

08

THE ROUTE TO THE GOAL, AND BACK AGAIN¹

Besides piloting, bees steer towards particular goals. They are, after all, heading somewhere. One of the lessons from human navigation is that several mechanisms are used and any cue can be useful. While circumventing obstacles, landmarks must be remembered, the general direction must be maintained and irrelevant things must be ignored. In early studies of insect navigation, with a single effect attributed to a single cause, the bees' use of several mechanisms in parallel led to confusion. As usual, positive results were explained by the first idea that came to mind and unsound theory was only slowly recognised, so controversies persisted unnecessarily.

Before the days of radar and satellite navigation, the human navigator had five main ways to navigate: by recognition of landmarks on a map; by dead reckoning, which summed the distances and the known currents noted in a log book; by compass directions; by sampling the depth, temperature and bottom of the sea; and by finding a position and direction from the sun and stars. He used all five, with a few extras such as the direction of the ocean swell or the smell of land. Insects also have several interacting mechanisms: 1) a measure of distance over the ground; 2) direction relative to the sun's position; and 3) the recognition of places or landmarks, which requires an efficient learning, discrimination and forgetting system. Less clear are 4) cues from odours, and 5) the Earth's magnetic field.

Early observations

About 1880, the famous entomologist J. H. Fabre took marked mason bees in a box for a few kilometres from their nest and noted the direction in which they disappeared. Although 20 out of about 40 set off in the right direction, less than half eventually found their way home and the fate of the rest was

unknown. Fabre, obviously an optimist, inferred an inner sense of direction! Darwin suggested that they used the Earth's magnetic field, but experiments on the bees with little magnets failed.

In a beautiful experiment, George Romanes (1885), who was a physiologist with a critical mind, took a hive of bees from far away to a house that he had rented for his family near a bare stretch of sand on the Cromarty Firth in Scotland. The hive was opened and the bees explored the garden and surrounding land, and all returned to the hive in the evening. The hive was then closed and the next day it was taken at most 250 metres across a stretch of empty sand where there were no landmarks, and again opened. This time every bee that emerged became lost. It was an excellent example of the power of an experiment in which the bees failed in a test. Romanes knew nothing about the sun compass of the bees. He concluded that the bees had no special sense of direction and they relied on local landmarks that they learned quickly. Modern critics will conclude that the bees did not compensate for the wind blowing over the featureless sand and the direction of the sun is little use if they have no reference point.

In the next decade, Albrechte Bethe (father of Hans Bethe), an indefatigable experimentalist, studied how bees found the entrance of their hive. He moved a hive sideways and put another in its place. The bees went to the introduced hive but soon came out again, then flew in again and out again, over and over. A few bees, however, started a procession that landed at the entrance of the new hive then walked home. When their hive was moved back by a short distance, the bees hovered in the air at the place where the entrance had been and eventually found it.

When their hive was moved back by 2m, an enormous swarm of returning bees congregated in the air at the place where the entrance would have been. When the hive was replaced, the whole swarm precipitated themselves into it. Bethe concluded that the bees were not guided by the sense of smell or hearing and that they could not recognise the hive by sight. To show that the bees were not guided by vision, he left large pieces of coloured cloth and paper near the hive or covering it, then changed the colour, only to find that the bees could still find their way. He went so far as to cut down a large tree that was close to the hive, and which the bees had to fly over, but with little effect on their homing ability.

Bethe then carried some marked bees from the hive into a meadow on one side of his house and some others into the narrow streets of the town of Strasbourg on the other side. Most of them headed in the correct direction when released and returned to the hive from places up to 3km away. From all this, Bethe concluded that *a totally unknown force* guided the bees for distances up to 3km. This was the period when x-rays, radio waves and radioactivity were discovered.

The age-old way to find a hive of wild bees is to catch a wild bee, feed it with honey until it is full and note the compass direction of the 'beeline' it takes when

released. Then, at another place, release another satiated bee. The hive will be found near the place where the two tracks cross. Bethe explained the beeline by the directing power of his new force. He was stumped, however, when he took some bees in a box and released them far away, finding that they flew high into the air and returned to the box from which they had been released. Of course, these bees had been moved to a place with no familiar landmarks and started to make exploratory flights.

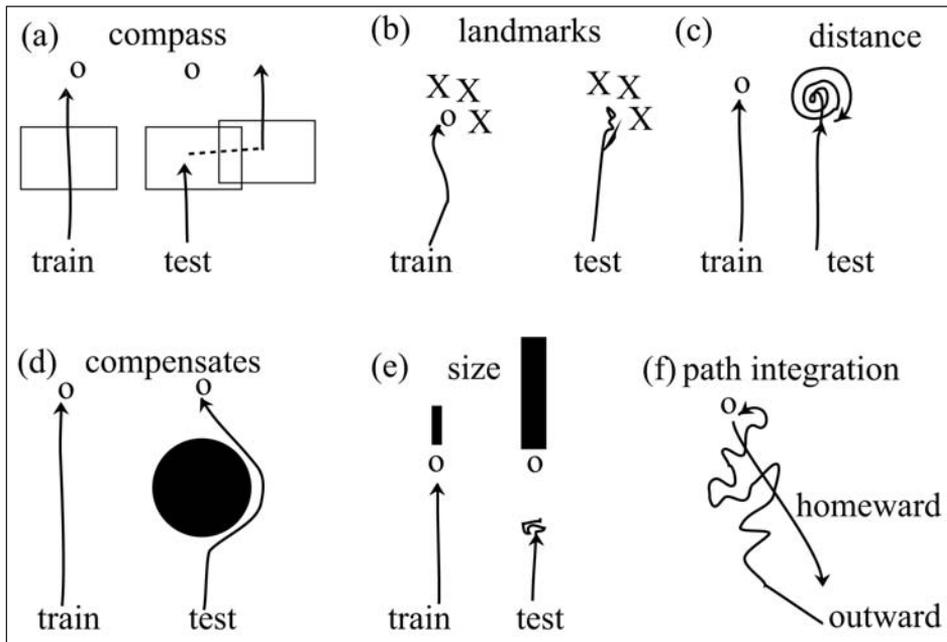
At the time, with almost no data, there was an argument between the empiricists and the intuitionists as to whether bees were automata or rational (von Butel-Repen 1900). The ability to learn and be adaptable made them look rational. It was argued that if they were not rational, bees would never adjust their daily tasks to the changes of the natural world about them. Because bees that are moved to a new place do not take a beeline home, von Butel-Repen ‘consigns the hypothesis of Bethe’s unknown and mysterious force absolutely and irrevocably to the realm of absurdities’ (Forel 1908:259). Forel (1908:229) was also very short with Bethe’s hypothetical force: ‘I am obliged to combat his conclusions as preconceived, one-sided, and of an absolutism quite contrary to the scientific spirit.’ Forel concluded that the bees familiarised themselves quickly with the appearance and direction of landmarks, both distant and nearby. At that time, researchers were familiar with the flights of exploration and saw the inexperienced bees point towards the hive as they flew in circles above it, as if to keep it as a reference point.

In 1905, the hive that had served for Forel’s experiments in 1901 was moved further away from the garden table where the family often ate breakfast on warm summer days. Forel recounts at length how in previous years the bees had never come to the table, but that year they discovered the marmalade—a recent introduction to Switzerland brought by English mountaineers. Experimentally, the table or the sweet things were moved or placed at times under covers. Forel showed that when forced to be versatile in their search, the bees quickly learned to give up their rigid return to the place of the previous reward. It would be another 50 years, however, before the mechanism of navigation came into view, and a further 50 before there was some understanding of how honeybee vision would be sometimes limited and rigid and sometimes flexible and adaptable.

In the century that followed, arguments that had started with Fabre, a creationist, Romanes, a physiologist and intuitionist, and Bethe, a physician and mechanist, would continue in France, Germany, the United States, Switzerland and eventually Australia. It is of interest that the arguments were not resolved earlier. It is amazing that so little was noticed by so many interested parties who had been doing experiments for a century or so. These men were not stupid! There were many anomalies they could have noticed, many simple experiments they might have tried, but, no, they repeated the partial explanation they had. The reason for the delay was not entirely the pig-headedness of the professors.

With hindsight, we now know that new physical principles remained to be discovered and the researchers were misled by the bees' ability to switch between different mechanisms. Nobody could imagine the answers. Lack of imagination and observation were not the only limiting factors.

Figure 8.1 Navigational options available to bees. a) When the path is shifted sideways, the sun compass retains the direction. b) If the reward is shifted, the bees search in the place indicated by the landmarks. c) They search for the reward after going the expected distance. d) They compensate after being deflected by an obstruction. e) They search for the reward at the place where the landmark has the expected angular size. f) The beeline.



Dead reckoning

By the beginning of the twentieth century, it was known that ants used landmarks, made directional odour trails and had at least one sense of direction. In a classical experiment, Piéron (1904) allowed ants of the genus *Messor* on their way to the nest to walk on to a piece of paper. With the ants on it unaware of the move, he then moved the paper sideways. The ants continued along the former direction (Figure 8.1a). When they had walked for the distance that had previously brought them to their nest site, they searched for the entrance (Figure 8.1d). They clearly knew the remaining distance to their home by dead reckoning and ignored landmarks, but their cue for the direction was unknown. A different ability—to repeat a set of manoeuvres by going through the same sequence of turns as previously—was called the ‘muscle sense’ and was distinguished from dead reckoning.

