

# MEMORY USE IN INSECT VISUAL NAVIGATION

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The navigational strategies that are used by foraging ants and bees to reach a goal are similar to those of birds and mammals. Species from all these groups use path integration and memories of visual landmarks to navigate through familiar terrain. Insects have far fewer neural resources than vertebrates, so data from insects might be useful in revealing the essential components of efficient navigation. Recent work on ants and bees has uncovered a major role for associative links between long-term memories. We emphasize the roles of these associations in the reliable recognition of visual landmarks and the reliable performance of learnt routes. It is unknown whether such associations also provide insects with a map-like representation of familiar terrain. We suggest, however, that landmarks act primarily as signposts that tell insects what particular action they need to perform, rather than telling them where they are.

Navigation provides a good arena for exploring the complexities of insect behaviour. The sensory processing, decision making, memories and in-built routines that are involved in insect navigation are expressed spatially in rich detail in the routes, search patterns and actions that insects perform when travelling over familiar terrain. This review focuses on the behaviour of individual social insects that bring food back to their nest for storage and for raising progeny<sup>1,2</sup>. Ants, bees and wasps learn to recognize the attributes of nest sites, foraging sites and the routes between them. Analysis of what these insects remember about places, routes and landmarks reveals robust and flexible navigation systems that depend on elaborate networks of learnt associations<sup>1</sup>. We show the importance of the associations between long-term memories in the operation of two basic navigational strategies — view-based guidance and path integration — that insects use to reach a goal that is fixed in space. Associations between memories are shown to have a basic role in the recognition of landmarks and in the ability of insects to follow familiar routes.

## View-based navigation

Fundamental to the visual navigation of insects is their ability to learn the appearance of landmarks from particular viewpoints. Insects are sensitive to and can learn

many visual features, including colour<sup>3,4</sup>, size<sup>5,6</sup>, edge orientation<sup>7</sup>, symmetry<sup>8,9</sup> and motion<sup>10</sup>, all of which could be involved in view-based landmark learning and recognition. The shape and position of a pattern on the retina can change with an animal's viewing position and orientation, making the recognition of landmark views problematical for a moving animal.

To some degree, an insect can recognize a previously learnt pattern, even with slight transformations in shape or shifts in retinal position. Generalization is helped by the relatively broad bandwidth of visual filters that are used to extract stimulus parameters such as orientation<sup>7,11</sup> and colour<sup>4</sup>. Evidence that insects generalize across retinal position comes from fruitflies that were held stationary, so that it was known what area of retina viewed a pattern. Wolf and co-workers<sup>12</sup> presented tethered fruitflies with two discriminable patterns, one 45° to the left of its midline and the other 45° to the right. The flies learnt to extinguish a heat beam by generating torque in the direction of one of the patterns. After training with this 'safe' pattern always in the same retinal position, flies were tested with the positions of the patterns exchanged. Their direction of torque shifted towards the safe pattern in its new retinal position. Positional generalization might be mediated, in part, by the large or elongated receptive fields of visual interneurons<sup>13</sup>.

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There are, however, other ways of increasing the reliability of pattern recognition. Insects can learn views of landmarks from several different vantage points, maintain consistency of views over multiple trips by following fixed routes, or use contextual cues to help them to recognize landmarks from new vantage points. These aids to recognition are explored below in the context of image matching.

**Image matching.** In approaching a goal that is defined by landmarks, an insect often starts out by using one of the landmarks as a beacon at which it aims<sup>3,14,15</sup>. The final approach to the goal is probably controlled by a form of image matching, in which the retinal position and appearance of landmarks as viewed from the goal are stored as a retinotopic 'snapshot'. Insects can then reach the goal by moving so that their current retinal view tends to correspond to their stored snapshot (as seen in ants<sup>16–18</sup>, bees<sup>19</sup>, wasps<sup>20</sup> and waterstriders<sup>21</sup>). Evidence for image matching in ants and bees comes from studies in which an ant's nest or a bee's feeding site is marked by an array of landmarks. When the array is enlarged, reduced or otherwise transformed, insects search for the goal where their two-dimensional view of the landmarks

matches the view that they normally see from the goal<sup>16,19</sup>. There is debate, fuelled largely by modelling studies, over many details of image matching, such as whether matching is local or global<sup>22</sup>, what features of the image are stored<sup>23,24</sup>, and whether retinotopy is essential<sup>22,25</sup>.

As insects often learn several goals and subdivide the routes to these goals, an important prerequisite of image matching is recalling the correct snapshot (one that corresponds to a particular place) out of a set of possible snapshots. We will see that recall of a snapshot is driven by a wider array of cues than those that are involved in the process of matching the snapshot and current image.

**The contents of snapshots.** Learnt visual features that can be used in matching a current retinal image to a snapshot are likely to include the retinal positions of edges<sup>18,19</sup> and spots of light<sup>21</sup>, and of the centre of gravity<sup>5</sup> and colour of an area<sup>26,27</sup>. Because the retinal position and appearance of nearby landmarks change appreciably with small movements, landmarks that are near to a fixed goal are the natural choice for pinpointing its exact position, whereas larger and more distant landmarks can guide an insect only to the rough area of the goal. Two types of evidence indicate that bees do place particular emphasis on information from landmarks that are close to the goal. First, the searches of bees in various tests are driven most strongly by landmarks that, during training, were near to the goal<sup>28</sup>. Second, the flights that bees and wasps perform when acquiring landmark information<sup>29–34</sup> appear to be designed to provide information about the appearance of landmarks near to the goal<sup>19,31</sup> (BOX 1). Bees and wasps perform highly structured orientation flights on their first few departures from their nest<sup>31</sup> or feeder<sup>32,33</sup>. A conspicuous feature of these flights is that the insect flies in a series of approximately semicircular arcs that are centred on the goal, turning at a similar angular velocity<sup>31</sup>. The visual consequence of this manoeuvre is that the goal and objects that are close to it are roughly stationary on the retina, while the distant panorama moves at the insect's rotational velocity, but in the opposite direction. The motion contrast between landmarks that are close to the goal and the background might result in a snapshot that emphasizes these highlighted landmarks.

