close to the goal-vector, to learn their appearance with at least the frontal retina, and then to approach them when they reappear on subsequent trips. Most of the animal's surroundings can be ignored. However, the details of the process are not well understood. What, for instance, does an insect learn about the retinal transformations of a beacon that occur during an approach? A bush at a distance will be viewed as a silhouette; the pattern of individual branches only becomes detectable once the insect is close. There are indications that bees will learn a series of transformations. Thus, bees trained over a route will store a sequence of visual patterns (Collett *et al.* 1993) and they can identify a familiar complex shape both by its internal structure and by its outline (Zhang *et al.* 1992).

Aiming at beacons may have developed out of an inbuilt 'fixation response' which causes insects to turn towards and to fixate small objects, such as potential mates or prey, or larger ones, such as plant stalks. The necessary elaboration is to link the fixation response to a learnt visual pattern. This is known to happen in *Drosophila*. A fly will learn to fixate selectively one of two patterns in order to extinguish an unpleasantly hot beam of light that is focused onto its abdomen (Dill *et al.* 1993). It then spends most of its time locked onto the cooling pattern.

In complex environments, when routes are specified by a sequence of beacons, it may be helpful to combine aiming at beacons with biased detours. Consider an ant in scrub with bushes directly in its path. Desert ants avoid walking under bushes, presumably because dense foliage will cause their celestial compass to malfunction. Instead, they skirt round

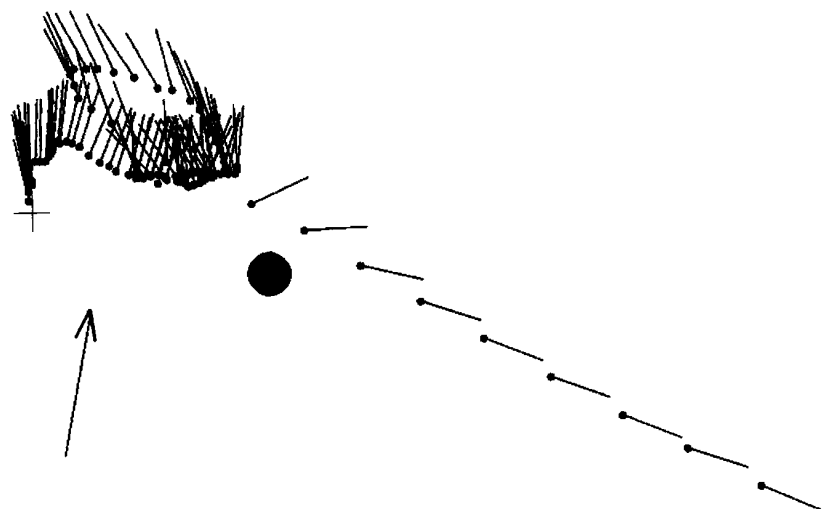


Fig. 3. The flight path of bee approaching a feeder (+) marked by a small black cylinder (●). The position of the bee's head is marked by the dot, the bee's orientation by that of the line. Arrow points north and its length represents 10cm on the ground. Two navigational strategies appear to be used during this flight. The bee first aims at the cylinder and then assumes a standard landing orientation (from Collett and Baron, 1994).