Many arthropods are known to keep an internal record of their path as they move about. As a part of their repertoire, as they progress, bees and ants integrate every turn and distance in their outward path so they have a continual measure of the direction and distance of home. To some extent, cumulative errors are avoided by turning alternately left and right.

To fly directly home along a novel track—the ‘beeline’—bees require landmarks, especially if there is a wind. Experienced bees and desert ants set out from the nest with an internal representation of the direction and distance to their goal (Figure 8.1f). As they go along, they check their direction by the sun and landmarks and measure the distance covered over the ground visually. As early as 1872, Lubbock (1893) was intrigued by the ability of a wasp to head directly to its nest after entering his room repeatedly via another way. Bethe (1898) used the beeline as support for his mysterious force that attracted the bee to the hive. Without considering dead reckoning, many have claimed that such action proves that bees have an internal map.

Having deviated around a new obstacle, desert ants and bees take the new direction directly towards the nest (Figure 8.1c). Experienced bees integrate the turns and motions of their own path and at all times know the direction of the hive or the goal. Their direction can be changed by an internal rotation of 180° to reverse the path either to food or to home. While returning home, ants that use vision remember the track for use on the next trip. Bees store vector memories that can be activated by the odour of the corresponding food source. They continually update the track direction from the sky compass and learn the relations between their path and the landmarks that are useful to them, particularly at the ends of the path. Under an overcast sky, desert ants (*Cataglyphis*) use dead reckoning along the ground, but experienced honeybees switch to the exclusive use of landmarks. If obvious landmarks are moved while the bees are in the hive, so that at the next flight they go in the wrong direction under an overcast sky, they follow the landmarks and return home by a direct route, but they have inferred the wrong direction of the sun from the displaced landmarks so they dance as if the sun had been moved and their recruits are misled.

von Frisch was in error in assuming that bees measured distance by the energy used on the outward journey. His bees flying uphill or carrying small burdens reported longer distances because they flew lower and registered more optic flow, not because they were working harder. The experiments of Harald Esch and Srinivasan in the 1990s showed that honeybees measured the distance travelled over the ground by integration of the optic flow, and those of Wehner and his colleagues showed that desert ants used the number of strides as well as the visual flow field.

Angular dead reckoning also plays a part under overcast skies and under forest canopy. The angular component in dead reckoning can be measured from the rotation of contrasts in the surrounding panorama, irrespective of landmarks

or of the compass. The fly *Drosophila* flies in shade and is not known to learn landmarks. When Martin Heisenberg placed one in a uniformly striped drum, it learned to face one way when the light was blue and at right angles when the light was green. The motivation to learn was provided by the temperature, which was controlled by the orientation of the fly. The regular stripes allowed the fly to measure the angles through which it turned but they provided no fixed landmarks. When the colour changed, the fly turned through the appropriate angle relative to the pattern. The fly acted as though it integrated its angular velocity relative to the drum and at all times kept a memory of its direction relative to its visual surroundings.

An important part of angular dead reckoning is the memory of the retinotopic position of an outstanding contrast or landmark on the eye, so that if disturbed, the animal can turn itself until the landmarks return to the same position as before. When this performance was analysed in the crab *Carcinus*, it was found that the positions of edges and areas were detected separately, and that vertical black/white edges were not necessarily distinguished from white/black edges (Horridge 1966a). This behaviour is a simple form of the visual recognition of a place by ants and bees by comparison with a memory of the retinal positions of two or more cues (Figure 8.1e). When dropped on a beach, a crab detects the direction of the movement of the sun within 10 seconds. Burrowing crabs show that they are aware of the direction of their burrow at all times when they are out of it.

The motivational state of the bee

Researchers were often puzzled by conflicting results before it was realised that bees must be in the appropriate motivational state for study. Primarily, they must be forager bees and known to be experienced or otherwise. Not surprisingly, when bees and visual ants that are on the move are displaced and released, they continue in the same compass direction as before. Those caught at the nest entrance when setting out are motivated to take their accustomed outward route. Conversely, when caught fully satiated at the foraging place, they are motivated to head homewards. Only when they are captured as they arrive home do they have no preferred direction.

Bees are motivated to learn only when they meet an unexpected difficulty or when presented with alternatives, one of which has the expected reward. Most learning involves active participation, but bees fixed in the opening of a small tube will learn passively in a single trial that one odour but not another is associated with a reward. Bees in flight presented with a choice hover and look first one way then the other. If at first they fail to find the reward when arriving at the expected place, they will hunt about for it (Figures 8.1b and 8.1c).

Landmarks

Landmarks are the most important guides for bees and wasps to find their foraging place and return to their nest. We can understand why this is so because they work on overcast days when no sun or blue sky is visible, and dead reckoning is not much use in a strong wind.

Local knowledge is acquired visually when bees explore an unfamiliar place. When a hive of bees is taken to an unfamiliar site, the emerging bees explore in the immediate vicinity. If individual exploring bees are removed from the hive during this process, their ability to return depends on the number of hours that they have previously explored. As days pass, their familiar area expands. In a short textbook, Rabaud (1928) described the use of landmarks and of the position of the sun by visual ants, but made no mention of the dance of the honeybee—probably because von Frisch had described the round dance as a mechanism for alerting the recruits to look for nearby food sources by their odour. Rabaud quotes results from Romanes, von Butel-Repen and Yung—all of whom conclude that bees learn the visual appearance of landmarks and improve their memory in successive journeys. Many observers had noticed that shifting a single prominent landmark might have no effect and the intuitive conclusion was that the insects memorised the general layout of conspicuous objects around the goal, particularly those on the skyline, and made the best visual match that they could. In fact, they recognise much less than this.

Baerends (1941) obtained new insights from intensive studies of individually marked female digger wasps (*Ammophila*) that carried caterpillars back to their nests. A female could have four to six nests at the same time, with an egg in each, so that she was obliged to visit them in turn. The wasp was familiar with local landmarks over quite a large territory, and when holding a caterpillar and carried in a box to another place, she had no difficulty taking the direct route to whichever of the nests was the former goal. It was 60 years before a similar ability was also accepted in the honeybee to remember the routes to several foraging places, and even then only after long arguments and the introduction of new radar-responder technology that recorded the tracks of individual bees in flight.

In recent decades, researchers have discovered several ways that bees use landmarks in the field. First, the bees learn only the tracks they need, not the whole surrounding district, unless forced to do so. If satiated bees are removed from a reward to the north of a hive and carried an equal distance to the south of the hive, they take a long time to get home or they become lost. On the other hand, bees can be trained to go to a reward that is 10m from the hive in a direction that is changed every 10 minutes. Then, when released from a box, they return to the hive quickly from any direction. If the hive is moved, however, they

lose it. The performance of a bee and the number of available routes available to it therefore depend strongly on what has actually been learned, making the memory of the landscape an elastic concept.

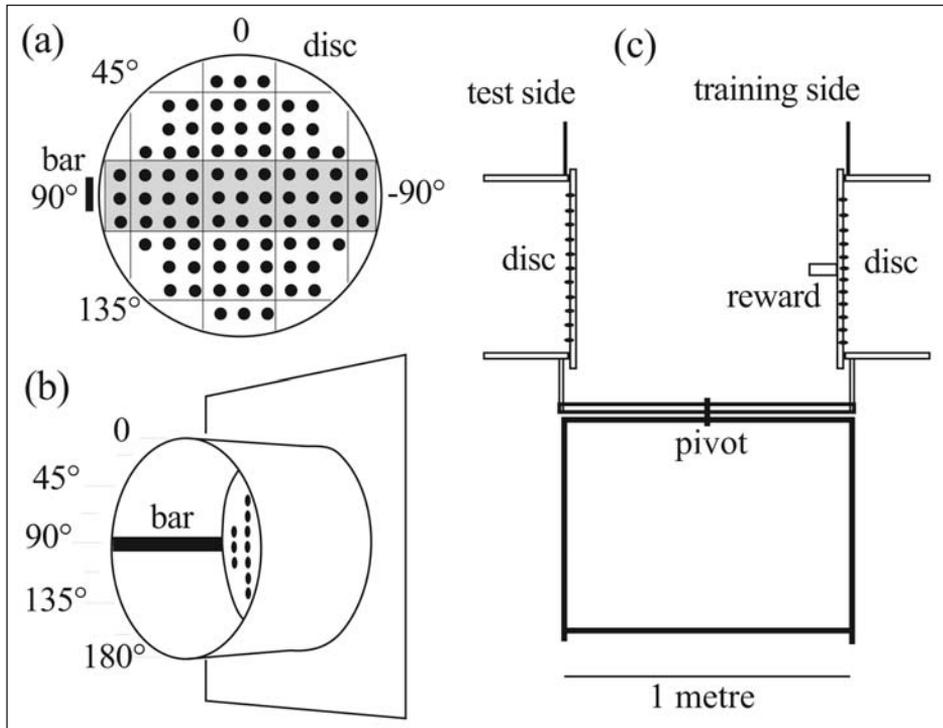
There is abundant evidence, from artificial landmarks in tunnels, mazes, tents or open featureless fields, that every familiar landmark tells the bee which way to go and how far to the next landmark. As found by von Frisch (1965), the memories of landmarks include directional vectors, as shown by the directional dances on overcast days. The track is therefore a chain of measured vector stages between landmarks, as well as a total vector and distance conveyed in the dance. In addition, the angular dead reckoning might help.

