

SPATIAL MEMORY AND NAVIGATION BY HONEYBEES ON THE SCALE OF THE FORAGING RANGE

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Summary

Honeybees and other nesting animals face the problem of finding their way between their nest and distant feeding sites. Many studies have shown that insects can learn foraging routes in reference to both landmarks and celestial cues, but it is a major puzzle how spatial information obtained from these environmental features is encoded in memory. This paper reviews recent progress by my colleagues and me towards understanding three specific aspects of this problem in honeybees: (1) how bees learn

the spatial relationships among widely separated locations in a familiar terrain; (2) how bees learn the pattern of movement of the sun over the day; and (3) whether, and if so how, bees learn the relationships between celestial cues and landmarks.

Key words: spatial memory, navigation, bees, cognitive maps, orientation, learning, sun compass.

Introduction

Animals that bring food to a central nest commonly face the problem of finding their way between their nest and feeding sites that may be hundreds or thousands of meters away. Over such distances, a forager is unlikely to be able to detect its goal directly. To set and maintain its course, it must therefore determine its position relative to the goal and then choose the appropriate direction of travel, in relation to environmental features detectable at its starting point and along the way. Visual cues such as landmarks and celestial cues provide reliable information for navigation over this scale. The challenge in using visual cues, however, is that the animal must learn the particular visual features that define the locations of important goals in its habitat. Thus, the study of how animals use such references has come to focus on how their nervous systems can store and use information that defines the spatial relationships among visually separated sites.

This paper reviews recent work on how honeybees and other nesting insects learn about the visual references they use for navigation on the scale of the foraging range. To put this work in the broad context of the study of animal navigation, I want to make three background points. First, the specific navigational problems faced by an animal depend upon the scale over which it has to move to find a goal such as a nesting or feeding place. A bee that has solved the large-scale problem of setting a course for its distant and unseen nest still faces the somewhat different problems of pinpointing the location of the nest relative to nearby landmarks and then recognizing the nest by its visual appearance. While recognizing that these problems differ, however, we should remember that there may be linkages among the visual and learning processes on each of these spatial scales.

Second, to set a course to a distant goal beyond its current line of sight, an animal must obtain two pieces of information from the environment (reviewed by Dyer, 1994): it must measure its orientation and it must determine its current position relative to its goal (hence determine which orientation is the appropriate one). To summarize these challenges, researchers often invoke the metaphor of a 'compass' for the ability to detect orientation and the metaphor of a 'map' for the ability to determine position. Although these metaphors have some heuristic value, they are also potentially distracting (Dyer, 1994). In particular, the concept of a navigational map is fraught with confusion. The term usually refers to a representation that defines locations relative to earth-based features of the environment, but there are many different ideas about the coordinate systems and geometrical operations that animals might use to develop navigational maps. Furthermore, some species can determine their spatial position without relying upon a map of locations relative to earth-based environmental features, but rather by path integration or 'dead-reckoning'. This process uses a directional reference (either an external compass reference or an inertial reference provided by vestibular or somatosensory feedback) to maintain a continuously updated egocentric representation of the animal's position relative to its home (Müller and Wehner, 1988; Séguinot *et al.* 1993).

Third, for insects moving about a large foraging range, the most important sources of navigational information are celestial cues (the sun and sun-linked patterns of polarized sky light) and landmarks (von Frisch, 1967; Wehner, 1981; Dyer, 1994). Celestial cues provide a true compass for insects that can compensate for the sun's movement relative to terrestrial

features. The celestial compass is also at the heart of an insect's ability to determine its position *via* path integration. In addition to relying upon celestial cues for navigation, honeybees can use them as the basis for communication in the dance language, whereby foragers can indicate to their nest mates the direction (relative to the sun) as well as the distance of food. As an expression of the forager's knowledge of the sun's position relative to her line of flight, the dance of the bee has played an important role in studies of how insects learn about the celestial reference (von Frisch, 1967; Dyer, 1987). Landmarks can be used to maintain a particular direction of travel. They can also be used to determine position independently of the path integration system, provided the animal has learned the spatial relationships between landmarks in different parts of the environment (reviewed by Dyer, 1994).