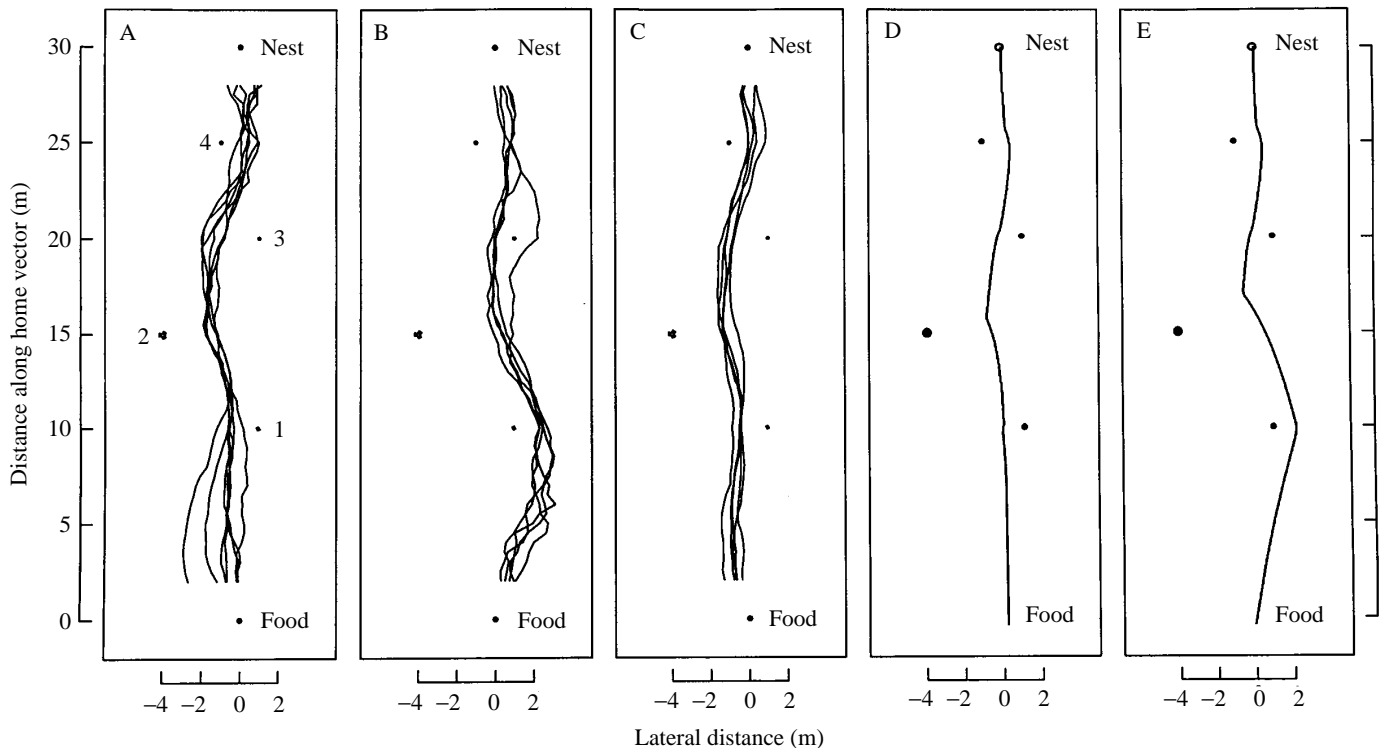


Fig. 4. Homeward trajectories of ants after several days of foraging at a fixed location. Four visually different landmarks were placed near to the direct path between food and nest as marked by numerals. (A,B) Superimposed individual trajectories from two different ants, one that habitually went to the left and the other to the right of the first landmark. (C) Mean trajectories of five ants that passed to the left of the first landmark. (D,E) Simulated ant trajectories. At each step, the simulated path was controlled by the landmark that had the largest apparent size and was less than 70° from the midline. The direction of each step was specified by a linear combination of (i) dead reckoning (turning tendency proportional to the angular difference between the ant's long axis and the home vector), (ii) aiming at beacons (turning tendency varied as the angular difference between the ant's long axis and the retinal bearing of the relevant landmark), (iii) biased detours (turning tendency to the left or right of a landmark was proportional to the retinal width of the relevant landmark). The simulated ant was instructed to go left (D) or right (E) of the first landmark (A–C from Collett *et al.* 1992).

them. A standard transition from the view of one beacon to the next will be helped by making detours in a consistent direction around each. Fig. 4 shows stereotyped routes of *Cataglyphis bicolor* recorded on flat desert terrain on which artificial landmarks had been placed. Initial attempts to simulate these trajectories using a combination of dead-reckoning and biased detours proved problematical (Collett *et al.* 1992). Trajectories are much easier to model accurately with a linear combination of aiming at beacons, dead-reckoning and biased detours, as Fig. 4D,E shows. Desert ants can navigate by landmarks without the use of reckoning (R. Wehner, personal communication) and, interestingly, the model continues to generate successful homeward trajectories when the simulated ant is driven solely by 'aiming at beacons' and 'biased detours'.