Bees are extremely sensitive to a whiff of the odour with which they mark a food source and to small differences in the distribution of light, polarisation and colour. Also, when forced, they learn to use remarkably small landmarks—down to a single small black spot. When the sky compass and all landmarks are removed, however, there is still some behaviour that can be attributed to the direction of the Earth's magnetic field (Lindauer and Martin 1968).

Signs along the route

Bees flying towards their goal don't only look ahead. Miriam Lehrer demonstrated that bees located themselves vertically relative to markers in their lateral vision when they were presented with a spatially complicated set of choices ahead of them. The bees were trained to look for a reward in one of 89 holes in a round target (Figure 8.2a). When presented with this target alone, the holes are in front of the eye, but the bees are unable to remember which one to enter and explore them at random. They have machinery to locate the centre of contrast in a local region of the eye (Figure 9.19) but not for memory of spatial layout of round holes. When given a single stripe at the side of the target as a marker, however, they locate the correct level and on this level they enter the hole at the correct range from the stripe. They use the map coordinates, not the map. They perform horizontally and vertically better with a stripe at each side. When the indicator stripe is moved in a test, the bees return to the hole that is indicated by the new stripe. In locating themselves relative to a stripe, the bees measure range from relative motion, not from apparent stripe size, and transfer the information to both eyes. Experiments with coloured stripes reveal that this use of markers in the peripheral field is colourblind and is done by the green channel of receptors, like vision of motion. These experiments are important evidence to show that the eye does not fix the spatial layout of the target into memory. Instead, lateral regions of the eye detect cues of range and direction of neighbouring landmarks. They triangulate but do not read the image.

Figure 8.2 The position and range of a landmark at the side direct the bee to the correct hole among many. a) Front view of the target; one hole leads to the reward. b) The bar at the side. c) The whole apparatus can be rotated to test the bees with a clean target and a different position of the bar.

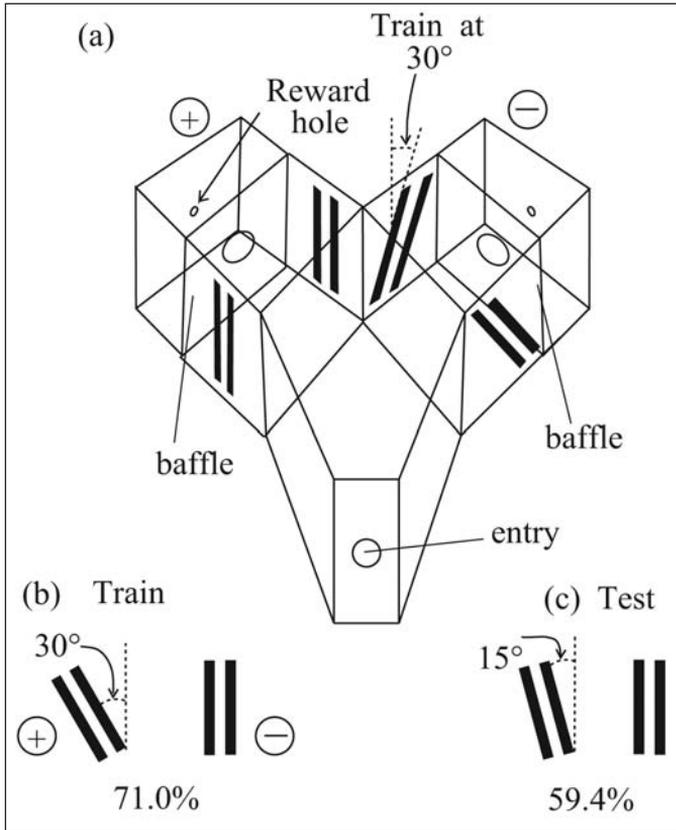


When bees are using the Y-choice apparatus, it is obvious that the narrow entrance hole excludes naive recruits, and even trained bees will not fly through a familiar hole that has been reduced in size. In 1995, I trained bees to pass between two black bars at each side before they passed the baffle (Figure 8.3a). The bars pivoted about their centre. Bees were trained with all bars vertical in one arm of the apparatus but inclined at an angle in the other arm. Left and right sides of the apparatus were interchanged every 10 minutes and there was no other cue. The bees quickly learned to fly between the bars with the orientation that was rewarded and could detect a difference of 15°.

In the next experiment, with the baffles in the normal position, bees were trained to discriminate between a vertical and a horizontal coarse grating (Figure 8.4b), and then tested with the grating replaced by a vertical and a horizontal black bar on each side of the holes in the baffles (Figure 8.4c). Although the task looks simple to us, the trained bees are unable to use the orientation cues of the bars, because they are in an unexpected place. When the bees are trained to fly between the oriented bars alone, however, they perform very well (Figure 8.4d).

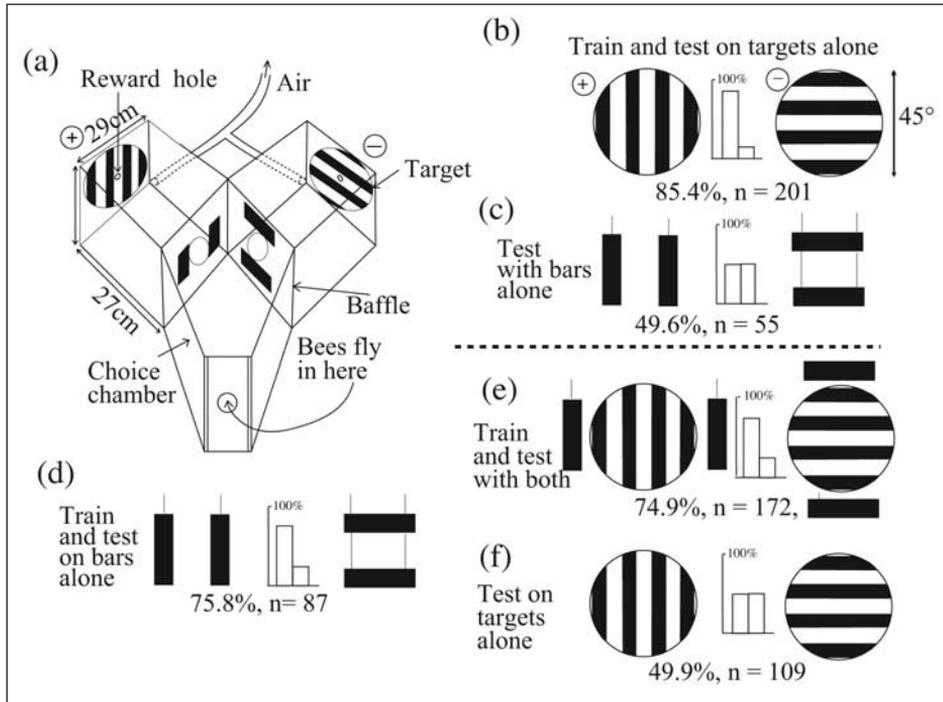
In fact, they prefer to learn the bars at the sides rather than the gratings in front, as shown by training them with both in place (Figure 8.4e) and testing them with the gratings alone (Figure 8.4f).

Figure 8.3 Detection of an orientation at the side. a) The Y-choice apparatus modified with bars at the side. b) When trained to fly between bars at an angle of 30° to the vertical, the bees respond to an inclination down to 15°.



From Horridge (1996b)

Figure 8.4 Orientation cues in front and at the side. a) The Y-choice apparatus modified with bars on the baffles. b) The bees discriminate the gratings very well. c) Bees trained on the gratings fail when tested with the bars. d) They discriminate very well when trained on the bars alone or (e) with both bars and targets together. f) Bees trained on the bars plus the gratings, as in (e), do not recognise the gratings alone.



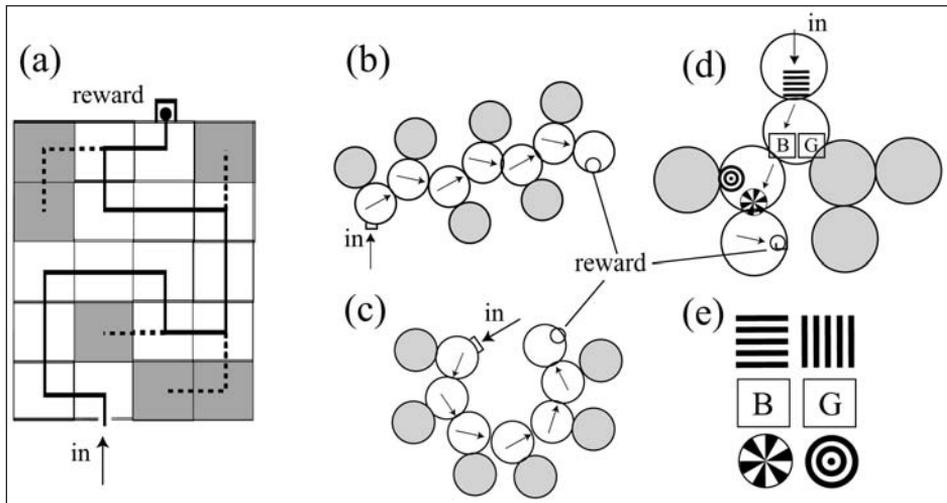
From Horridge (1996b)

Maze learning by bees

Ants find their way through a maze by laying down directional odour trails that carry a signal like an arrow on a road. Walking bees will learn the correct route to get a reward and then walk back for more. After all, bees have to negotiate through a nest in a hollow tree and sometimes fly through a dense wood. A maze was at first just an apparatus to reveal the performance and was only recently used to find out where the bees looked, to analyse what cues they recognized and how long they remembered them. Flying bees can use an odour or a visual cue to tell them which way to turn at a choice point in a maze (Weiss 1953). When the cues were identified in the 1990s, Zhang Shaowu started an investigation of maze flying by bees using boxes that could be arranged side by side on the floor, with holes communicating between neighbours. A maze is constructed by blocking some of the holes so there is

only one correct way through (Figure 8.5a). The boxes can be replaced in tests to prevent the bees using odour cues. Bees learn to fly through holes marked by a cue. The cue can be an instruction to turn right or left at the next choice or alternative cues can be displayed on the alternative holes. At the end, the bees escape by a back door.