**Storing multiple views.** It can be difficult to recall or to match a retinal image to a snapshot from vantage points that are distant from the point at which the snapshot was learnt. Experiments on wood ants<sup>18</sup> that were trained to approach a goal from a short distance away indicate that they subdivide the path into a sequence of path segments, with each segment guided by a different snapshot. So, anywhere along a route, the current retinal image will always be similar to one of the stored snapshots. The ants were trained to find food at the bottom of a cone. In tests, the cone was replaced by a card on which a single black–white edge was oriented so as to match the left or right edge of the cone (FIG. 1). The direction of the ant's body axis was recorded during the approach to see where on the retina (assuming that the head moves little with respect to the body) the ant placed the bottom of the edge. The ant tended to hold

#### Box 1 | Techniques for monitoring spatial behaviour

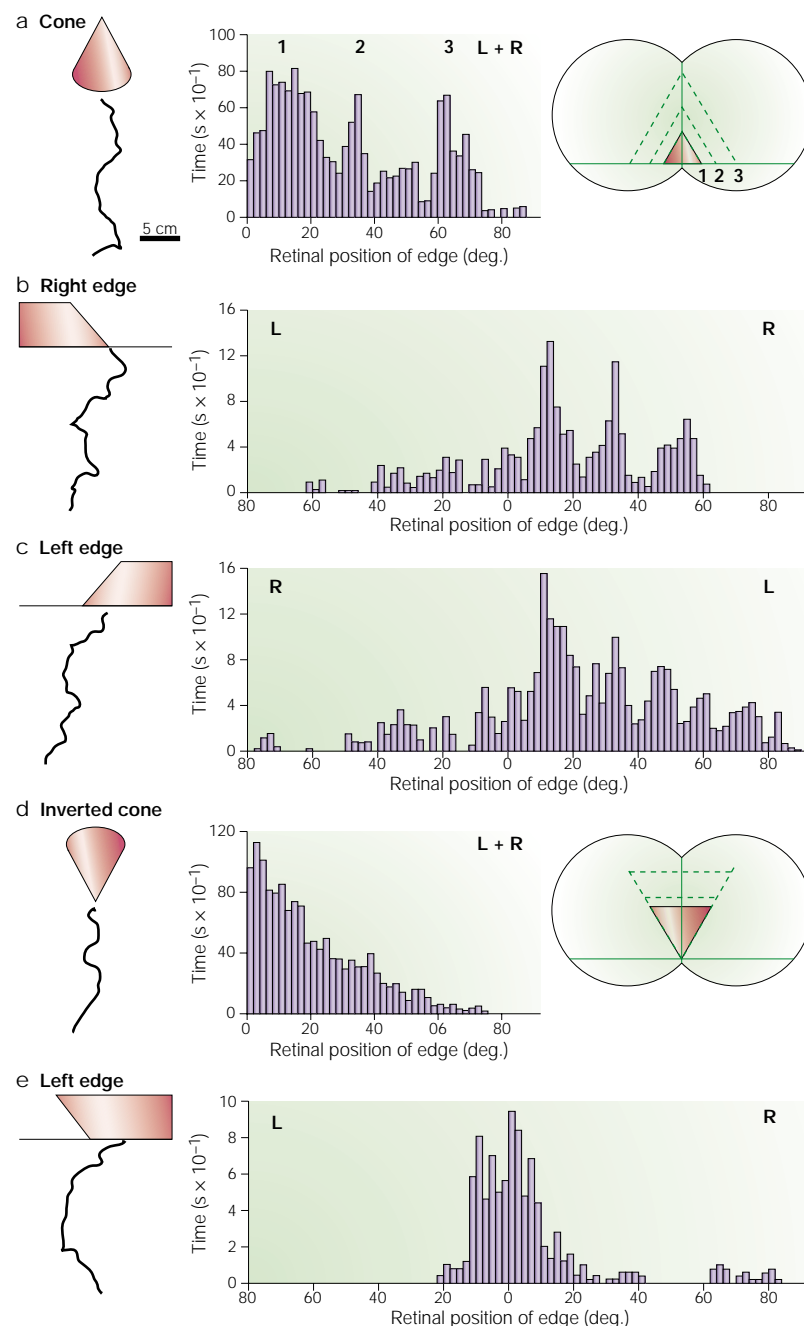
Entomologists have long appreciated the significance of an insect's ability to remember routes, and their methods of recording them have gradually improved. Recently, an insect's orientation, as well as its position, has been monitored so that it is possible to infer where the insect looks during its route.

Cornetz<sup>105</sup> recorded the details of many ant paths in a dusty Algerian town square by walking behind an ant and marking with a stick in the sand the path that the ant followed. Other old-fashioned methods included dropping markers (small stones, improving on Hansel and Gretl) along the ant's trail. In the 1970s, Wehner and colleagues<sup>16</sup> recorded the trajectories of desert ants by painting a grid on the sand and then monitoring the ant's movements over the grid on squared paper. This method is still used (FIGS 2 and 6c).

More recently, routes have also been video-recorded. One method is to keep the camera in a fixed position and pan with it so that the ant is held in the centre of the viewfinder. The ant's position is then given by the camera's azimuth and tilt angles<sup>109</sup>. With the advent of cheap servo-controlled cameras and image processing, this method has been automated<sup>110</sup>. A single ant walking indoors on a white floor can be tracked over at least 5 m with a video image that is large enough to give the orientation of the ant's longitudinal axis (FIG. 6a).

Flying insects are more difficult to track. Over short distances, video-recording in two or three dimensions provides positional and rotational information. Even more precise data has been obtained by attaching separate coils to an insect's head and thorax, and having the insect fly within a uniform magnetic field<sup>111</sup>. Independent rotational movements of head and body can then be derived. Over a much larger scale, harmonic radar now makes it possible to follow a bee for about 1 km over open terrain and to obtain positional fixes every two or three seconds<sup>112</sup>.

More indirect methods are also used. Honeybees communicate the distance and direction of a feeding site to potential foragers through the waggle dance<sup>3</sup>. Human observers can read the dance to infer where the insect has been foraging, but not the route that it has taken. The direction of the start of a bee's route has been recorded by monitoring the bee's position on the horizon (its vanishing bearing) when it disappears from view a few hundred metres away<sup>67,90</sup>. Janzen deduced segments of the route taken by particular orchid bees by recording their punctual daily arrival at different points along the route<sup>113</sup>. Information about routes and route learning has also come from making ants or bees walk or fly through mazes, and recording the insects' decisions at various choice points.