The first section of this review addresses the question of how bees use landmarks to determine a course to a distant goal and, in particular, focuses on what bees learn about spatial relationships among widely separated locations in a terrain. Then I will discuss how bees compensate for the movement of the sun relative to terrestrial cues. Finally, I will consider the relationships among celestial and landmark references, in particular the question of how these two reference systems are linked by bees in obtaining navigational information from the environment.

Landmark maps

Over the past century, abundant evidence has accumulated suggesting that nesting insects can use landmarks to navigate over distances of hundreds or thousands of meters (reviewed by Wehner, 1981). Even early researchers assumed that insects could learn their way using landmarks, but the first direct evidence for landmark learning on the scale of the foraging range came from Baerends' (1941) studies of digger wasps (*Ammophila campestris*). Previous studies of *Philanthus triangulum* digger wasps (Tinbergen and van Kruyt, 1938) had shown that wasps learn to use landmarks near the nest to guide their final approach to the nest. Baerends found that digger wasps also use landmarks (e.g. rows of trees) to set a homeward course when neither the nest nor landmarks in its vicinity can be seen. He proposed the following relatively simple explanation for these abilities. As the insect travels through the environment, it memorizes the sequences of visual images experienced on routes that lead it to food and back to home. When a homing wasp finds itself on one of these routes, having arrived actively or through displacement caused by the wind or by the experimenter, it compares what it currently sees with an image previously memorized and sets an appropriate course. Baerends found that wasps could learn more than one route connecting the nest to places in the habitat, but that they learned nothing about spatial relationships among different routes.

Subsequent research supported and extended Baerends' interpretation of large-scale landmark learning in insects (e.g. Wehner, 1981, 1983; Collett *et al.* 1992), and linked the learning processes used on the scale of the foraging range to those used

for the smaller-scale task of pinpointing the location of a goal relative to nearby landmarks (Cartwright and Collett, 1983, 1987). In both contexts, insects appear to guide themselves by following the paths that produce the best match between current and remembered images of landmarks. Navigation along a route entails using a sequence of visual images analogous to the one used to guide the final approach to a goal.

About 10 years ago, a controversy developed over the issue of whether, in addition to learning sequences of landmarks encountered on each familiar foraging route, insects also learn spatial relationships among different separately traveled routes. In other words, do they construct a large-scale mental map that charts the relative positions of familiar locations in a common coordinate system? Gould (1986) provided evidence that honeybees do form such maps. His results proved hard to replicate (Menzel *et al.* 1990; Wehner *et al.* 1990). I was able to replicate them (Dyer, 1991), but found that the behavior that Gould took as evidence for maps is actually consistent with Baerends' suggestion that insects do not incorporate their experience on different routes into an integrated map of the terrain. However, as I shall now discuss, attempts to resolve this controversy have clarified the concept of mental maps and have led to several new insights concerning the use of landmarks for navigation on the scale of the foraging range.

The ability to learn the relationships among widely separated sites in a terrain is puzzling, because it implies that the animal can memorize spatial relationships that it experiences only over time, as a result of its movement through the environment. Consider that, although we may draw a picture of the landscape as if viewing it from above, an animal near ground level (e.g. a walking insect or person, or a bee flying at a normal height of a few meters) cannot experience it in this way. If the animal is to develop a knowledge of spatial relationships on the scale of the terrain, it must construct it from its egocentric perceptions of spatial patterns seen in successively encountered parts of the terrain.

Fig. 1 illustrates schematically some ways in which an animal may learn spatial relationships among locations in a familiar terrain. If a 'map' is defined as a representation of spatial relationships in some geometrical framework, then any of these schemes may be called a map. My aim is to differentiate among them in operational terms, while exploring possible hierarchical relationships among different mapping schemes. In this illustration, as in Baerends' original hypothesis, the elements of large-scale maps are the local images of the spatial patterns that can be seen from specific vantage points in a terrain. Roughly, each local image corresponds to the panorama of landmarks visible along a given portion of a familiar route. The local image surrounding a given goal, such as the nest, is equivalent to the 'snapshot' that bees use to guide the final approach to the goal (e.g. Cartwright and Collett, 1983). The spatial extent of the local image would depend upon the insect's visual resolution and the structure of the visual surround where the image is recorded. For example, the image could be of the surrounding hills that a bee sees when flying through a valley or of the

