How honeybees find a place:
Lessons from a simple mind

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Foraging honeybees find their way from their hive to their food in a stereotypical manner using up to four place-finding servomechanisms in sequence: (1) They first fly a vector (straight-line distance and direction) from their home to the vicinity of the target. Direction is determined by the sun compass and by distant landmarks, while distance is estimated by visual flow. (2) They then beacon in on a landmark near the target location. (3) En route toward the landmark, they may adopt a sensorimotor trajectory that takes them toward the target. (4) Near the expected target location, they attempt image matching, which involves trying to put surrounding landmarks at the correct positions on their eyes. In doing image matching, they fly facing a stereotypical direction, a strategy that makes it unnecessary to translate retinal coordinates into another coordinate system.

The honeybee is a eusocial species (Seeley, 1985, 1995; von Frisch, 1953). Reproductive labor is divided within the colony. One bee, the queen, has the sole job of laying eggs for future generations. The vast majority, the workers, are infertile females who do the rest of the work necessary to raise the young and keep the colony viable. Each worker does all the necessary jobs, at different stages of its life, a pattern known as *age polytheism*. The jobs include cleaning the cells, feeding and capping the brood, attending the queen, grooming and feeding nestmates, ventilating the hive, receiving nectar and pollen, and, last but not least, foraging (Seeley, 1985, 1995). How and why a worker bee decides to forage is a complex process, as is the question of what the bee forages for (nectar, pollen, or water). These topics have been amply reviewed by Seeley (1995). Foraging is usually the last job in the worker's life. From the viewpoint of animal learning and behavior, it is the job that is the most studied. A comprehensive overview of the learning capabilities of the worker bee has appeared recently in this journal (Bitterman, 1996).

Getting to previously visited locations is an important problem in the lives of many animals. Research on ways of finding places has been amply reviewed recently, in a special journal issue (Wehner, Lehrer, & Harvey, 1996), a book on spatial cognition (Healy, 1998), and review chapters in books on animal cognition (Gallistel, 1990; Roberts, 1998; Shettleworth, 1998; Vauclair, 1996). The neuroethology of spatial cognition in bees has been reviewed recently by Capaldi, Robinson, and Fahrbach (1999). I aim to present here the basic story of how one creature does its place-finding job, elucidating the steps start to finish. The review will draw together research on different aspects of navigation, done by different researchers.

Place-finding is an essential task for the survival of the beehive. As is often done when animals confront a complex task, the job is broken down into a series of subproblems, each of which is simpler to solve. The worker bee forages by following a series of place-finding servomechanisms. A place-finding servomechanism (Cheng, 1995) contains a specification of the goal (G) that can be considered as the target that the system "aims for" (Figure 1). Different servomechanisms specify the goal in different terms. The system also takes a "reading" of the animal's current position (P), which is specified in the same terms as G. Comparing the two gives a measure of error (P − G). The system moves the animal so as to make P match G. At that point, the servomechanism has done its job, and the next system can take over. The last servomechanism brings the animal right to its target.

Four kinds of servomechanisms have been identified in research so far. Together, they take the bee from its hive to its foraging spot (Table 1). The first step is to get to the region of the food source. This is done by following a vector or route. The bee attempts to fly a particular distance in a particular direction. The goal is thus specified in terms of a direction and a distance to be covered from exiting the hive. This requires determining direction and measuring distance traveled en route. The second step is to use nearby landmarks to get near the food source. The bee heads toward or beacons in on identified landmarks near the target. The third servomechanism, used optionally, is striking another vector, this time a much shorter sensorimotor trajectory. It is called sensorimotor because a visual input, a particular view of the landmark toward which the bee is beaconing, triggers a motor output, the vector that should take the bee toward the expected target location. If the bee can spot the target, typically a small dish of sugar water in experimental foraging situations, the bee beacons in on that. If the target cannot be seen, as on
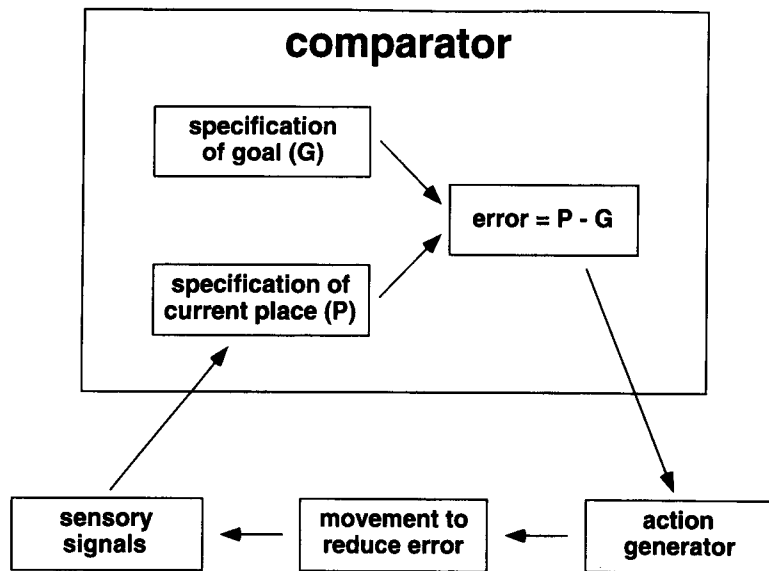
Figure 1. A place-finding servomechanism compares a specification of the goal location (G) with a "reading" of the current position of the animal (P). The system reacts so as to reduce the difference between P and G.