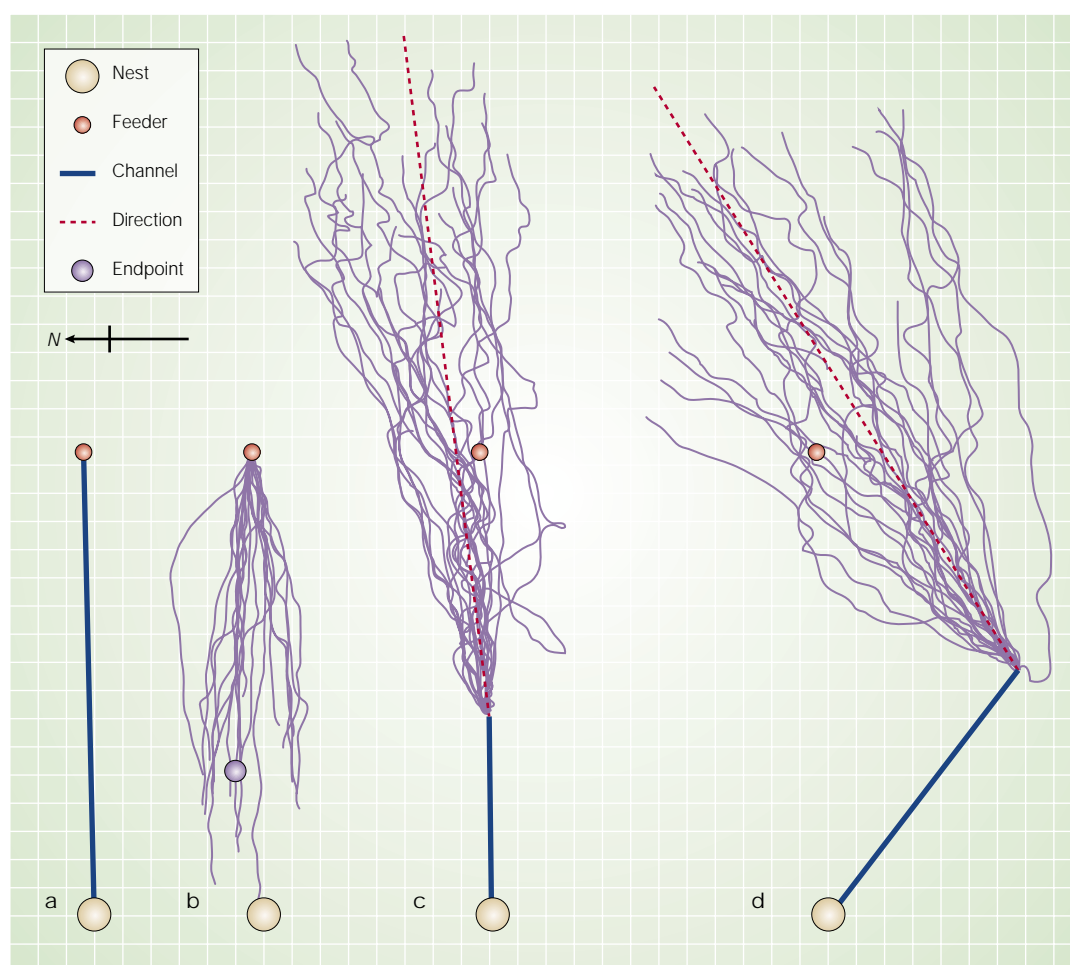
**Figure 1 | Image matching in the wood ant, *Formica rufa*.** Wood ants are trained to approach the bottom of a cone (height 12 cm, base 8 cm) for food. **a** | The track of a single ant walking towards the cone. The histogram plots the horizontal positions of the bottoms of both edges of the cone on the ant's retina (L, left; R, right). Data are accumulated from 14 such approaches by the same ant. The sketch on the right illustrates the hypothesis, derived from the multimodal distributions, that an ant stores several snapshots of the cone that it has taken while fixating the centre of gravity of the cone. **b, c** | Similar data obtained during multiple approaches of the same ant to a single black–white edge on a piece of vertical card. The edge is much longer than the cone, but is oriented at the same (15°) angle to the vertical, corresponding to either the left or the right edge of the cone. The ant places these left and right edges on its left and right retinae, respectively. The distributions of the horizontal position of the bottom of the edge on the retina are, again, multimodal. Note the correspondence in the positions of the modes in the ant's approaches to these different stimuli. **d, e** | Similar plots and data for ants trained to approach an inverted cone. If an ant were to record snapshots when facing an inverted cone, the apex of the cone would fall on the same position at the front of the retina, wherever the snapshot was recorded. During approaches to inverted cones or to a single black–white edge, the horizontal position of the apex of the cone or of the bottom of the edge on the retina was, indeed, mainly at the front of the retina. Adapted, with permission, from *Nature* (REF. 18) © 1998 Macmillan Magazines Ltd.

the edge in a limited number of preferred retinal positions, so that a histogram of dwell times of the retinal position of the corner of the edge during the approach was multimodal, with each mode possibly corresponding to a separate snapshot (FIG. 1b,c).

Other examples of insects learning the appearance of an object from more than one distance come from honeybees that acquire one set of visual features when they are close to an object and a different set from further away. Bees that are trained to approach a stimulus that contains both a macro-pattern, which is visible from a distance, and a micro-pattern, which is visible only from nearby, learn both patterns so that they can recognize the stimulus over a range of distances<sup>35</sup>. The chromatic properties of a stimulus change with image size. When bees are distant from a coloured target so that the target's angular subtense is small, they perceive only its achromatic contrast against the background, using green receptors. Bees can appreciate the colour of the target only when they are close enough for the target to subtend more than 15°. For recognition throughout the approach, both the chromatic and the achromatic properties of the target are learnt<sup>36,37</sup>.

**Consistent views of snapshots.** Visual-pattern learning in insects takes several trials<sup>38</sup>. If the same view of an object or a scene is to be recaptured during learning trials and later during recognition, an insect must look at the object or scene in a similar way from trial to trial. The insect's tendency to treat an object as a beacon<sup>3,14,15</sup> helps to provide consistent views. View consistency can be enhanced by always fixating an object's centre of gravity<sup>39</sup> during an approach. Details of the approach of wood ants to features of upright and inverted cones (FIG. 1) suggest that, during learning, the ants might fixate the cone's centre of gravity and at that time store details of the edges of the cone. An ant that has learnt to approach an inverted cone for food tends to keep the apex of the cone on the front of the eye during its approach. When approaching a single edge that corresponds to the bounding edge of the inverted cone, the ant tends to fixate the lower corner of the edge. An ant that is trained on an upright cone, and tested with a single edge that is oriented to match either the left or the right side of the cone, holds the bottom corner of the edge in a series of preferred retinal positions on the left or on the right retina, respectively. Until the ant gets close, the preferred positions on the two retinae are symmetrical about the midline (FIG. 1). The symmetrical peaks suggest that the retinal positions of the edges are learnt while the cone is centred.