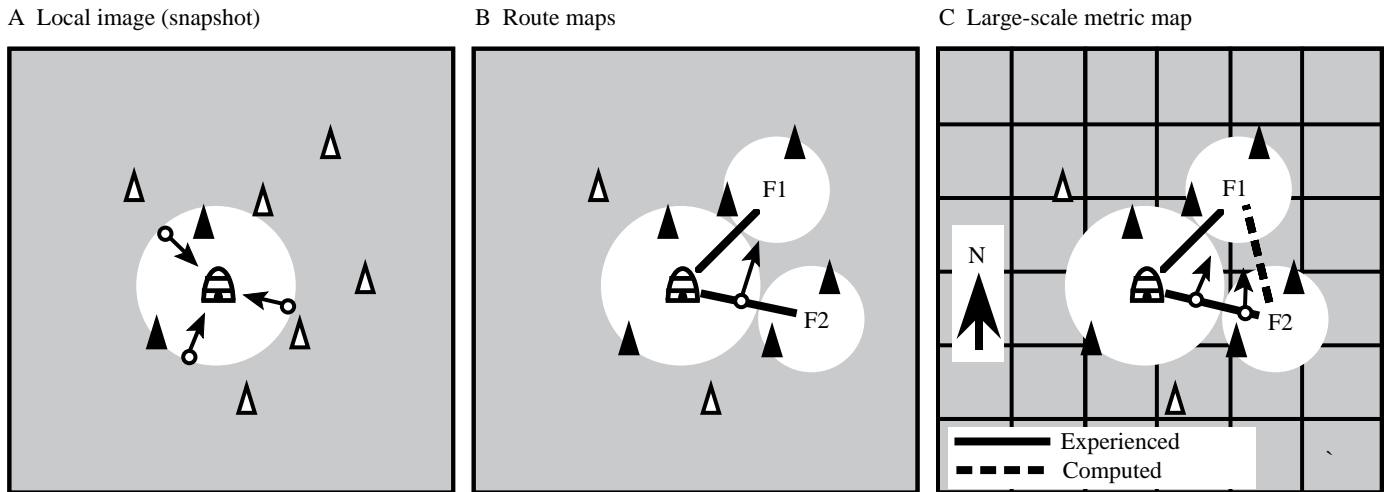


Fig. 1. Three ways in which an animal may learn about spatial relationships in its foraging range. Shaded regions are *terra incognita*; black triangles are known landmarks, white triangles are unknown landmarks. Arrows originating at small circles indicate paths that bees can select towards home (A) or towards feeding site F1 (B and C) from various starting points. (A) Local image, or 'snapshot', of an array of landmarks surrounding a given goal; bees can use such snapshots to approach the nest from a variety of directions (Cartwright and Collett, 1983). (B) Route maps for two feeding sites, F1 and F2; each route map consists of two local images encountered in sequence along the path to the food. Bees can use such maps to head for an unseen goal (e.g. F1 when it is their current feeding site), even if they have been displaced so that they see the landmarks associated with the route to their goal from new vantage points (Dyer, 1991; Dyer *et al.* 1993). (C) Large-scale metric map, in which bees have encoded the directions and distances separating familiar sites in reference to a common coordinate system, shown here in a Cartesian format. A metric map would allow a bee to compute a novel course to F1 even if she found herself near F2, from which she could not see any landmarks associated with the route from the nest to F1.

surrounding trees that she sees when flying through a pasture. From the work of Cartwright and Collett (1983, 1987) and others, we know that bees using the local image of the landmarks around a goal can set a course to the goal from a variety of directions (Fig. 1A). In studies of rodent spatial memory in analogous tasks (e.g., the Morris water pool task), this sort of flexibility is often taken as evidence of a 'cognitive map' (reviewed by Leonard and McNaughton, 1990). I want to emphasize that whatever processes are used on this small scale (and they remain to be elucidated for insects as well as mammals), it remains an open question how larger-scale spatial relationships might be encoded.