The end of the journey – landmarks for pinpointing places

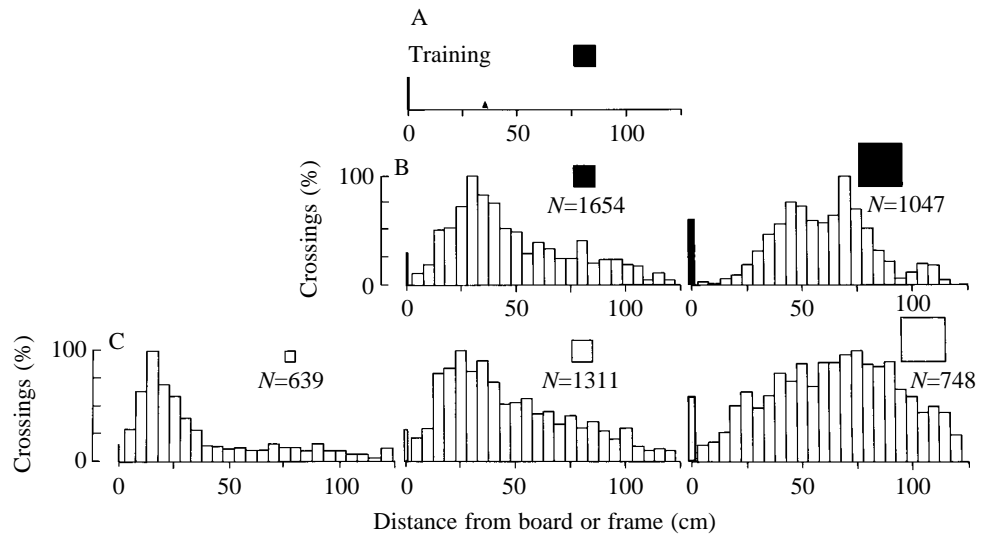
The final goal may itself be inconspicuous and only locatable by its spatial relationship to nearby objects. One technique of regaining such a position is by image matching.

An insect first stores a view of the panorama surrounding a goal that it wishes to retrieve. It can then guide its return by moving until its current view matches its stored view. This method has the advantage that an insect will be attracted to its goal from any direction, provided that the discrepancy between the current and stored images is not too large (for reviews, see Collett, 1992; Wehner, 1992).

Data consistent with such a mechanism come from experiments in which bees, ants or wasps have been trained to learn the position of a goal that is specified by an array of landmarks. After training, the array is distorted and the insects' search is recorded. In many cases (but not all, see Brännert *et al.* 1994; Cartwright and Collett, 1979; Zeil, 1993b), the pattern of search fits the hypothesis that an insect spends most time where it finds the best possible two-dimensional match between what it has stored and what it sees.

Findings such as those illustrated in Fig. 5 suggest that bees do not literally store raw retinal images but rather a processed version that emphasises edges. In this experiment, bees were trained to search at a set distance from an upright, square board. If the square is made smaller, bees search closer and if larger further away from it. Search distances are not altered or made

Fig. 5. (A) Searching distance after training to forage at a feeder (triangle) placed 35 cm from a square black board with 25 cm sides. Histograms give the distributions of positions at which the bee's flight path crossed an imaginary line segment passing through the position of the feeder and the board during tests with the feeder removed. (B) Search distributions with a solid 25 cm or 50 cm board. The board seen end-on is indicated by the solid rectangle. (C) Search distributions with a 12.5 cm, 25 cm or 50 cm frame. The frame seen end-on is indicated by the outline rectangle (from Cartwright and Collett, 1983).



more variable by substituting an open frame for the solid square. Bees in a variety of circumstances parse visual patterns for oriented edges (for a review, see Srinivasan, 1994). Edge detection is probably crucial for segmenting the visual world, as is emphasised by a bee's ability to identify the same edge through colour, luminance and motion contrast (Zhang *et al.* 1995).