Learning, recalling and matching a snapshot are all made easier by facing in a consistent direction. Using compass cues that are available from the sun<sup>3,40</sup> or the Earth's magnetic field<sup>41</sup>, bees and wasps often take up a preferred compass orientation when they are close to the goal<sup>15,20</sup>. With rotation controlled independently by compass cues, the discrepancy between snapshot and current image can be reduced by translational movements alone. This simplification is possible for flying insects because they can move in any direction relative to their long axis. Ants, whose direction of movement is



**Figure 2 | Food vectors in the desert ant, *Cataglyphis fortis*.** **a** | Training route. Ants travel 15 m along an eastward-pointing channel to a feeder. **b** | Homing trajectories of ants taken from the feeder. Trajectories are in the normal homeward direction. The large, yellow circle shows the position of the fictive nest. The smaller, blue circle indicates the mean endpoint. **c** | Foraging trajectories on open ground after leaving a shortened channel that pointed in the same direction as the training channel. The small, red circle marks the usual position of food, which is absent in these tests. Mean direction is along the channel. **d** | Foraging trajectories on leaving a channel that points 38° to the east of the training channel. Mean direction is to the east of the direct path from the end of the channel to the feeder. Grid lines are spaced at 1-m intervals. Adapted, with permission, from REF. 61 © 1999 Elsevier Science.

always aligned with their long axis, require other mechanisms<sup>42</sup>. The preferred compass orientation of bees and wasps is chosen to suit the geometry of a particular task<sup>43</sup> or the position of landmarks relative to the goal<sup>44</sup>. In the absence of compass cues, honeybees can use as a reference bearing a consistent approach direction from a fixed starting point to a landmark<sup>45</sup>.

**Contextual cues and recognition.** The distant panorama that is viewed from the goal has complementary properties to those of nearby landmarks. Because its appearance changes little with an animal's movements in the vicinity of the goal, the panorama in which local landmarks are set is easy to recognize over a relatively large area, so panoramic cues can provide natural support for the recognition of local landmarks.

The role of panoramic cues in the recall of snapshots is evident from a study<sup>46</sup> in which honeybees were trained to find a small drop of sucrose on each of two 2-m<sup>2</sup> platforms that were located 40 m apart, with

a distinctly different view of buildings and trees from each platform. The small amount of sucrose that was available on each platform encouraged the bees to visit both platforms on every foraging trip. The location of the sucrose drop on each platform was specified by nearby landmarks that, in colour and shape, were specific to each platform and were moved to different positions on the platform between trials. On one platform, the food was a few centimetres to the west of the local landmark, and on the other to the east. When these landmarks were swapped between platforms, bees ignored the changed appearance of the landmarks and searched in the usual position relative to the training landmarks on that platform. The panorama, and not the local landmarks, determines which snapshot is recalled. And because it occurs in the right context, a landmark of unusual appearance is taken as an acceptable stimulus for matching, and its image is placed in the retinal position that is appropriate to the recalled snapshot.



The previous example shows how contextual cues allow the image-matching system to operate with badly matching visual features. The next two examples highlight the role of contextual cues in selecting the correct target from several potential targets. Honeybees will learn to approach one petal on an artificial flower at one time of day, and another petal on the same flower a few hours later<sup>47</sup>. The visual scene is more-or-less the same throughout the foraging period, but time-related cues signal which petal is the appropriate target. In another study, honeybees were trained to go to one place in the morning, where they approach a blue target for food, and another place in the afternoon, where a yellow target means food. In tests, bees that were given both coloured targets in each place chose the colour appropriate to the place, irrespective of time of day<sup>48</sup>. In this case, the distinct spatial cues override temporal cues in determining the target.

#### Navigation using path integration

When a honeybee or desert ant leaves its nest, it continually monitors its path, using a sun and polarized-light compass<sup>40</sup> to assess its direction of travel, and a measure of retinal image motion (bees<sup>49–51</sup>) or motor output (ants<sup>52</sup>) to estimate the distance that it covers. This information is used to perform path integration, updating an accumulator that keeps a record of the insect's net distance and direction from the nest<sup>53,54</sup>.

The memory of the insect's global position relative to the nest, which is stored in the state of the accumulator, is temporary in the sense that it changes whenever the insect moves. It allows the insect to return home directly from any point on its foraging path. A test that was first performed almost a century ago<sup>55</sup>, in which an ant is displaced during a foraging trip to another location, shows that, in these circumstances, the homeward trip is not guided by landmarks. On release, the ant is given food and performs what is termed a home vector: it runs in almost a straight path in a direction and for a distance that would have returned it to its nest had it not been displaced (FIG. 2b). If the ant is kept in the dark for several hours before release, the direction of the home vector is unaffected by its period of captivity<sup>56</sup>, implying that there is compensation for the daily movement of the sun through the sky<sup>3,57–59</sup>.

Honeybees store the coordinates of a feeding site for long periods. When a bee returns from a food site, it will signal through its waggle dance the direction and distance of the site, and thereby recruit other foragers to it. Von Frisch<sup>3</sup> cites examples of bees advertizing a food site that they have not visited for days or even weeks. By having bees arrive at a feeder at one distance from the nest and then moving them to another distance, Lindauer<sup>60</sup> found that the bees' waggle dance reported the outward rather than the return journey, indicating that bees record the path-integration coordinates of the feeder when they are at the site.

There is some evidence that honeybees can remember the coordinates of more than one site. Lindauer<sup>57</sup> trained a group of bees to forage at one site in the morning and at another in the afternoon. By feeding the bees with

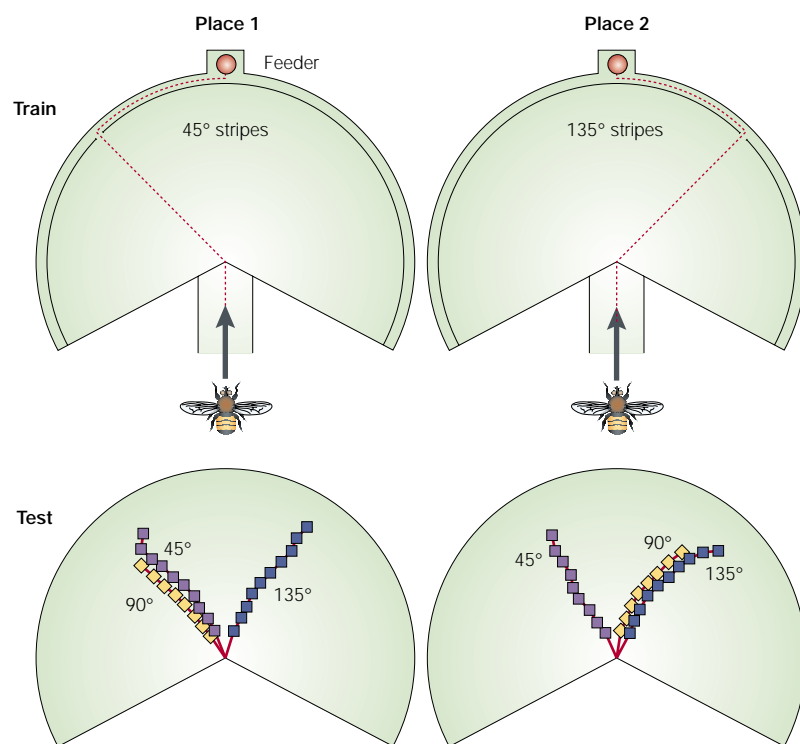
sugar water, he induced a few of these bees to dance at night, when they do not forage. Early in the night, their dances signalled the afternoon feeder, but as morning approached, they signalled the morning feeder. The number of sites that a bee or an ant can remember in terms of global coordinates is unknown.