The simplest sort of map larger in scale than a local image is a route map, a sequence of two or more local images seen along the path between two locations (Fig. 1B). These separately experienced images constitute a map of the route only if, as Baerends suggested, the animal can use a given image to get to the next in the sequence. Conceivably, an insect would only have to encode the appropriate direction to travel relative to the features of each visual image, and would not have to learn the sequence in which it encounters the images, although there is evidence that insects can encode sequence *per se* (Collett and Kelber, 1988; Collett *et al.* 1992). An insect would also not have to memorize other geometric parameters such as the compass orientations (relative to external references) of each local image, the distances of each local image from the ends of the route (but see Chittka *et al.* 1995) or the angles separating different routes. The result would be a geometrically simplified, but nevertheless reliable, record of

visual guideposts along each route, referenced to egocentric (e.g. retinal) coordinates. Given adequate memory capacity, an insect could use several such route maps to navigate homeward from any location in a large area around the nest.

A geometrically more complex map could be formed by learning the spatial relationships among separately traveled routes (Fig. 1C). Humans do form such maps in memory. One way we exploit our mental maps is to estimate novel shortcut paths between points on different familiar routes (Byrne, 1982). This ability presumably requires not only learning the visual features of each route but also orienting each route in a common frame of reference, such as one defined by an external compass reference. The map can then be used to calculate the direction and distance that would lead to a point on any other route. An animal with this ability is said to have a 'metric' map (Gallistel, 1990) or a 'vector' map (Byrne, 1982) referenced to an allocentric coordinate system (see Gallistel, 1990). A spatial representation referenced to allocentric coordinates would be computationally more demanding than one referenced to egocentric coordinates, because it would need to be constructed from images recorded in egocentric (retinal) coordinates (see Dyer, 1994).

Gould (1986) proposed that honeybees can construct mental maps that encode large-scale metric relationships in allocentric coordinates (see also Gallistel, 1990). His evidence came from experiments in which bees were displaced from a familiar route. Such bees corrected for their displacement by flying straight towards their current goal. It should be clear from Fig. 1, however, that an ability to set a straight course for a goal after

displacement is not sufficient evidence for a large-scale metric map. Cartwright and Collett (1987) and Collett and Baron (1994) have shown that the flexibility that bees exhibit in using a local image to guide their final approach to a goal can be explained without assuming that bees have placed the landmarks constituting the snapshot in an allocentric reference system. Presumably each local image constituting a route map can be used with similar flexibility (Fig. 1B). Gould did not clearly exclude the possibility that released bees had a view of landmarks associated with the route that they were about to travel when displaced. Hence, his bees might have been guided by such landmarks rather than by a large-scale map. A more convincing test requires releasing bees at a location on a different foraging route not in view of the current foraging route. This would test whether bees could compute a novel course on the basis of their memory of the relationships among the separately traveled routes. In an experiment that presented bees with this problem (Fig. 2), I found that bees could not solve it (Dyer, 1991). Thus, there remains no evidence that bees can combine information from two separately traveled routes.

By establishing that bees use route maps but not large-scale metric maps we have barely begun to solve the puzzle of how they find their way over long distances using familiar landmarks. Many questions remain open. For example, exactly what computations underlie the bees' ability to compensate for modest displacements that still leave them with a view of landmarks associated with their current foraging route, but not necessarily with a view of portions of the route near their destination (Dyer *et al.* 1993)? How do they build up their memory of the terrain during their orientation flights (Becker, 1958) and early foraging flights? Given that experienced bees can learn a new terrain (Becker, 1958) or new nesting sites within a familiar terrain (Robinson and Dyer, 1993), how is new information about landmarks integrated with information previously stored in memory?

Learning and celestial navigation

So far we have considered experienced bees that have already acquired knowledge about specific routes and landmarks. Often, however, bees must navigate in unfamiliar terrain by means of their celestial compass. This is true, for example, of bees recruited to a novel feeding site by dances. Dancers inform prospective recruits about the direction (relative to the sun) and distance to the food, but not about the landmarks encountered on the route to be flown. Also, to discover new sources of food, foragers must be able to explore previously unknown parts of the terrain. This requires the animal to measure the directions and distances traveled on each segment of the search path and then to use this information to compute its position relative to home. As mentioned, the celestial compass provides the directional reference for this path integration system (see Müller and Wehner, 1988).