Figure 8.5 Mazes. a) A maze made from square boxes; the dashed lines are deadends. b) A zigzag maze made from cylinders. c) A turn-left maze. d) A maze for successive alternatives. e) The series of pairs of cues for the successive choices in (d).



In the maze, bees can learn by trial and error to follow a trail marked by one cue at each choice point and then use the same cue through a different maze. Bees trained to use one colour through a particular maze can switch to another colour because they have learned ‘any colour’ not ‘this colour’. They can also use an unfamiliar colour to negotiate an unfamiliar maze. If the maze has a fixed route, the bees soon learn to negotiate it correctly although the cues are removed. The cue can be indirect—for example, the bee can learn to turn right when the back wall is green and left when the back wall is blue, and bees trained to do this can thread novel mazes guided by the same colour cues. They can also learn to choose to turn left and right alternately (Figure 8.5b) or always to the right (or left, as in Figure 8.5c). Bees can also learn an unmarked maze, but they learn more slowly.

Maze learning by bees shows that the cue is an instruction to turn in a given direction at that place and then go a certain distance, and they can learn a sequence of several choices. There is no reason to suppose that this ability is restricted to small mazes. The experiments in which bees take a definite track

through space show that angular orientation also follows a learned motor sequence—called the muscle sense—as demonstrated by the persistence of turns in the track when obstacles are removed.

In the next series, the bees learn to turn left or right according to whether the back wall of the box is blue or yellow. Next, one colour is placed above the entrance to a choice chamber, so that the sight of it precedes the decision, and the bees remember what they have just seen, with similar results. In other experiments, the colour cue is placed on one side of a narrow tunnel through which the bees must walk—yellow to turn one way and blue to turn the other. The trained bees are tested with the cues on the opposite wall of the tunnel and it is shown that in this situation the bees can transfer a colour cue from one side to the other (Zhang et al. 1998). In these and similar experiments, the choice can be learned according to the time of day.

The experiments became more sophisticated. A sample cue, A or B, was exhibited outside the entrance to the choice chamber. The bees must look at the cue and then inside the choice chamber they must choose the hole with the same cue, although the sample outside is changed randomly between A and B. (In other experiments, other bees must not choose the same cue.) Having learned this, the trained bees are given a sample of quite a different cue outside the choice chamber, such as a horizontal or a vertical grating, and inside they must choose the same cue (or not the same cue, if they have learned to avoid the cue).

Finally, one of two cues—for example, horizontal or vertical bars—is displayed over the first hole as an instruction for how to make the next choice—for example, between blue and green (Figure 8.5d). The correct choice—in this case, blue—then instructs the bees how to make the next choice, between circles and sectors. The correct choices are in the left column in Figure 8.5e. The trained bees are able to use this series of cues starting at any point in the sequence.

In all these experiments, the mazes were fixed and the bees were successful, so it was difficult to say what the bees in fact detected and remembered because they were not tested. It was all performance, no analysis. The bees detect a cue and act on it, and a delay is essential to correlate the cue with the reward. The bee learns the minimal cue. For example, it learns that there is a colour, not *the* colour, just as, in experiments with patterns, it learns less than the whole pattern. The bee learns whether to follow or avoid the sign on the door, sometimes irrespective of what the sign is.

There is no case for inferring that the bees learned a ‘concept’ of sameness or difference because they were not tested to see what they had in fact learned. In other examples where the performance looks remarkable at first sight, analysis reveals that the bees have learned a simple cue that is just adequate

for the next choice—not a general solution that suggests some kind of insight. The descriptions of the performance in mazes scarcely began to analyse the feature detectors and cues or what the bees really detected (Chapter 9).

The celestial compass

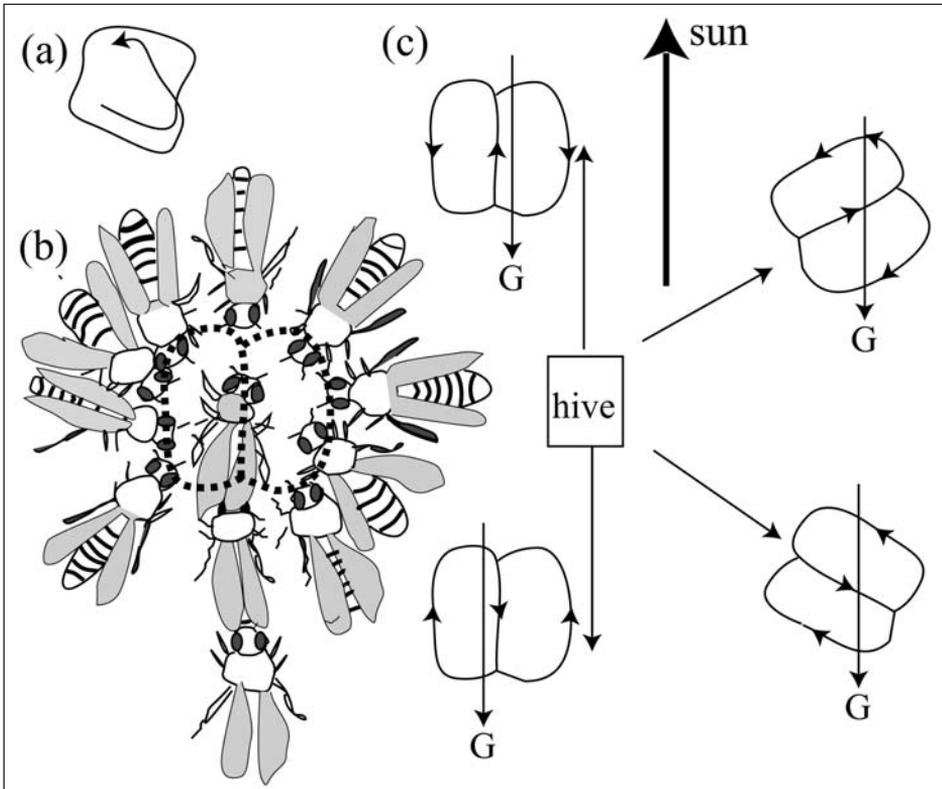
At the beginning of the twentieth century, workers on ants described the use of the sun, as well as landmarks, to provide a reference direction. Ants with large eyes can be expected to use landmarks, the sun compass, dead reckoning and odour trails, but the majority have not been investigated. Felix Santschi (1872–1940), an Italian physician, described several examples between 1900 and 1920, when he changed the perceived position of the sun with a mirror and showed that the tracks were deflected accordingly. The best example, however, was the desert ant *Cataglyphis*. Santschi showed that when placed at the bottom of a featureless drum, this ant could use a small patch of the blue sky to take the correct direct route homewards. A ground-glass screen spoiled the performance, but Santschi did not know why; it was the polarisation of the sky. Extensive analysis of this splendid animal in recent times by Wehner and his group at Zürich has shown that its navigation mechanism is very similar to that of the honeybee.

Aristotle, and presumably many beekeepers, thought that the dancing forager bee led the recruits back to the food. In 1923, von Frisch already knew, from a famous little book by M. Maeterlinck, that this was not true. He described the round dance (Figure 8.6a) as a signal for nectar and showed that returning foragers excited recruits to go out and search nearby for food with the same odour. He missed the sun compass, thought that the figure-of-eight dance signified pollen and turned to other topics. After 20 years, while living in seclusion from the Nazis in his country house beside the Wolfgangsee in Austria, he turned again to the study of the dance. For some years, he believed that the recruited workers were guided by the odour that the returned foragers carried from their foraging. After numerous experiments, he discovered the relation between the figure-of-eight dance and the direction and distance of the food source relative to the direction of the sun (Figure 8.6). When the direction of the sun was used as a compass, to find the direction on the Earth's surface, the dancing bees made an adjustment according to the time of day. They recognise the sun as a bright light free from UV polarisation.

After returning for more food at least once, the forager dances on the vertical comb in the hive or on a flat surface outside the hive, in either a circle or a figure-of-eight double loop with the straight piece in the centre giving the direction. On a horizontal surface, the direction of the central run in the figure of eight points in the direction of the food source. On a vertical surface, the angle between the central run and the vertical is the angle between the direction of

the food and that of the sun (Figure 8.6). The bees detect the direction of gravity by hair sensillae in the neck joint. They detect the vibration of the dancer by Johnston's organs at the base of the antennae.

Figure 8.6 The dance of the returning foragers. a) The round dance. b) Potential recruits stand close behind the dancer, while others stand around within the area of vibrations of the comb. c) The direction of the central bar in the figure of eight relative to gravity on the vertical surface indicates the direction of the food source relative to the direction of the sun.