Equipped with the recalled coordinates of a food site and a temporary memory of its current coordinates, an insect that uses path integration can steer itself towards the site. The direction of the site from the insect's current position is given by the difference between the coordinates of the two memories. The details of vector storage and vector subtraction have still to be worked out. However, the results of the subtraction can be seen, for instance, in the way that an ant will head in the correct direction after an imposed detour on either its outward<sup>61</sup> (FIG. 2) or its homeward<sup>62</sup> journey.

**Local vectors.** The target of the path-integration system (the positional coordinates of a goal) is not directly observable, and some further stimulus is needed to recall the target. As Lindauer's nocturnal dance experiment shows, when bees are in an appropriate motivational state, the target of the path-integration system can be evoked by time of day. Another way of recalling a target is by associating it with a particular landmark.

In addition to measuring the total distance travelled from their nest, honeybees also use prominent landmarks to segment routes and to measure separately the distance travelled along each segment. This local vector, which spans the distance between landmarks, is attached to the view that is seen at the beginning of the segment, such that when the bee recognizes the view, it recalls the associated local vector that takes it to the next landmark. For instance, bees can be trained in a multi-compartment maze to perform a vector of one length in one compartment when they see a pattern of stripes that is in one orientation, and to fly a vector of a different length in another compartment on seeing stripes in an orthogonal orientation. When the order of the stripe patterns is changed, the associated vectors change too<sup>63</sup>. Similarly, bees flying within a channel can be trained to fly one distance to a feeder when a pattern is on the left wall of the channel, and a different distance when the pattern is on the right wall<sup>64</sup>. In both examples, bees recall the local vector when they see the appropriate stimulus.

Panoramic cues are important in the recognition of the visual cues that trigger a local vector<sup>65,66</sup>. The experiment that is illustrated in FIG. 3 adds to the examples of the previous section in showing that context can enlarge the range of what bees categorize as an acceptable cue. Honeybees learnt in one place to fly to the left on viewing a pattern of black-and-white stripes oriented at 45°, and in a second place to fly to the right on viewing stripes oriented at 135°. They continued to follow this rule in tests in which the positions of the 45° and 135° stripes were swapped. When the bees were tested with 90° stripes, they treated them like 45° stripes in the first place and like 135° stripes in the second place<sup>65</sup>. Part of the burden of recognizing the striped pattern was carried



**Figure 3 | Pattern recognition and spatial context in honeybees.** The task is shown in the top row. Bees are trained in two places to fly through a cylindrical compartment (radius 70 cm) and exit through one of two holes in the back wall. The direction to be taken depends on the stimulus that covers the entire back wall. In place 1, bees fly left if the wall is covered with 45° black-and-white stripes, and to the right when the wall is plain yellow. In place 2, bees fly to the left when the back wall is blue and to the right when the back wall is covered with stripes that are oriented at 135°. Bees are then tested with 45°, 90° or 135° stripes in both places. Mean trajectories, which are plotted in the bottom row, show that bees responded correctly to 45° and to 135° gratings in both places, showing that they were sensitive to grating orientation. But bees treated a vertical (90°) grating differently in the two contexts. In place 1, they flew left as though it were a 45° grating, and in place 2 they flew right, as if it were a 135° grating. Adapted, with permission, from REF. 65 © 1997 Springer Berlin Heidelberg.

by the panoramic cues that were associated with each place, so although bees were sensitive to orientation, they accepted an unusually broad range of orientations as a suitable match to the training pattern.

**Averaging local vectors.** Without the assistance of panoramic cues to bias recognition in favour of a particular visual stimulus, ambiguous stimuli can lead to the simultaneous recall of several vectors. The behaviour illustrated in FIG. 4 occurred when bees were trained in a single spatial context to perform two local vectors. One vector was linked to 45° diagonally oriented black-and-white stripes, and the other to 135° stripes<sup>63</sup>. Stripes oriented at angles that lay between the two training stimuli induced vectors that were a weighted average of the two learnt vectors, indicating that the two vectors were recalled and combined in the bees' motor output.

Might this kind of interpolation ever be useful for navigation? A possible instance was explored by Menzel *et al.*<sup>67</sup> in which bees approach a single goal, the hive, from two locations within an open environment; a conical hill 2 km northeast of the hive was the most prominent landmark. Individual bees followed two routes. In

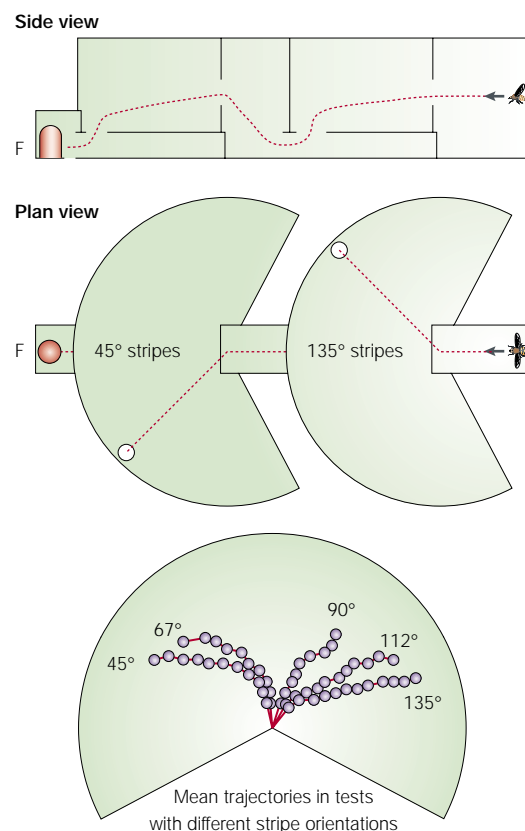
the morning, they flew from their hive 630 m southeast to one feeder, and in the afternoon the same bees flew 790 m northeast to a second feeder. In tests, bees that arrived at the nest in the morning, after feeding, were taken to either the morning or the afternoon feeding site. Their vanishing bearings from the release site pointed to the hive. Bees were also taken to an intermediate site 720 m east of the hive. From here, the vanishing bearings were more dispersed, but were still directed at the hive.

One of several possible interpretations of these findings is that one local vector is associated with the landscape that is viewed from the morning site, and another vector is associated with the afternoon site, and that the mountain is an important component of both remembered scenes. At the intermediate release site, the mountain is seen from an intermediate direction; both the morning and afternoon landscapes are recalled and an intermediate vector is performed<sup>67–69</sup>. Such interpolated responses could allow bees to navigate continuously within open terrain using a few memories, each recorded in a different, discrete location.