To use the sun as a compass, however, a navigator has to compensate for the shift of the sun's azimuth (its projection onto the horizontal plane) relative to earth-based coordinates

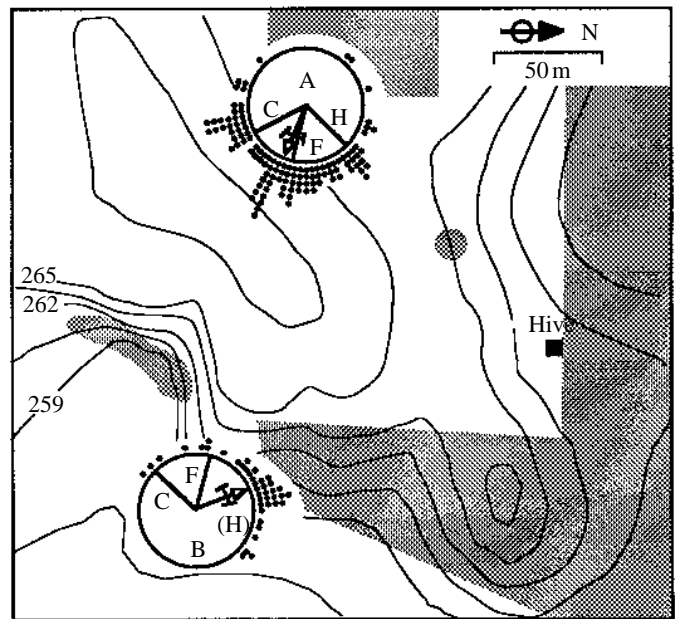


Fig. 2. Experimental demonstration that bees cannot solve the problem presented in Fig. 1C, hence do not have large-scale metric maps of a familiar terrain. Shaded area is trees, open area is grass. Contour lines show elevations in meters. Polar histograms show vanishing bearings (with mean bearing $\pm 99\%$ confidence interval) at each of two release sites for bees that had been heading from the hive to a feeder placed at the other release site when they were caught. From each release site, bees might fly towards the hive (H), towards the current feeding site (F) or in the compass direction that they were about to fly when they were captured (C). From site A, bees had a view of landmarks that they could see along their current foraging route (from the hive to site B) and they were able to compensate for the displacement by heading directly towards site B. From site B, by contrast, bees could not directly see any landmarks associated with their current foraging route. These bees were unable to compensate for their displacement by selecting a course for the food. They headed homewards instead, suggesting that they were familiar with the landmarks at site B, but had not encoded these landmarks into a usable metric map of the positions of site A, site B and the hive. See Dyer (1991) for details.

(for a review, see Wehner, 1984). For navigation on the scale of the home range, this means compensating for the rotation of the azimuth relative to landmarks and routes traveled between the nest and food. What makes this task particularly challenging is that the azimuth changes at a variable rate over the day; the rate of change is slow as the sun rises in the morning and sets in the evening, and rapid as the sun crosses the local meridian at midday. Furthermore, this pattern of daily change, or the solar ephemeris, varies with season and with latitude.

Honeybees deal with these challenges by learning the current local ephemeris during their early experience as foragers (Lindauer, 1959). The spatial frame of reference for detecting and learning solar movement is probably the panorama of landmarks surrounding the nest (Dyer and Gould, 1981; Dyer, 1987), and the temporal reference is provided by

the bees' endogenous time sense, which is entrained by the light-dark cycle (reviewed by von Frisch, 1967). The question I want to deal with here is how bees learn such an apparently complex pattern.

One way to solve the problem of learning the sun's course would be to compile in memory a list of time-linked solar positions observed during the day. Since the 1950s, however, we have known that many species behave as if they can estimate the solar azimuth at times of day (or night) when they have never seen it. For example, Lindauer (1959) reared honeybees in an incubator and exposed them only to the afternoon course of the sun while training them to find food in a particular compass direction. When he opened the hive for the first time in the morning (in a novel terrain so that the bees could not use familiar landmarks for navigation), bees with several days of flight experience in the original terrain searched for food mainly in the compass direction in which they had been trained. Other studies have revealed an ability to estimate the sun's position at night by the European honeybee *Apis mellifera* (Lindauer, 1957), Saharan desert ants *Cataglyphis* sp. (Wehner, 1982) and the Asian giant honeybee *A. dorsata* (Dyer, 1985). Thus, the learning processes underlying the development of the sun compass in these species allow the animals to fill in gaps in their experience of the sun's course.