The elimination of a mismatch between a stored and a current view is likely to exploit the direction and magnitude of error signals rather than to rely simply upon random movements. Directed error correction can be seen happening in waterstriders (Junger, 1991). These insects take up a fixed position facing upstream in fast-flowing water so that they can catch drifting prey trapped in the water surface. They keep in one spot by using nearby objects as markers and controlling their rowing movements to hold the image of these objects in a fixed position on their retina. In an artificial stream, they will adopt a single point-source of light placed above and in front of them as a landmark. If the point-source is raised, so shifting it upwards from its currently preferred retinal position, the insects will immediately allow themselves to drift backwards with the stream until the image of the source falls onto its previous retinal location. Conversely, if the point-source is lowered, the insects increase their stroke rate until the light is recaptured. Thus, waterstriders detect the direction in which the landmark has moved from its learned position and make appropriate corrective movements.

Image matching assumes that views are stored primarily at the goal, and some evidence for this supposition is given in the next section. However, simulations (Krackauer, 1995) show that search patterns similar to those generated by an image matching procedure can be produced by a different mechanism in which an insect takes views of local landmarks from several vantage points and associates with each view a vector pointing at the goal. A mechanism of this general kind contributes to path-following relatively close to a goal (Collett *et al.* 1993; Collett and Baron, 1995). However, it and image matching

have complementary strengths and weakness so that the two strategies would work well in tandem.

One shortcoming of image matching is the restricted area over which it works (Cartwright and Collett, 1987). An insect must recognise a pattern away from the goal and then move so as to improve the fit between image and stored pattern. However, simple algorithms for improving the fit succeed only if the patterns to be matched are reasonably similar. Thus, longer-range guidance strategies, like aiming at beacons (Fig. 3) or goal-vectors linked to scenes, are required to bring insects close to the goal where a partial match is assured.

Once the insect is near to the goal, care must be taken not to overshoot it. The elimination of overshoots is an intrinsic feature of image matching, but it is expensive to achieve with goal-vectors linked to scenes. To do so, local views must be stored at positions all around the goal. However, this is unlikely to occur. For example, the learning flights that wasps and bees perform in order to memorise the location of a goal typically cover a restricted sector of space around the goal (Zeil, 1993a; Lehrer, 1993).

Landmarks and pattern learning

Landmark guidance depends upon an insect's ability to learn visual patterns and it may well have been one of the driving forces in the evolution of pattern learning by insects. However, the various methods of landmark guidance have distinctly different requirements so that pattern learning may have been steered along several divergent paths.

There is, for instance, conflict over the most appropriate objects to choose as landmarks. When the details of an insect's path are guided explicitly by the position of landmarks, as in image matching, insects depend primarily upon objects that are near to the goal, because these can supply accurate positional information (Cheng *et al.* 1987; Zeil, 1993b). Scene recognition is different. It is less likely to be compromised by small shifts in an insect's position if it is based upon objects in the scene that are relatively distant from where the view is learnt.

Differences are also likely to occur in the process of acquisition. A beacon must remain recognisable as an insect moves towards it and learning may thus occur over much of the approach. A wide temporal window of acquisition would lead to a smearing of the spatial position of edges on the retina, though for many patterns individual edges will have a consistent orientation. And indeed tests on bees that have learnt to approach simple patterns in a Y maze suggest that spatial position may not be critical (Srinivasan, 1994).