**Segmenting routes and linking segments**

When ants and bees have a reliable source of food, they travel repeatedly between their nest and the food site, often following a fixed route that they divide into segments, using prominent objects as sub-goals. Von Frisch<sup>3</sup> observed that honeybees tend to head for isolated trees along their route, even if doing so takes them off their direct course. Similarly, Chittka *et al.*<sup>14</sup>, when training bees to a feeder in a desert environment, found that foragers flew towards a prominent landmark (a pick-up truck) that was placed 20 m to the side of the feeder, before turning to the feeder. As we have seen, studies of small-scale routes in honeybees indicate that these insects attach to each landmark a local vector that spans the distance to the next landmark along the route. Studies of more natural routes in bees<sup>14</sup> and desert ants<sup>70</sup> also indicate that local vectors are linked to visual cues. These results indicate that the basic structure of each route segment is a landmark and an associated local vector or some other stereotyped movement (for example, turning left)<sup>71,72</sup>. This view of learnt routes emphasizes that the primary role of a landmark is to serve as a signpost that tells an insect what to do next, rather than as a positional marker that gives the insect its current location within a large-scale coordinate system<sup>73</sup>.

Segmenting the route improves accuracy and robustness in several ways. First, if bees are led astray on one segment by some imprecision in their local vector, they will still be attracted to the next landmark along the route, so the subsequent segment will be unaffected by their error. Second, because short local vectors are more precise than a long global vector that covers the whole route<sup>74</sup>, the uncertainty of reaching the goal through local vectors depends on only the length and directional accuracy of the final local vector. Third, local vectors that run between landmarks mean that insects will approach each landmark from a consistent direction, making landmark recognition easier.



**Figure 4 | Trajectories of honeybees trained in a two-compartment maze in a single place.** Bees are trained to fly to their right in the first compartment, which has 135° stripes covering the entire back semicircular wall, and to fly to the left in the second compartment, where 45° stripes cover the back wall. In tests, the responses of bees to different stripe orientations are recorded in the first compartment. Top: plan and side view of maze and training conditions. Bee's route to food (F) at the end of the maze is shown by the dashed line. The bee leaves each semicircular compartment through a hole in the transparent Perspex floor. Bottom: average trajectories in the first compartment of bees that view different stripe orientations. Stripes of intermediate orientations elicit vectors in intermediate directions. Adapted, with permission, from REF. 63 © 1996 Springer Berlin Heidelberg.

To show that the accuracy of a path-integration vector does decrease with its length, Srinivasan *et al.*<sup>74</sup> trained bees to fly along a narrow channel to a feeder, and measured how far down the channel each bee searched when the feeder was removed (FIG. 5). The uncertainty of the bee's search position increased with the distance of the feeder from the channel entrance<sup>75</sup>. A landmark that was placed along the channel narrowed the bees' search distribution, indicating that the precision of the search was determined by the length of the vector running from the landmark to the feeder. This possibility was examined in tests in which the landmark was moved back 120 cm towards the entrance. The peak of the search distribution then shifted by the same amount (FIG. 5).

Foraging routes of honeybees gain reliability from the formation of associations between memories of landmarks in neighbouring segments. Several experiments

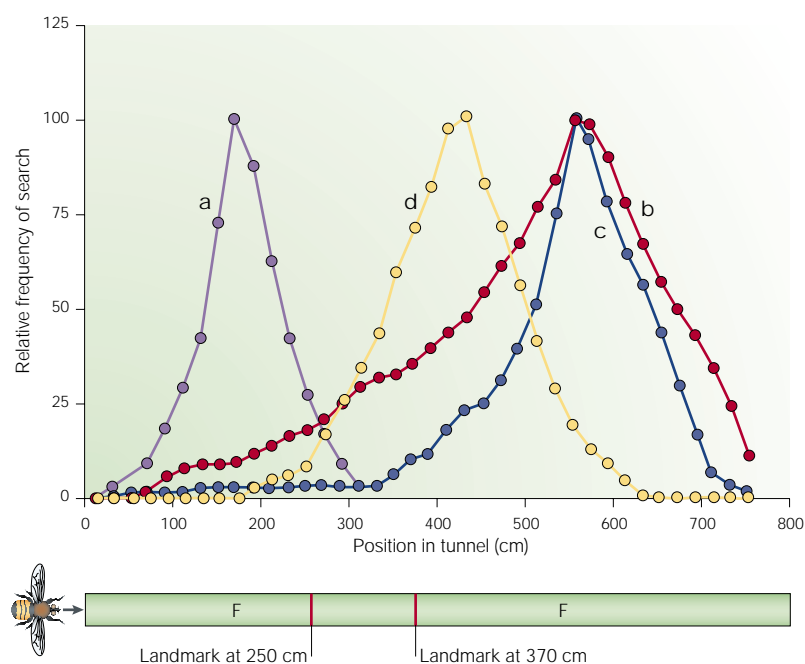
in honeybees have shown that viewing a landmark can prime the recognition of the next landmark along the route in both small-scale<sup>76,77</sup> and natural environments<sup>78</sup>. Experimental demonstrations of sequential priming of sensory cues in mazes have used bees that have learnt to recognize two different priming stimuli in the first compartment of a maze. One or other priming stimulus is present on each trial and determines which of two simultaneously presented targets should be selected in the next compartment of the maze<sup>76,77</sup>. Associative links also form between local vectors, so that the performance of one vector can trigger the next in the sequence, even if the landmark that normally evokes the vector is missing or not noticed<sup>79,66</sup>.

#### Learning routes

Insects have a range of navigational strategies for reaching a goal. Some strategies are usable with little or no learning, but these off-the-shelf strategies might be slower or less accurate than those that require experience, such as visual guidance along a learnt route<sup>17,80,81</sup>. Off-the-shelf strategies are used by naive foragers, but give way to memory-based strategies as a forager gains experience with a particular route. In the meantime, the off-the-shelf strategies can supply both the constant environment that is required for multi-trial learning (see above), and the training signals for learning the succession of stimuli and actions that will later come to govern the route.

The shape of the route that an insect acquires is to some degree fixed by the positions and types of objects along its path, and by the insect's in-built responses to those objects. Insects tend to approach isolated objects<sup>3,14</sup> (FIG. 6a,b) and then to detour around them<sup>81</sup>. If a honeybee flies between two objects, it will tend to balance the optic flow that is created by the objects, and so to fly midway between them<sup>82</sup>. Similarly, if a desert ant walks between two landmarks, the ant picks a path that balances the retinal elevation of the tops of the objects on the two sides<sup>83</sup> (which maximizes the ant's view of the sky). Such instinctive tendencies help to create the paths of naive insects. Through repetition, these tendencies can be consolidated into a sequence of memories of path segments.