Most attempts to explain such behavior have assumed that the animals somehow measure the sun's position, and perhaps its rate of movement, at times of day when it is visible and then derive from these observations a uniform rate of shift of azimuth which can be used to estimate the sun's course during a time when it has not been seen. Three specific computational hypotheses have been advanced: (1) bees might 'interpolate' at a uniform rate to find the sun's position between two known positions (New and New, 1962; Wehner and Lanfranconi, 1981); (2) they might extrapolate forward in time from the sun's position and rate of movement as measured at earlier times of day (Gould, 1980; Dyer, 1985); or (3) they might extrapolate 'backwards' from the sun's position and rate of movement at later times of day (as observed on previous days) (Dyer, 1985). Of these, the interpolation hypothesis was best supported by data, but the two extrapolation models could not be excluded as explanations for certain results. Some data, such as Lindauer's (1959) original results, were consistent with more than one model.

To decide among these hypotheses, Dyer and Dickinson (1994) developed an approach that exploited the dances of bees to infer how they estimated the course of the sun at times of day when they had not seen it. We allowed incubator-reared bees to see a small portion of the sun's course in the late afternoon each day. During this period, we trained the bees to a feeding site. Otherwise we denied the bees an opportunity to fly or to see the sun, although we exposed them to a normal light-dark cycle to avoid disrupting their sense of time. To find out how these bees estimated the morning and midday course of the sun, we allowed them to fly in the morning only when the sky was overcast and observed their dances when they returned to the nest from the food. The dance indicates the

angle of flight relative to the sun and thus reflects the bees' knowledge of the sun's position. Clouds deny bees a view of celestial orientation cues and thus prevent them from measuring the sun's position directly (Dyer and Gould, 1981). To perform dances on cloudy days, bees that have been exposed to the sun's full course use a memory of the sun's changing position relative to familiar landmarks (Dyer, 1987). We challenged the bees to estimate the sun's position relative to familiar landmarks in cloudy weather at times of day when they had never seen it, and we assumed that their dances would reflect how they made this estimate.

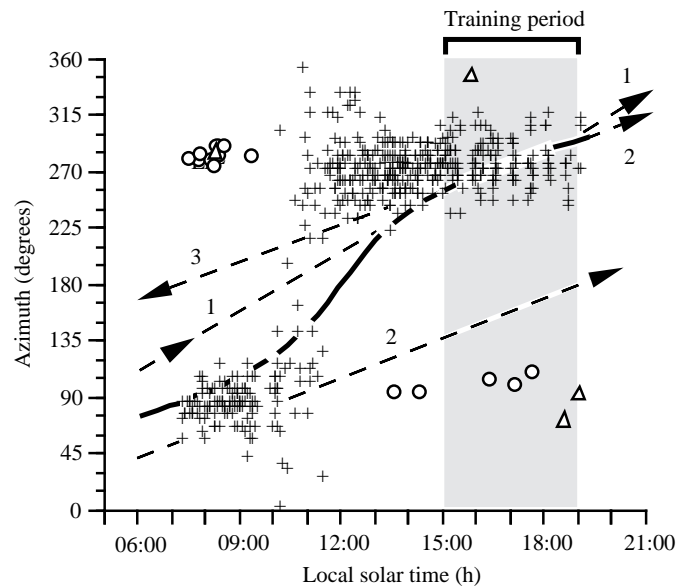


Fig. 3. Solar positions estimated by partially experienced (incubator-reared) bees during an entire cloudy day. The heavy curving line shows the actual course of the solar azimuth. The bees had previously only seen the sun during the late afternoon, from 15:00 h to approximately 19:00 h (sunset). When they flew for the first time in the morning, the sky was cloudy; hence, celestial cues remained obscured. To set a dance angle, they had to estimate the sun's position by compensating for its movement since they last saw it. Each symbol is the solar azimuth inferred for a single dance. We recorded a total of 554 dances by 46 different bees. Most bees behaved during the morning as if they expected the sun to be about 180° from where they saw it the previous afternoon and then abruptly switched to the use of the afternoon azimuth at midday. The mean azimuth (\pm S.D.) inferred from dances performed before the midday transition was $88 \pm 14^\circ$ ($N=109$). The mean azimuth inferred from dances after the midday transition was $277 \pm 18^\circ$ ($N=350$), a change of 189° (or 171°) from the morning angle. The open symbols show the data from two bees that departed qualitatively from this basic pattern, starting with the afternoon angle and then switching to the morning angle (see Dyer and Dickinson, 1994). The dashed lines show the predictions of three different computational mechanisms that have been proposed to underlie the ability of bees to fill gaps in their experience of the sun's course: (1) linear interpolation between the sun's positions at sunset and at the beginning of the training period; (2) forward extrapolation of the sun's rate as measured at sunset on the previous days; (3) backward extrapolation into the morning hours of the sun's rate as measured at the beginning of the training period on previous days.