The dancer indicates the direction to the final goal as learned on its homeward flight, together with the total length of the outward flight, and these two components can be influenced separately. For example, a segment of the outward flight along a narrow tunnel, which increases the optic flow for a given length of flight, increases the apparent distance to the goal, but has no effect on the direction of the homeward flight.

The distance measured on the outward track is the sum of the optic flow over the flight irrespective of the real track. The bee sees its surroundings passing by, integrates the angular velocity over the whole length of the outward flight and in the dance reports only the final total. This is exactly what the other bees need in order to follow for the right distance, as long as they take the same direction

and have similar preferences for flight height and treatment of obstacles. Odours are not essential for success. Of course, if new to the track, recruits require the sun or blue sky to follow the vector in the dance and then might need an odour to discover the real place. Experienced bees can recall the whole track from the odour of the food on the dancer. If new to the track, newly recruited bees quickly link the landmark vectors and separation distances into their memory. Experienced bees can switch between the memory of the total vector and the expected landmarks, which explains why omission of a landmark might have no effect and why they can ignore landmarks and take the beeline home.

In 1996, David Sandeman showed that the figure-of-eight dance on the surface of the comb was not a run in which other bees followed, as described in most accounts (Tautz et al. 1996). The dancer faces in the appropriate direction but in fact takes only one step while wagging the abdomen from side to side. The further away the food source, the longer the waggles last. With a source 1200m away, this step takes 1.2–1.8s to cover 8mm. The duration of the waggles and the direction of the food are conveyed by vibrations through the comb and the legs of the follower bees, not by following the dancer. In other situations, however, longer directional runs of a few centimetres are made over hard surfaces or the backs of other bees.

The calculation of the direction outside allows for the movement of the sun, which is in opposite directions in the northern and southern hemispheres, as migrants to Australia discover for themselves. When transported across the Equator by air, the experienced bees do not learn to compensate for the reversed direction and become lost for ever. The direction of compensation was learned once in these bees' lifetime, but they were not given a second chance. The hive survives because young bees learn the task afresh.

There are two components to navigation by the sun compass—one innate and one learned. Lindauer found that bees that had seen the sun only in the afternoons could immediately use the position of the sun if released in the morning, so they had an innate expectation of where to find it in relation to the time of day. Bees are genetically programmed to expect the sun to be at a constant position in the eastern sky in the morning and at another position in the western sky in the afternoon, although the azimuth position of the sun in fact rotates from east to west at an average of 15° per hour. Inexperienced bees, shut in a box during one of these periods, make predictable errors when released. About noon, the bees tend to come to training sites less frequently. Inexperienced foragers learn the motion of the sun and get a better measure of compass direction with the aid of landmarks, as indicated by the improved alignment of the axis of their dance. To exclude the sky compass, experiments must be done indoors or under a heavily overcast sky—as was done by accident for a century or so—forcing the bees to use landmarks.

The recruits are influenced by the odour of the food source on the dancer. From earlier Russian work, von Frisch knew that, even without a dancer, bees could be induced to leave the hive and search in the correct places when the odour of familiar flowers was blown into the hive. While much of Europe was in ruins, von Frisch published quite a lot about this—and the Nazis probably considered his work useful for directing bees towards pollinating useful crops.

The bee wars

Soon after von Frisch's publication of the figure-of-eight dance, bitter controversy broke out when Adrian Wenner (1967) reported that bees were able to locate the food source when exposed only to its odour in the hive. As said, this was already in the non-English literature. Wenner found that the bees that followed the dance were unable to locate the food source without assistance from its odour. They were presumably inexperienced bees, while those working for von Frisch were better trained. Wenner found it impossible to publish further work until after the Nobel Prize was awarded to von Frisch, Lorenz and Tinbergen in December 1973. Wells and Wenner (1973) then correctly pointed out that von Frisch's original claim—that the dance alone was sufficient to convey the direction and distance—was not controlled against memories induced by odour cues.

This little 'bee war' aroused unexpected indignation, but not on account of the merit or otherwise of the experiments, which all had typical weakness of design, confusion arising from multiple causes, ignorance of the previous experience of bees and intuitive inferences with no confirmatory tests. Wenner was rightly indignant that his publications were blocked (how or where has not been revealed), but he should have read the German literature. No doubt, von Frisch was indignant that his authority was questioned and he saw nothing new in Wenner's claims. After all, von Frisch had made a new observation; Wenner had not.

More of a colonial skirmish than a war, this difference of opinion was at the time not seen as another incident in the long defeat of Kantian intuition by the requirement for empirical proof. John Stuart Mill was not mentioned. To observe the performance and infer that the mechanism was inadequate; experiments were required. James L. Gould took the matter up. He arranged for the dancers to display the direction in the dance according to the gravity stimulus, while the followers interpreted the direction according to the celestial stimulus and were therefore fooled into searching in the wrong direction. This showed that the dance alone could be an effective directional signal as well as a message to leave the hive. After that, Gould lost interest in the odour stimulus, but the controversy was kept going and served a useful function as a warning that proper controls were advisable.

In his later polemics, Wenner produced no new data to show that the dance was ineffective, only arguments that it had not been proved to be effective, except as an urge to make the bees go and search. When work on the measurement of range, optic flow, bee navigation and piloting began in Canberra about 1988 and again in 1995, I was astonished that the data that had been argued about were so incomplete. One of my former students, Professor David Sandeman, who worked mainly on Crustacea, by chance studied the bee dance and found that it was not a walk or a dance, but just one step with a waggle (Tautz et al. 1996). After 1995, the correlation of the number of waggles in the dance with the bee's odometer—as tested in tunnels, over water or in the open—produced a wealth of data that might have been gathered earlier with less talk and more business. One millisecond of waggle encoded about 18° of image motion on the eye—leaving Wenner without a leg to stand on. As further tests showed, the bees could use dance, odour, landmarks or the sun compass, depending on the situation (Vladusich et al. 2005, 2006).

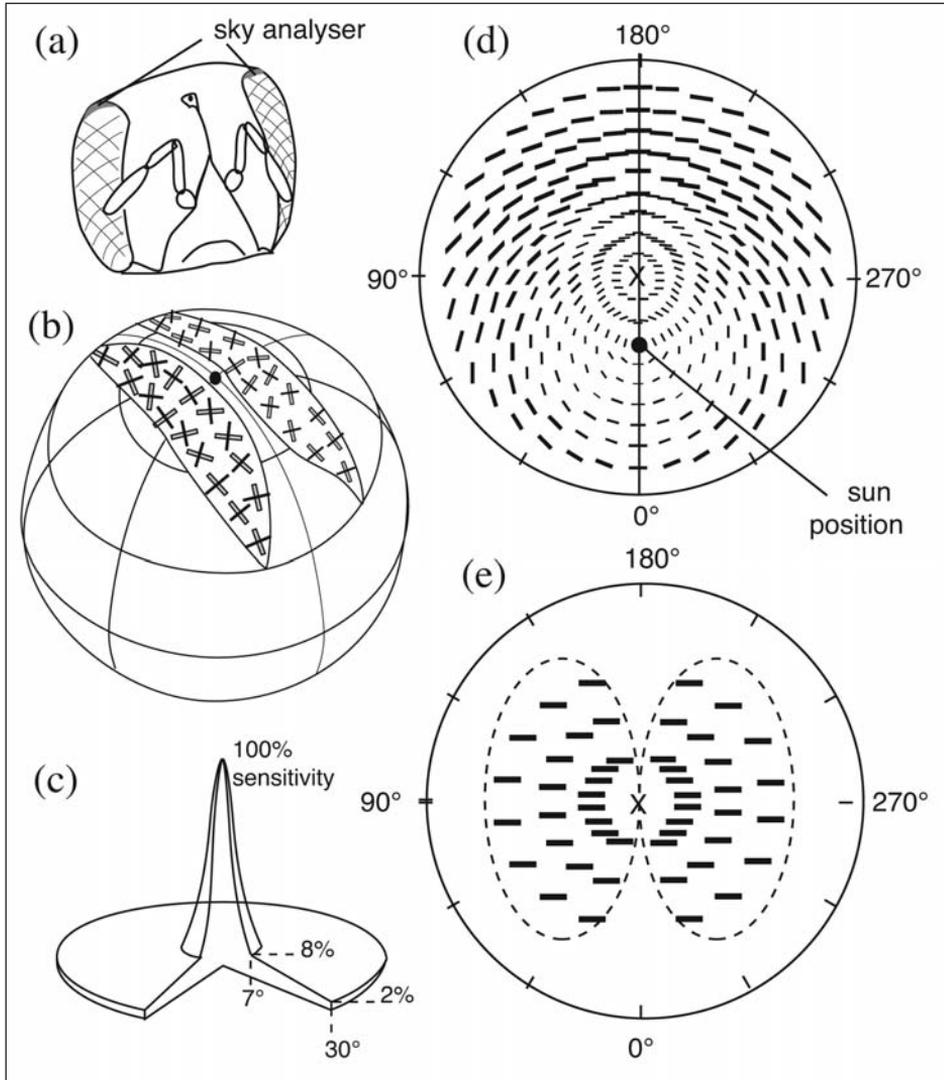
The signposts in the blue sky

In August 1869, at the top of the Aletschhorn in Switzerland, the English scientist J. Tyndall scanned the sky with his Nicol prism and found that the direction of maximum polarisation of light from the blue sky was always perpendicular to the direction of the sun (Figure 8.7d). This observation was explained by elongated and horizontally floating dust particles that scattered the light preferentially, and was eventually published in *The Forum* for February 1888—such was the speed of scientific advance in those days. Scattering is inversely proportional to the fourth power of wavelength. At large angles to the sun, the sky provides sufficient ultraviolet to be useful for detecting small dark objects against the sky with the improved lens resolution of the bee ommatidium that the shorter wavelength allows.