The acquisition of visually guided routes can also be aided by scent trails. Ants that follow a scent trail require no knowledge of landmarks along the path. To keep to the trail, an ant must continually antennate close to the ground, and progress is relatively slow. Foragers of some ant species switch from using chemical to visual cues, doubling their travel speed, as they become familiar with landmarks along the trail<sup>84</sup>. Naive and experienced ants will then behave differently when given competing information from chemical and visual cues: naive ants follow the scent trail, whereas experienced ants ignore the scent trail and follow visual landmarks instead. The scent trail provides a means of stabilizing the route of an ant over several trips. It might also aid learning by providing a training signal, so that the ant knows to learn landmarks while it can detect the scent.



**Figure 5 | Honeybees learn the distance of a feeder from a landmark.** Bees are trained to a feeder (F) at either 180 cm or 560 cm from the entrance of a 760-cm-long channel. The curves show search distributions in a test channel with no feeder. Curve **a** shows the search distribution after training to a feeder at 180 cm, curve **b** after training to a feeder at 560 cm, and curve **c** after training to a feeder at 560 cm with a landmark at 380 cm. Note that curve **c** is narrower than curve **b**, indicating that distance is measured from the landmark. This supposition is confirmed by curve **d**. Training was as for curve **c**. In tests, the landmark was displaced by 120 cm and the bees' search shifted by the same amount. Adapted, with permission, from REF. 74 © 1997 The Company of Biologists Ltd.

In desert ants, the role of scent trails in leading naive foragers along a route is largely replaced by path integration. If they are unfamiliar with a landscape, desert ants rely on path integration, with its limited precision, to reach a feeding site or their nest. Desert ants forage individually for dead insects. On finding one, an ant stores the path-integration coordinates of the site, and on its next foraging trip returns to the position that is defined by those stored coordinates<sup>85</sup>. If more food is not found there, the ant either searches around that location or continues in the same direction until it is successful<sup>85</sup>. The ant, by repeating its previous journey, has given itself the opportunity to learn the appearance of landmarks<sup>17,80,81</sup> that it encounters *en route*, and to associate memories of local vectors with those landmarks<sup>70</sup>. With experience, local vectors take precedence over global vectors when the directions indicated by the two mechanisms conflict<sup>70</sup>. Path integration might also provide a training signal by indicating that memory acquisition is appropriate whenever the individual moves in the rough direction of its path-integration target<sup>86</sup>.

If insects can obtain continuous landmark information along the route from an extended landmark, such as a solid barrier or wall, their path is less constrained by the landmark. An ant can learn to take a path that is parallel or oblique to a barrier<sup>87</sup>. The paths shown in FIG. 6c are from desert ants that were forced to detour round a high vertical barrier on their way home<sup>88</sup>. On rounding the barrier, the direct route given by path

integration goes from the end of the barrier to the nest. Ants will learn the appearance of the barrier viewed along this direct route in terms of the retinal elevation of the top of the barrier<sup>87,89</sup>. They will then adjust their path to keep the barrier at that elevation, and can follow the same path relative to the barrier despite the absence of useful information from path integration or the sky compass<sup>87,88</sup>. So, the path of an ant along a barrier that has been rotated through 45° from the training arrangement is also rotated by about 45° (FIG. 6d).

#### Homing and cognitive maps?

Over the past hundred years, entomologists have tested the effects of displacement on the ability of insects to find their way home. Recent studies on honeybees' vanishing bearings<sup>90,91</sup> or entire paths, as monitored by harmonic radar<sup>92</sup>, show that displaced bees often take a direct path to their hive. One issue that keeps re-emerging<sup>91,93</sup> is whether such homeward trips after displacement reveal map-like representations in which spatial memories are associated together in some kind of a global network. Map-like representations have been implemented in modelling studies<sup>94–96</sup>. Two relevant examples are: a connected network of local views with local movements<sup>97</sup>; and associations between global path-integration coordinates and landmark memories<sup>93,98</sup>.

About 15 years ago, a controversial paper by Gould<sup>99</sup> claimed that bees might use cognitive maps for navigation. This paper immediately provoked several further studies that seemed to support the alternative and more generally accepted conclusion that bee navigation is essentially route based<sup>100–104</sup>. All these studies involved bees that were trained to specific routes. More recently, Menzel *et al.*<sup>91</sup> have suggested that bees might indeed assemble a more global (cognitive map-like) memory of familiar terrain, but that this memory is masked in bees that predominantly follow one fixed route.

The directed homing behaviour of bees after displacement is, of course, consistent with a map-like interpretation<sup>91,92</sup>. But without direct neurophysiological evidence for the existence of map-like memories in insects, the challenge to cognitive-map adherents is to show that homing behaviour cannot be explained in terms of mechanisms, such as the three discussed below, that require an insect to have only a piecemeal and fragmented spatial memory of its environment.

One possible mechanism is attraction to routes. When ants<sup>17,105</sup> or walking digger wasps<sup>106</sup> are displaced and released close to a familiar route, they are attracted to the route and then follow it very precisely back to their nest. Joining a route is probably accomplished by recognizing and approaching landmarks that are near to the route. In desert ants, multiple paths from a single ant that follows a route to a feeding site fall within a narrow corridor of about a metre<sup>17,80,81</sup>. With small landmarks that are viewed from the ground, the attraction of a displaced ant to a familiar route might be limited to a small area that flanks the corridor. As honeybees fly several metres above the ground, they might often use landmarks that are somewhat distant from the route. In consequence,



their routes would be less precisely demarcated than those of desert ants. The only detailed information about the routes that are taken by bees comes from a study of bumblebees in which the corridor that was formed by multiple paths of a single bumblebee to a cluster of feeding sites was tens of metres wide<sup>107</sup>. One

might expect that bees would be attracted to such a broad corridor over distances that are still larger.

A second potential mechanism is image matching with distant landmarks. Although a snapshot that is centred on a nest containing nearby landmarks will attract insects to the nest hole from only a small area, a