Image matching, however, depends upon the memory of patterns of defined size and shape. Such learning does occur. If bees are trained to enter a narrow tube containing a food reward that is some distance in front of a visual pattern, they will hover in front of the tube entrance in a standard posture before entering. Later choices between test patterns indicate that visual patterns are recorded during hovering and that the spatial position of pattern elements is stored in retinal coordinates, with a pattern only recognised when seen by the same region of retina that viewed it during learning (Wehner and Flatt, 1977; Wehner, 1981).

To employ such a retinotopic system in natural behaviour, an insect must control its position in space so that it experiences its surroundings from the same vantage point, both when acquiring visual patterns and when using the stored information. Viewing direction also needs to be fixed. Bees and wasps hovering in front of a horizontal tube have their orientation imposed by local features of the environment, in this instance the direction of the tube (Wehner and Flatt, 1977). However, bees are also capable of recognising patterns in situations where local features cannot reliably specify the bee's orientation (Lindauer, 1960). They then learn patterns with reference to directional cues supplied by celestial (Dickinson, 1994) and by magnetic compasses (Collett and Baron, 1994; Frier *et al.* 1995). Retinotopic memories can function in such situations, because bees tend to have preferred viewing directions that are probably set by compass cues. By this means, insects can keep retinotopic and Earth-based coordinates in register (Collett and Baron, 1994).

The learning flights that bees and wasps perform when they first leave a goal to which they will later return may be involved in acquiring the information needed for several guidance mechanisms. The complex geometry of the flights (Zeil, 1993a) may thus be an attempt to meet the separate demands of these different navigational strategies. The first portion of a honeybee's learning flight on leaving a feeder appears to be adapted to the task of learning about objects from vantage points close to the feeder, for bees often fly close to the feeder for several seconds before moving away (Fig. 6).

In the initial phase of the learning flight, bees and wasps fly through arcs, pivoting about the goal while simultaneously turning. Both the insect's orientation and the angle of the vector connecting the insect to the goal change at about the same rate (approximately 200°s^{-1} ; Zeil, 1993a). Consequently, the area immediately surrounding the goal will be kept relatively stationary on the retina. There is a slight phase lag between changes in the direction of the vector and

the insect's orientation so that the retinal area fixating the goal tends to be 45° or more away from the midline (Zeil, 1993a; Fig. 7). Insects may thus automatically stabilise the retinal image of those objects that are near to the goal and so well suited to act as beacons on the return.

If image matching is organised retinotopically, insects should take up the same orientation when acquiring and when using the information. On this argument, views for image