These experiments yielded a striking result (Fig. 3): none of the three previously proposed computational models was adequate to account for dancers' cloudy-day estimates of the morning and midday course of the sun. Instead, with remarkable consistency among bees, dancers used a solar azimuth in the morning that was approximately 180° from the azimuth that they had learned on previous afternoons. They maintained this dance angle until midday, when they changed their dances by approximately 180° and began using the afternoon angle. Thus, rather than using a particular constant rate of solar movement to estimate the sun's course during the time when they had not seen it, the dancers behaved as if they used an innate, approximate representation of the sun's actual non-linear pattern of movement during the day. In the approximate ephemeris, as in the real one, the sun rises in the direction opposite from where it sets, the azimuth changes relatively slowly during the morning and during the afternoon, and it moves from the eastern to the western half of the sky at midday. Initially this approximate ephemeris resembles a 180° step-function. As bees acquire experience with the sun at other times of the day, however, they develop an internal representation that more closely conforms to the real ephemeris (see Dyer and Dickinson, 1994). Essentially the same phenomenon has been implicated in a study of *Cataglyphis* ants (Wehner and Müller, 1993).

These studies suggest that bees and ants are equipped with an innate template that specifies the approximate dynamics of solar movement over the day and that is modifiable with further experience. This offers them a fairly accurate and computationally undemanding mechanism for estimating the sun's course even if they have sampled only a small portion of it. Indeed, in the tropics, where honeybees evolved, this template closely matches the actual course of the sun and would scarcely need to be modified as bees acquire additional experience during the day. Furthermore, because the bees' innate ephemeris approximates the actual pattern of solar movement as observed at any latitude or any season, it could simplify (and speed up) the process by which an individual insect learns the current local solar ephemeris.

This new model not only accounts for the results of the recent studies of bees (Dyer and Dickinson, 1994) and ants (Wehner and Müller, 1993) but is also consistent with data that have previously been explained by the interpolation (New and New, 1962; Wehner and Lanfranconi, 1981; Wehner, 1982) and extrapolation (Dyer, 1985) hypotheses. Further studies are needed to evaluate whether these other mechanisms are actually involved in the development of the bees' memory of the sun's course.

Integration of celestial and landmark references

The two previous sections have dealt separately with each of the honeybee's two principal reference systems – celestial cues and landmarks. Experienced bees can use these reference systems independently to obtain directional and positional information during a foraging flight. As mentioned, they can

use the celestial compass for maintaining a compass course and for path integration even when in unfamiliar terrain. Also, by using familiar landmarks, bees can find their way on completely cloudy days, when the celestial reference is unavailable. However, although celestial and terrestrial cues can be used independently, the two systems sometimes operate in concert. We have already seen that the visual panorama provides bees with the frame of reference for learning the sun's pattern of movement, and that once they have learned this relationship, they can exploit it for dance communication on overcast days (Dyer and Gould, 1981; Dyer, 1987). Recent work has focused on the question of whether bees use the memorized relationship between landmarks and the celestial compass for orienting their movements through the environment, analogous to the way that birds have been found to integrate different references (e.g. magnetic compass and celestial cues) during navigation (Able and Able, 1990).

The ability to exploit the memorized relationship between landmarks and celestial cues would be very useful when landmarks provide ambiguous navigational information by themselves and when the ambiguity could be resolved with the help of the celestial compass. Recent experiments have shown that bees apparently do consult their celestial compass when using landmarks to guide the final approach to food, but do not do so when using landmarks for the large-scale task of setting a homeward route.