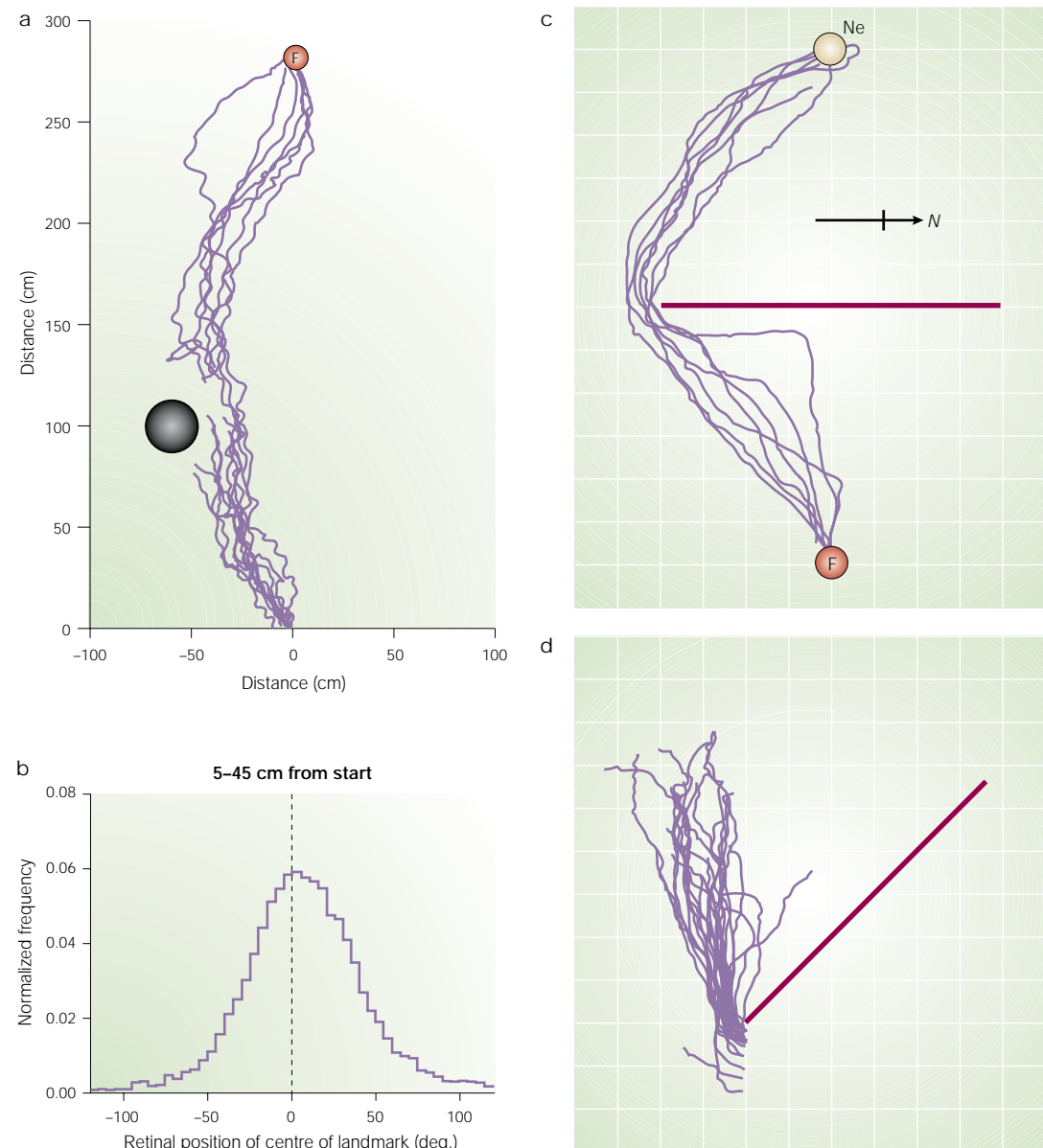


Figure 6 | The different shapes of routes taken by ants when trained with discrete or with extended landmarks.

**a** | Recorded trajectories of a single wood ant in an indoor arena in which a black cylinder was placed to the left of the direct path between start and feeder (F). Gaps in the trajectory occur when the tracking camera is trapped by the landmark. On each trial, the ant first heads directly at the cylinder before deviating to the right. The shape of the route depends on the position of the landmark. However, once the ant is trained to this route, the landmark can be removed in tests, and the shape of the trajectory remains approximately the same, showing that the stability of the route is enhanced by learning other visual cues that keep the ant to the same track. **b** | Histogram showing the retinal position of the centre of the cylinder during the initial part of the trajectory (data are from several ants). **c,d** | Recorded trajectories from the desert ant, *Cataglyphis fortis*, as it negotiates a barrier. The ant goes from its nest (Ne) to a feeder, detouring around a 50-cm-high barrier. **c** | Homeward routes during training. Once the ant has rounded the barrier, its path is straight to the nest. **d** | The routes of ants that are collected when they have almost reached the nest and displaced to a test ground with a similar barrier that has been rotated through 45°. The ants' path relative to the barrier is very similar to their path in training. Ants ignore compass cues and instead use the visual cues provided by the barrier to set a path that would normally lead them straight to the nest. Adapted, with permission, from REF. 88 © 2001 The Company of Biologists Ltd.

snapshot that contains prominent and distant landmarks might be able to guide insects directly towards the rough area of the nest from release sites over a much wider region<sup>98</sup> (see REF. 17 for a possible natural example).

A third possible explanation is averaging local vectors. As already mentioned<sup>67–69</sup>, in environments with prominent landmarks that are visible over large distances, bees that have learnt the routes between two feeding sites and their nest can, in principle, home directly from novel release sites between the routes. If a release site between two routes contains visual features that are common to both, the bee might recall and average local vectors from the two routes, and so fly directly towards the nest. For now, the question of cognitive maps in insects remains unsettled. However, in the past, bees have often confounded sceptics, so perhaps there is still a new chapter to be written.

### Conclusions

One purpose of this review has been to point to the importance of multiple memories and associations between memories in aiding the reliable recognition of landmarks. Perceptual mechanisms exist for recognizing visual features from new retinal positions, but these mechanisms are supplemented by the explicit storage of a scene from different vantage points, and by the association of contextual cues with landmark memories. Insects might solve the problems of landmark recognition more through the use of a rich store of

interconnected memories than by the use of elaborate computational devices.

Another purpose of this review has been to consider the ways in which familiar terrains are represented by an insect's spatial memories, and the navigational skills that these representations can support. Ants and bees have two distinct systems for storing information about places. Path integration provides insects with a global coordinate system that is centred on the nest and can be used for storing the coordinates of significant places in long-term memory. Memories of visual landmarks provide a second method. These memories specify places in a coordinate-free way, in terms of the view seen from each position. There seems to be no evidence, as yet, that these two ways of defining places are combined so that views are associated with global positional information from path integration. By contrast, links between memories of visual landmarks and movements, such as local path-integration vectors, mean that landmarks can direct insects along specific paths. It seems that the principal role of a landmark might be to instruct an insect to perform a particular action, rather than telling the insect where it is within a large-scale coordinate system. Simon<sup>108</sup>, in a famous passage, contemplated an ant walking on the beach and asked whether the ant's winding path over the sand simply reflects the complexity of the world through which it wanders. We now know that not only the ant's path, but also its memories, mirror some of the world's complexities.

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## Online links

FURTHER INFORMATION  
Department of Neurobiology, University of Zürich:  
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Insect Vision, Navigation and 'Cognition' Laboratory:  
<http://cvs.anu.edu.au/insect/insect.html>  
Sussex Insect Navigation Group:  
<http://www.cogs.susx.ac.uk/users/paulgr/SING/>  
The Menzel Research Group — Navigation of Honeybees:  
<http://www.neurobiologie.fu-berlin.de/Menzel-Gumbert-Kunze.html>  
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