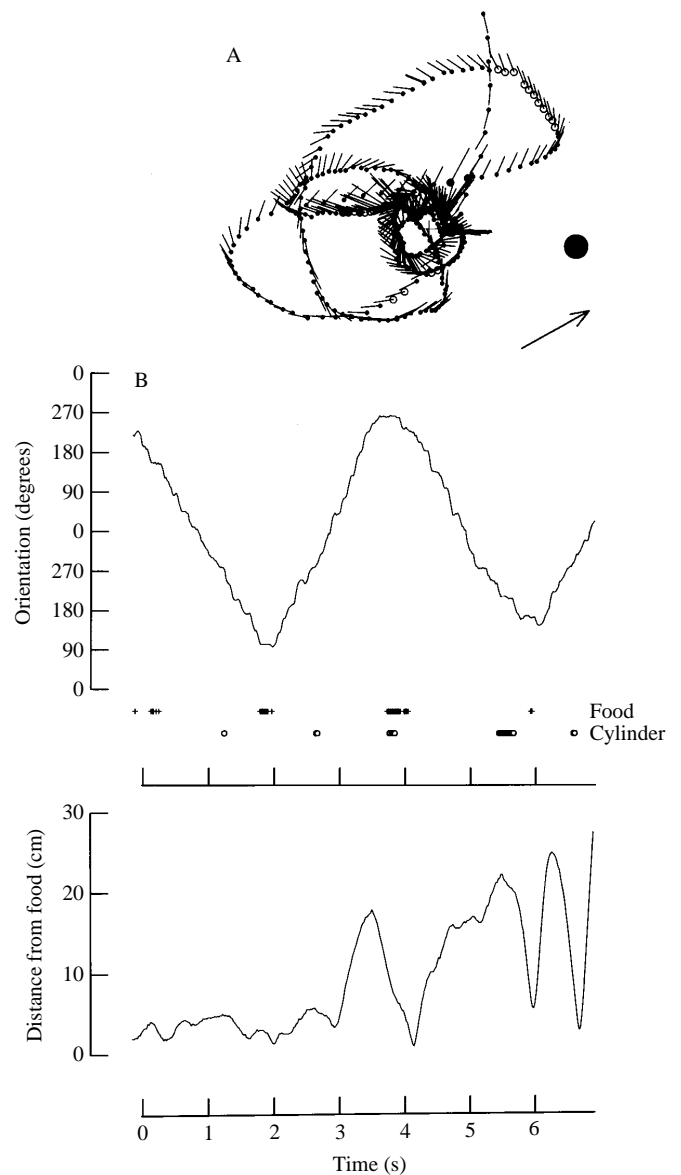


Fig. 6. The learning flight of a honeybee when leaving a feeder (+) with a black cylinder (●) placed nearby. (A) The bee's position and orientation in a horizontal plane is shown every 20 ms. Extended tails and enlarged circles show when the bee pointed within $\pm 10^\circ$ of the feeder. Open circles indicate when the bee faced within $\pm 10^\circ$ of the cylinder. Arrow points north and its length represents 10 cm on the ground. (B) Time course of the bee's orientation and distance from the feeder. Times at which the bee faces the feeder and cylinder are marked by + and ○ respectively (T. S. Collett and H. J. Frier, unpublished data).

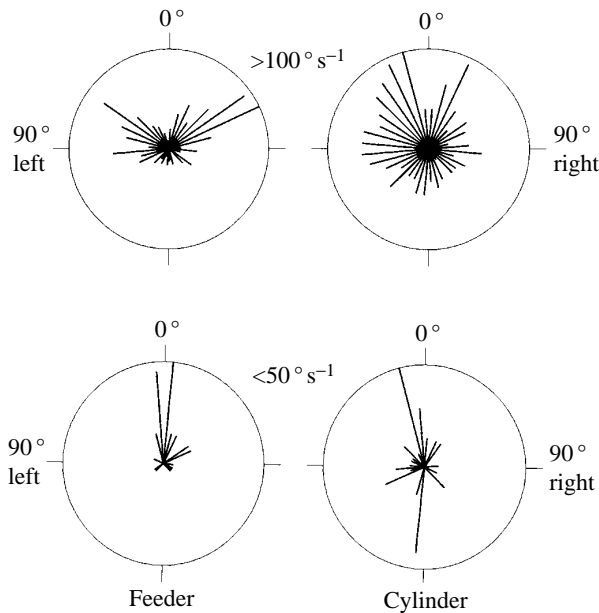


Fig. 7. Frequency distribution of the position of the feeder and the cylinder on the bee's retina when the bee turned at angular velocities of more than 100° s^{-1} (267 frames) or less than 50° s^{-1} (41 frames). Data from flight of Fig. 6.

matching should be stored when the insect looks at the feeder, for the preferred orientation of a social wasp at these moments is correlated with its preferred orientation when it is close to the feeder on return flights (Collett, 1995). It is helpful for image storage that inspections of the feeder tend to occur at the peaks and troughs of the orientation plot when the insect's angular velocity is low (Figs 6, 7; Collett and Lehrer, 1993).

It is more difficult to analyse how insects acquire the information needed for scene recognition; possibly this occurs in the last phase of the learning flight when they circle high above the ground, tantalisingly out of range of the camera and the naked eye.

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