Unaware of the earlier work by Santschi on ants, von Frisch discovered that a small patch of blue sky light was sufficient to direct the orientation of the figure-of-eight dance. A physicist colleague in the faculty at the University of Graz, Han Benndorf, advised von Frisch to consider the polarisation pattern of the sky and, in 1945, the observation was published. Knowing the time of day and the direction of polarisation, the bees had another compass.

The mechanism within the eye took more trouble to unravel. In each ommatidium of cockroaches, butterflies, dragonflies and the honeybee, there are one or two retinula cells with sensitivity peak in the ultraviolet. These cells are probably responsible for UV-specific behaviour, such as the escape response towards the open sky. In the drone bee, which pursues the virgin queen against the background of the sky, and dragonflies that catch flying prey from below, the dorsal part of the eye is predominantly UV sensitive.

Figure 8.7 The solar compass and its detector. a) The position of the polarisation-sensitive (POL) area. b) The pattern of the planes of the orthogonal pairs of UV receptors in the dorsal rims of the bees' eyes. c) The angular sensitivity curve of the single receptor has a wide skirt that integrates over an extended area of sky. d) The pattern of the e-vector of polarisation of the blue sky. e) The orientations of the detectors that were inferred from the behavioural experiments.



Scientific theories often appear in imperfect form and are refined. From Santschi (1911) onwards, knowledge of the mechanism of the bee eye for detecting the polarisation plane was a real dog's breakfast. A selective scattering or reflection to convert the polarisation pattern into an intensity pattern *outside* the eye was suggested in the late 1950s, but none could be found. Other mechanisms *inside* the eye—for example, a Nicol prism in the cornea or cone—were suggested in

the early 1960s. Later, one such was in fact found in some fossil trilobites. These theories were forgotten when the intrinsic properties of the visual pigment rhodopsin were discovered. By illumination of vertebrate rods and cones from the side in tissue slices, it became clear that molecules of rhodopsin absorbed more light polarised in one direction than in the perpendicular direction—that is, the molecules were dichroic and were lined up (as in Figure 5.3). In the 1960s, electron microscopy revealed the structure of insect rhabdomeres as organelles made of parallel microvilli. It was generally accepted that the rhodopsin molecules were oriented in the plane of their lipid membranes and it was assumed that the whole compound eye detected the plane of polarisation by having different retinula cells with microvilli (and therefore rhodopsin molecules) oriented in different directions and repeated in other ommatidia. To mimic this, von Frisch had models made with a hexagonal mosaic of polaroid so that when held up to the sky they showed different intensities in each piece of the mosaic. They were even proposed for military use, to direct missiles.

There was much discussion about how the responses of the retinula cells could be integrated. There was further discussion about how the rhodopsin molecules in the microvilli could be oriented to have more than double the sensitivity in the best direction than in the worst direction, because the value of only 2 is the maximum to be expected from rhodopsin molecules that lie randomly in the plane of the membranes. Later, the basal (ninth) retinula cell of the bee ommatidium was proposed as the sensor because it was sensitive to ultraviolet and had a high sensitivity to the plane of polarisation (explained by filtering by cells above it). There was a lot of discussion about twist in the bee rhabdom, which, if true, could abolish the sensitivity to the plane of polarisation. There were experiments with discriminations of patterns composed of polarisation directions. Direct recordings showed that all bee retinula cells had some polarisation sensitivity, but the ninth (basal) cells remained mysterious. There was great excitement in the 1970s as these discoveries were worked into a mechanism for navigation.

The efforts were not entirely rubbish. The data were valid, but the conclusions drawn at the time were led astray by the historical context. The explanations were based on known components, but ignored the possibility of a completely different explanation, which arrived too late to be in the excellent book by James L. Gould (1982).

The dorsal rim receptors

Many insect groups have a specialised region along the dorsal edge of the compound eye (Figure 8.7a) where the microvilli in the rhabdoms are aligned in cells with poor optics, large fields, blue or UV sensitivity and high polarisation sensitivity—first properly described in the cricket. During the 1980s, it became

apparent that in the bee the ommatidia along the dorsal rim of the eye have poor spatial resolution but are very sensitive to the plane of polarisation in the ultraviolet. The critical experiment showed that bees could not dance or navigate correctly when only this dorsal band of ommatidia was covered—a splendid example of evidence of absence. These special receptors sensitive to the polarisation plane are used to determine the position of the sun when it is not visible.

The dorsal rim cells have angular sensitivity fields with a wide skirt around a central peak (Figure 8.7c). Single cells therefore integrate the polarisation over fields at least 45° wide. The ratio of absorption, and therefore sensitivity, in the plane of the e-vector to that at right angles (see Figure 5.3a) can be as great as 15. This shows that the rhodopsin molecules are lined up in the parallel microvilli. The receptors in the rest of the eye have a ratio less than 2. The 140 or so dorsal rim ommatidia of the honeybee (Figure 8.7b) look upwards, and each contains nine long, straight retinula cells.

Tom Labhart (1980) found that the axis of sensitivity to the polarisation plane had a special pattern in the dorsal band (Figure 8.7b). So, as Wehner, Rosell and colleagues in Zürich concluded during the 1980s, the dorsal rim cells acted as fixed-feature mini-detectors for an expected visual task. Two types of cell at each place had orthogonal axes. In tests with the polarisation pattern of the sky, the dorsal band acts as a functional unit and the detector axes appear to be parallel (Figure 8.7e). All the bee has to do is rotate itself until this sensitivity pattern of the dorsal rims of its eyes makes the best fit with the pattern in the sky, then it is facing the sun. The best fit would depend on the coincidences of a number of independent feature detectors, any of which can be omitted. Either eye would serve. In the locust, the signals from the dorsal rim cells reach the central body in the protocerebrum, where they are laid out as a close-knit topographic representation of the e-vector panorama in the sky (Heinze and Homberg 2007). Presumably the bee is similar.

Observation of bees suggests that they read the compass direction from the sky without turning themselves. To do this, there would have to be an internal analyser of neurons in the brain. Three such macro-analyser neurons have been found in the central body of the locust brain; they are binocular, with large fields. In all three, light polarised in one plane is inhibitory to light polarised in another, with peaks of maximum sensitivity 60° apart. The function is clearly not to see the polarisation pattern of the sky. The task is to show the direction to go, for which two other sets of data are required—the land coordinates from the distant landmarks and the expected position of the sun at the time of day—both of which are learned by each individual bee. It is likely, therefore, that individual bees also learn the polarisation patterns that are useful to them, from the coincidences in a distributed array of high-level neurons.

The visual estimation of distance flown

By an accident of the terrain, von Frisch (1965) placed a food source at the back of a projecting ridge of a mountain and found that the dances of the returning foragers indicated the direct direction to the food source, and the total distance flown around the detour on the way home. The bees following the dance fly off in the correct direction, meet the detour, which they circumvent, and find the food at the expected distance flown. Therefore, the information they received was just what was needed. These results were confirmed for other detours.

von Frisch noted that the bees reported a shorter distance when flying downhill than when flying uphill and for many years he believed that they measured the distance by the energy expended on the homeward flight—an intuitive inference that became fixed in textbooks. Harald Esch, who worked with von Frisch, never believed this proposal, but he had no opportunity to prove otherwise until long after he was obliged to move to the United States. While Srinivasan was first experimenting with bees flying along tunnels in 1995, Esch and Burns (1995) published the result of a now-famous experiment. They trained bees to fly to a food source on the ground. Then they raised it with a balloon. Later, they flew bees between the tops of tall buildings. The homeward distance reported in the dance was less as the bees flew higher above the ground, showing that the perception of distance was dependent on the scene. The bees measured the distance they perceived visually over the duration of the flight. They had a visual odometer, but clearly they did not indicate a fixed unit of distance for each waggle in the dance.

The next year, Srinivasan published the account of how bees, flying along a tunnel towards a food source, measured the distance to the position of the food source by integrating the visually perceived angular velocity of the walls and floor (see Chapter 7). The distance to the place where the bees searched was independent of the pattern on the walls and tests with a wind along the tunnel, or moving walls, showed that the bees summed the apparent angular velocity over the flight, not the total number of edges or time passed.

The next logical step was to calibrate the dance in terms of the perceived motion. In 1995, there was new enthusiasm among grant-giving bodies for collaboration between distant laboratories, so it was easy to bring experts on the waggle dance to Australia and send experts on bee tunnels to Europe, resulting in a flurry of detail published by Srinivasan, Collett, Esch, Zhang, Tautz, Vladusich and Lehrer and their colleagues at both antipodes. Outdoors, the bees gave about 1.6ms of waggle dance per metre travelled, and 1m of flight in a tunnel 30cm wide was equivalent to 25m outside. In both situations, one millisecond of waggle encoded about 18° of image motion on the eye.