To begin with the small-scale task, consider a bee that has to learn to find food relative to a symmetrical landmark such as a single tree in an open field. An egocentrically recorded visual image of such a landmark does not unambiguously specify the location of the food; at best, the landmark specifies an annulus of surrounding locations from which the landmark appears the same. Lindauer (1960) found that honeybees can use a symmetrical landmark to pinpoint a feeding site unambiguously, and he suggested that bees might refer to a compass reference to do so. Dickinson (1994) has recently provided direct evidence that they use the celestial compass in this task; on sunny days bees found the position of the food, but on cloudy days they searched randomly around the landmark. Collett and Baron (1994) found that bees use a magnetic field for the same task.

These results might be interpreted as evidence that bees do encode their memory of landmarks in an allocentric frame of reference, explicitly recording the compass bearing of the food relative to the landmark (Gallistel, 1990). This would allow them to use the landmark to find the food independently of how the image of the landmark projected to their eyes. However, Collett and Baron's (1994) observations suggested that bees use the compass reference in a simpler way. They found that bees searching for food adopted a characteristic orientation (usually facing south) relative to the compass reference. Their interpretation was that bees do this to standardize the viewing angle from which they record, and later use, an egocentric snapshot of the landmark as they approach the food. With a constant body orientation, bees can find the food unambiguously by matching their current view of a single

landmark with a retinally localized image recorded on previous visits. Thus, there is no reason to assume that the compass reference is used to provide an allocentric coordinate system to record the spatial arrangements of landmarks independently of how they project to the eyes.

For the large-scale task of selecting a homeward course relative to an ambiguous landmark, bees seem not to consult their celestial compass at all, even when they would benefit by doing so (F. C. Dyer, in preparation). I trained bees to use two differently oriented lines of trees to fly home from distinct locations in a familiar terrain. I then displaced the bees to a novel terrain containing a line of trees that resembled each of these familiar lines of trees and, hence, that was ambiguous as a source of navigational information. The test tree line was parallel to one of the training tree lines, however, and thus bees could have used it to set an unambiguous course if they could recognize its compass orientation. Bees were confused by this task on both cloudy and sunny days, suggesting that they could use neither celestial cues nor any other compass reference in conjunction with their memory of the landmark.

Thus, bees have a rather limited ability to exploit the relationship between celestial cues and large-scale features of the terrain for navigation. That they cannot do it at all for setting a course to a distant goal suggests that they lack a way to organize their memory of large-scale landmarks in an allocentric coordinate system of the sort advocated by Gould (1986).

Conclusions

The research reviewed here shows that the impressive navigational abilities of honeybees are based on a minimalist cognitive architecture. The spatial relationships among locations in the foraging range, as well as the spatiotemporal dynamics of solar movement, appear to be encoded in highly simplified formats, with only partial integration of information derived from these two important reference systems. The apparent simplicity of these insect systems may be advantageous because they impose low computational demands on an animal whose capacity for processing spatial information is presumably constrained by its small nervous system (Wehner, 1991). Another possible advantage of simpler representational mechanisms, however, is that they may allow more rapid learning of useful navigational information than mechanisms that encode more complex spatial relationships in the environment. Mechanisms that allow rapid development of spatial memory would be highly beneficial to a short-lived animal like a honeybee, which collects food for its colony for only about 10 days before it dies.

Lest we too readily dismiss the bees' 'small-brained' learning strategies, I would like to emphasize some remarkable properties of the bees' navigational and learning abilities. In using familiar landmarks to compensate for displacement from their current foraging route, bees choose an appropriate response, flying towards the food if they can see landmarks associated with their current route and flying towards home if

they cannot (Fig. 2), and they make this decision very rapidly. Bees generally select a course within 5 s of their release (Dyer, 1991). Clearly the underlying spatial information is encoded in memory in a highly accessible manner.

Even more remarkable to me is the ability of bees and other insects to fill in unknown portions of the sun's course (Fig. 3). This highlights the limitations inherent in the common conception of insects as simple robots whose learning abilities are restricted to the formation of associative links between sensory stimuli and motor responses. To explain the bees' ability to learn the sun's course we have to postulate internal computational processes that organize (incomplete) sensory information into a coherent model of the environmental pattern. Path integration (Müller and Wehner, 1988) illustrates the same point (see Gallistel, 1990; Dyer, 1994). Such behavioral abilities amply justify efforts to develop neuroscientific theories that account for cognitive abilities in insects as well as in vertebrates (Gallistel, 1990; Churchland *et al.* 1994).

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