Later, a tunnel provided a convenient way to add a large deviation at right angles to the path to a distant goal. In the dance, the bees that were deviated by

a tunnel measured the total optic flow on the outward journey and the compass direction of the hive in a straight line from the food source. Bees would not fly through the tunnel on the return to the hive or switch between tunnels at right angles, showing the influence of their dead reckoning.

When bees fly slowly against the wind or faster with the wind, they still measure the impression of the distance travelled over the ground. As the contrast is reduced—for example, at dusk—the odometer continues to function normally down to contrasts of about 20 per cent of that in sunlight. When flying over water, the odometer registers less than the usual distance (Tautz et al. 2004).

When desert ants travel up and down hill, they remember only the horizontal component of the distance walked. Bees flying in tunnels measure and remember the total distance travelled, even in the vertical direction in a vertical tunnel. This is reminiscent of the earlier finding that flying bees measure the angular velocity of passing contrasts irrespective of their direction of motion. Some species of stingless bees direct the recruits to the correct height of a food source by scent marks.

The bees appear to reset their odometer at the transition at the entrance to a tunnel. A landmark placed in the tunnel before training improves the accuracy of measurement of distance in the tunnel, and when the landmark is moved, the search place moves with it. They reset their odometer at each landmark and the flight is divided into sections, each with identified beginning and length. The bees would not search beyond a landmark that was placed in the tunnel after training, just as they would turn away from a landmark that displayed an unfamiliar cue. Conversely, bees overshoot the goal when a familiar landmark was removed. In a tunnel, the landmark positions overrule the visual odometer (Vladusich et al. 2005), which is what happens in their natural terrain, but paper tunnels are far more convenient for manipulation of the visual scene and for experiments with positions or numbers of landmarks or a controlled wind.

Practical route finding by foraging bees

Last century, Lubbock described how displaced wasps flew higher and higher until they recognised a distant large landmark then headed towards home. The pattern of the horizon is certainly important. The largest landmarks are preferred—even distant mountains. When there are two or three similar landmarks, bees learn how many to pass, but normally they judge distance from the perceived ground speed.

Bees that are recruited at the dance fly out from the hive using the sky compass, learning landmarks as they go. They can do this under an overcast sky by inferring the sun's position from known landmarks. At the distance indicated, they search for the food scent picked up from the dancing bee. They also look

out for other bees to follow and they will land beside bees that have settled. The results from maze learning show that bees learn routes from very small cues, but Romanes' (1885) experiment shows that the sky compass and dead reckoning are not sufficient by themselves in a windy place.

Experienced bees in a busy visual environment use the sun compass if it is available and the shifting of a landmark under a blue sky does not disturb them. They can use one set of local landmarks at one location and another set somewhere else, and learn to visit each foraging area at the appropriate time of day. They can select an odour cue according to time of day or location, but different colour cues only according to location. When some of the local landmarks that mark a goal are displaced, the bees search in a spot that shows that they are placing the remaining landmarks in the expected directions relative to their own eye. There is strong evidence of assistance from the horizontal vector of the Earth's magnetic field. Similarly, they perform faster if they regularly fly along a particular path.

By definition, a landmark cannot be recognised by its position; it must be recognised uniquely by its shape, size or colour and then it indicates a position. Bees can fly towards and past an obvious isolated landmark that they have learned, then to another one and so on to the goal, then directly back home. Commonly, if they fail to find the reward, they return to the previous local landmark and make their approach again. Some landmarks are like beacons on which they rely. With these, if the landmark or the feeder is moved, the bees show that they have not learned the compass direction and, not finding the goal, they cast around until they find it. They then calculate a new compass direction towards home and remember the additional information needed to correct the error they made.

Each bee repeatedly flies along the same track and the landmarks fall on the same regions of the eye each time. On the other hand, the sun and its polarisation pattern move across the sky, so the bees must adjust for the time of day. A landmark is a local cue indicating which direction to fly relative to the sky compass at that place. Bees that are displaced to a new location under a clear sky continue in the direction they were going but quickly begin to search for familiar landmarks. Bees displaced under an overcast sky can recognise tall landmarks from unfamiliar directions, which is the only way they can head towards a food source or home. In these experiments, it is essential to distinguish between bees returning to the hive or food source and those setting out.

From comparisons of the turn-back-and-look behaviour with route finding, bees and wasps apparently take snapshots with the side of the eye and bounce from side to side of an imaginary corridor that they have committed to memory. Experienced bees also use the apparent size of the landmark, having first learned where it is located. As Collett showed, if landmarks were made larger, the insect searched further away from them; if local landmarks were moved, the target was sought at a place from which all landmarks had the best approximation to

their expected size, appearance and directions (Figure 8.1b). Movement of local landmarks relative to distant ones confuses the insects. All of the evidence put together shows that the actively moving insect quickly discovers which way to go to bring individual landmarks into the desired arrangement as seen from the goal. Many insects apparently can do this while flying in circles. Perhaps a single saccade can put a snapshot of all surrounding landmarks into the 360° visual system. The landmarks change as the insect moves along the route home and natural changes in landmarks are tolerated. The mechanism is flexible because there are alternative cues (Figure 9.21).

Detailed study of what cues bees really use in order to recognise a landmark shows that they detect landmarks in the same way that they discriminate patterns in the Y-choice maze. They detect only a few simple features that are summed into cues and they recognise them in the places where they were in the training. The enormous number of observations can probably all be explained by the same few feature detectors and cues listed in Chapters 9 and 10—perhaps with a few other undescribed cues.

The orientation flight

The first flight of a young bee from the hive is an orientation flight in larger and larger loops up and away, returning within a few minutes. Older bees that emerge to an unfamiliar scene from a displaced hive make a new orientation flight. If carried away from the hive, most bees that have taken only one orientation flight return eventually, but bees that had no orientation flight always become lost. After the orientation flights, bees can distinguish some landmarks by colour, height of the centre, angular size, range, orientation and by their angular directions relative to each other, but not by compass direction from the point of choice. This implies that near the hive the landmarks do not carry an attached homeward direction towards the hive.

When a hive is moved, all the bees in it must make new orientation flights. Experienced bees learn the direction of the hive from any point in their area and, when the sky is clear, they progressively shift their reliance from landmarks to the integrated vector path as guided by the sun compass and distance over the ground. On overcast days, landmarks take precedence and if the landmarks are moved the bees are either fooled or they make new orientation flights. The orientation flight is a performance, not a mechanism. How their several navigation systems are coordinated has not been analysed.

Turn-back-and-look flights

Turner (1908) described the curious way that bees turn back and look (TBL) to acquire or update their memory of the location on leaving a nest or food site:

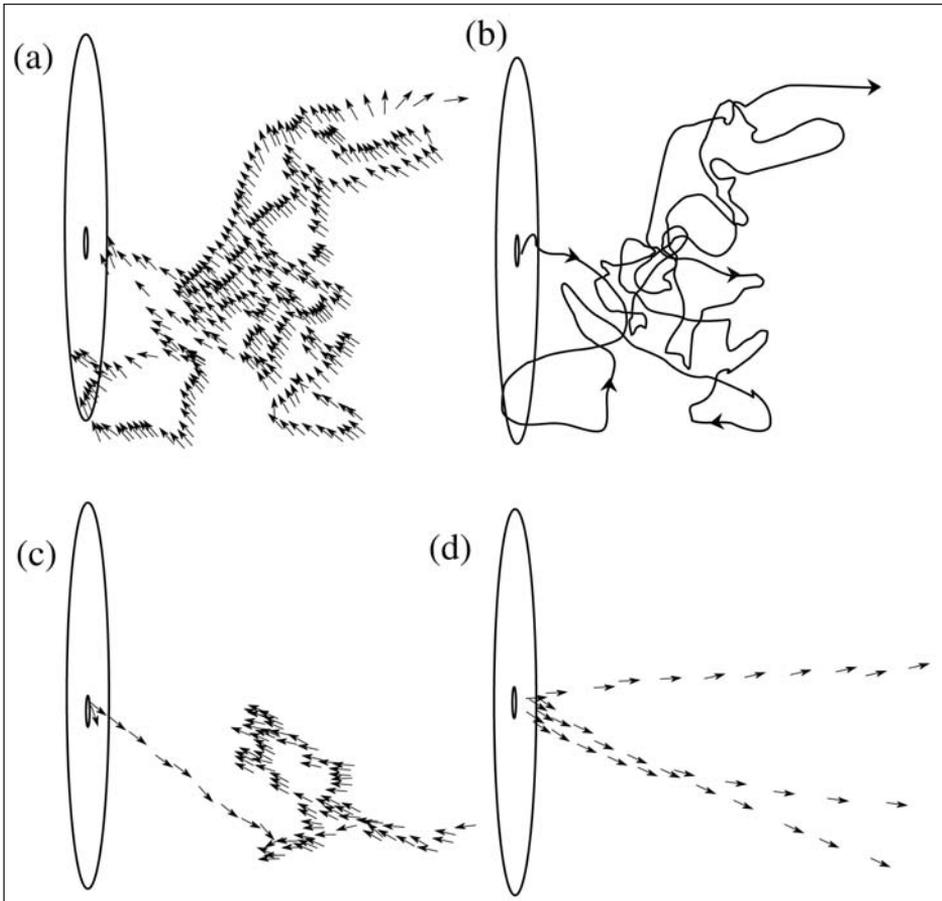
When a bee had discovered one of my honey producing artefacts and collected therefrom, it would make a flight of orientation and then fly home...After the association had been well established, the bees usually departed for home without making a careful flight of orientation. If however I had made a marked change *in the position* of the artefact since the last visit of the bee, then a careful flight of orientation was always made.

It was not clear until the 1990s what the insects were doing. The details are more obvious in wasps than in bees. Wasps leaving a new food source back away and swing from side to side in flight, along a series of successive short arcs centred near the goal, and learn the location by making inspections from successively greater distances along a line from the target in just one or two directions (Figure 8.8). The detail suggests that the wasps store a series of landmark sizes, directions and ranges, which they can use in reverse order to return to the food—a kind of inversion of the desired flow field. The ground speed increases as the insect backs away in successive arcs, so the turning speed is visually controlled at 100–200°/s irrespective of the radius of the arc. The body angle is fairly constant relative to the landmark. The null in the visual flow field falls on the landmark and on a particular eye region as the insect swings around in flight, while the foreground and background move in opposite directions. They do not zoom and loom. Shadows, which being flat have no motion parallax, have no effect. Parallax can be a crucial cue, if available. The relative locations and ranges of nearby landmarks are learned during one manoeuvre, but there is insufficient time to learn the pattern around the goal. For a bee, if the TBL manoeuvre is prevented, the size of the target becomes the cue.

When the approaching bee centres its vision on a symmetrical target or on the colour of the goal, it can learn its size, minimum cues and colour on the approach and then depart without making a TBL manoeuvre, but the bee can also learn the cue or colour of the goal in a TBL if the cue is put in place just before the bee leaves. If shown one colour, cue or size of target on arrival, and another on leaving, they retain the first cue only, so the TBL is not primarily for learning colour, pattern or size, but for range, landmark size and depth. In the Y-choice maze (Figure 9.1), bees do not make TBL manoeuvres as they look first at one target and then at the other, because they already know where they are.

Some of the angular manoeuvres are repeated when the insect returns, so that it places itself in the same postures as before, looking in the same directions, and the flow field swirls around the same null points, landmarks fall on the same eye regions, while the goal is brought to the null point at the front. There is no evidence that the area around the goal is compared with a retinotopic memory.

Figure 8.8 The turn-back-and-look behaviour. a) When departing for the first time, the bee flies backwards in a convoluted path while facing the target. b) The track without arrows. c) At the second departure, the bee departs sooner. d) When familiar, the bee leaves without looking back.



In later visits, these actions progressively disappear and experienced insects arrive and leave directly. The nature of the manoeuvre and its effect on the visual flow field suggest that a sequence of ranges, sizes and locations on the lateral part of the eye is remembered. If the goal is moved, the bee returns but cannot find it, but if the pattern on the goal is modified the bee might not notice, because the place is learned, not the pattern. It is just one of many acts of looking that suggests that patterns are equivalent to landmarks.

Navigating with one eye

Many of the visual tasks of ants and bees can be carried out with one eye. This is not surprising because to a large extent each eye appears to act independently

of the other, and even each local region of each eye detects separate cues or landmarks. Naive bees trained to measure a distance along a tunnel with one eye can transfer the information to the other eye. They can also be trained to measure one distance along a tunnel with one eye and a different distance with the other eye. There remains some uncertainty about how the eyes interact in the natural situation, because bees in flight see a different scene with the two eyes, but they turn around for the return flight (Srinivasan et al. 1998). When one wall of the tunnel is blank and the other displays a pattern, the bees estimate the distance of the reward along the tunnel almost as well as when both walls are patterned.

There are strange discrepancies between investigations of this topic and it seems that insufficient notice has been taken of the overlap of the visual fields of the two eyes. Early work showed that the ant *Cataglyphis* could navigate by the polarisation of the sky or by landmarks with only one eye and could then find its way home with that eye. When trained to home with one eye and then tested on the other eye, they can navigate by the polarisation of the sky but not by using landmarks (Wehner and Müller 1985). Similarly, bees can learn a colour or an orientation cue when presented to one eye but cannot transfer when tested on the other eye (Giger and Srinivasan 1997), and they can use the position of a laterally placed bar but they do not recognise it with the other eye. They can, however, transfer relative motion of the cue and the eye between the two eyes (Lehrer 1994) and also a colour when it is a cue for the direction of the next turn (Zhang et al. 1998). The experiments are descriptions of the performance, not an analysis of mechanisms, there have been too few tests to reveal the cues and each group of trained bees was given only one kind of test, which was successful, so there is the probability that they learned during the test procedure.

Cognitive maps

If a cognitive map is defined as any internal representation of an extended world, however rudimentary, most active animals have it built into their visual responses. If, however, a map is defined as an internal representation of the geometric layout of objects in the surrounding environment, such that an animal can place itself in the right place by recognising landmarks or other cues and then take a novel shortcut to its goal, it is simply a matter of the scale of the map. In a test, an animal with an internal map must be able to take the shortest distance along a novel track to any goal in its territory.

On a small scale in the Y-choice maze, bees quickly learn the layout of the whole apparatus and when they receive no reward at one target they quickly fly to the other target without going back to the last landmark, as though they know very well the relative locations. On a small scale, they learn a map of sorts when the location of the goal is randomised, which suggests that to make the bees learn a large-scale map, nothing more is needed than training with the reward in many

possible places. In a maze, the bees that take the wrong turning soon learn to take the alternative turning, as though they have an appreciation of the spatial layout of the maze. Again, they learn a sort of map when necessary.

Bees can learn to go to one feeding place in the morning and another in the afternoon. If bees that are departing from the hive are taken to the wrong feeding site and are allowed to feed, they set out in the correct direction when they return to the hive, showing that they associate the landmarks they see with the compass direction to the hive. If they are taken to the wrong place and not fed, they usually do not fly off in the direction of the other place, but they usually return to the hive and then set off again or they go scouting around for another food source, then fly their beeline home.

As seen in Bethe's old idea of a homing force, there have been contending opinions for more than a century. So far, there is no suggestion that ants have maps of their territory. For wasps, the detailed studies of Baerends and many others before him showed that wasps carrying food could head directly to one of a dozen goals when displaced to anywhere in their territory, probably by use of landmarks learnt in numerous exploratory flights. In 1986, Gould produced evidence that displaced bees did not merely continue along their previous compass course, but were able to 'make use of novel and efficient routes on the basis of map-like cognitive representations' of local landmarks. The next year, Gould went too far in claiming that the dance of a returned forager was interpreted by the recruits in terms of their own internal map based on landmarks.

Most unusual and out of character, one of Gould's former students questioned the conclusion and suggested that distant landmarks indicated the direction of the hive. Also, the idea of an internal map was so objectionable that two professors, not known for previous amicability, collaborated to throw it out. In 1990, they jointly reported new experiments in Europe and the United States in which marked satiated forager bees continued along their compass directions when displaced. These bees eventually searched around or flew up high and circled before returning home, so were apparently using distant landmarks as a backup. It was concluded that bees used only the local landmarks close to their day-to-day tracks, but when lost, they revealed reserve memories of distant landmarks.

In 1998, Randolph Menzel found that when the foragers were fed at one site in the morning and a different site in the afternoon, they were able to take a novel shortcut back to the hive when displaced from the hive, but not when displaced from the feeding sites.

Notwithstanding this earlier conclusion, in 2000, Menzel and others found evidence of memory of a wider area within which bees could return to the hive from any point, and in 2006, they measured the time it took for bees to return

home after being displaced. Bees that had been trained to a feeder that was regularly shifted in any direction at a distance of 10m from the hive all returned quickly, but bees familiar with only one flight track took longer. Finally, they brought into use a method for continually tracking the position of a bee in flight by attaching a radar transponder to it—invented by Osborne et al. (1996). After being displaced under an overcast sky, bees can use familiar landmarks to take a novel shortcut to where they ought to be. The results reveal ‘a rich, map-like organization of spatial memory in the navigating honey bees’ (Gould 1986). The displaced bees can choose between at least two goals. They can take straight and rapid flights directed either to the hive or first to the feeding station and then to the hive. In the featureless landscape used, moveable tents act as landmarks, but apparently the varied textures of the ground provide sufficient information for navigation when the landmarks are shifted.

To my mind, these results show that the bees learn as much as they need in order to know the direction of home at all times. When the destinations are shuffled, they learn the positions of all possible places to look, exactly as in the Y-choice apparatus. They are able to extend the scale of the exploratory flights and build up a memory of the vector directions to two or more goals from a larger number of landmarks, as inferred by Baerends for the way that the experienced wasp can take a caterpillar to one of several nests from any point in her territory, and also demonstrated by the way that bees fly through complicated mazes.

The present opinion seems to be that when bees make orientation flights, they are learning to associate the directions of landmarks with the sun-compass direction of home. The beeline home therefore does not prove the existence of a two-dimensional map in the brain of the bee. Departing bees, going either way, have a strong internal signal for distance, which is all used up in arriving bees. Then, after finding the food site—sometimes by scent or by seeing other bees feeding—the new bees learn the local landmarks at the food site and also associate them with the direction of home. We have no idea how or where this sequential memory is coded.

The reader might note that researchers on navigation were interested in the mechanisms, as well as the performance (that is, what the bees could do).

Endnotes

1. For further information, see the recent works of Menzel, Srinivasan or Wehner.