tests in experiments in which the reward has been temporarily removed, the fourth servomechanism, image matching, is called upon. The bee does basically two things in image matching: flies facing a stereotypical direction and attempts to put nearby landmarks at the correct retinal position. The goal is specified in terms of where landmarks should appear on the eye. The correct position is the position at which the landmark was seen when the bee was at the target, facing the direction it has adopted. Because the bee flies facing one direction, correct retinal positions of landmarks specify the correct positions of landmarks in the world. This stratagem bypasses the need to translate retinal coordinates of landmarks into some other coordinate system and demonstrates one simplifying tactic adopted by foragers.

What follows are expanded discussions of these servomechanisms, concluding with some reflections on what they imply about learning and other aspects of cognition. The review concentrates on how the bee gets to a chosen target, visited on previous occasions, and not on how the bee chooses one location over another. The choice behavior of honeybees has been reviewed by Bitterman (1996). Good evidence from different areas of behavioral research on the honeybee can be presented for each of the servomechanisms in Table 1. What I am claiming in this review, over and above the evidence, is that these servomechanisms are used sequentially to accomplish that task, completing a logical story. Two reviewers took me to task on this point, and rightly so. I have little to say on how one servomechanism gives way to another. Empirical evidence on transitions between servomechanisms and on conditions under which each servomechanism is called into play is lacking. The theme of transitions should form a focus for future research.

FOLLOWING A ROUTE RATHER THAN A MAP

In a paper published in *Science*, Gould (1986) claimed that honeybees possessed a cognitive map of their familiar terrain. What was meant was that they could chart their way from any point in their territory to any other point. The evidence provided was the ability to make a detour. The foragers were first trained to fly from their hive (H) to one of two different feeding stations, A or B. The two feeding stations differed in their direction from H. The crucial detour tests came when Gould captured bees en route from H to A and transported them in a dark container to B. These bees, when released at B, flew in the direction B → A. Bees en route to B and derouted to A likewise flew in the direction A → B. The interpretation was that the bees have a map-like representation of the three points, A, B, and H, and could figure out the path from A to B or from B to A.

Since Gould's (1986) paper, a number of failures to replicate the results have been reported (Dyer, 1991; Wehner, Bleuler, Nievergelt, & Shah, 1990; Wehner & Menzel, 1990). A more accepted interpretation now is that landmarks near A or B, visible from a distance, guided Gould's bees to the correct route between A and B. Dyer (1991) replicated Gould's experiments closely in another setting. A was up a hill from B. From A, landmarks near B were visible. From B, however, nothing near A was visible. The detour experiment produced asymmetric results. Bees en route to B and derouted to A headed off in the direction of B. Bees en route to A and derouted to B, however, did not head to A. They either continued in the direction they were heading in (that is, on a course parallel to H → A) or else flew homeward. In separate experi-

Table 1
Servomechanisms Used by the Honeybee to Find a Place

Servomechanism	Brief Description	Requirements
Route or Vector	Fly in a particular direction for a particular distance from the hive	Remembering vector Determining compass direction Measuring distance flown
Beacon	Fly toward a landmark near target location	Identifying a landmark Approaching a landmark
Sensorimotor Trajectory	Take a particular trajectory with a particular view of the beacon being approached	Remembering vector Measuring direction Measuring distance
Image Matching	Put surrounding landmarks at the correct retinal positions	Remembering landmark positions and features Adopting a particular direction to face while flying Determining distance and direction to landmarks

ments, Wehner and Menzel (reported in Wehner et al., 1990; Wehner & Menzel, 1990) also failed to replicate Gould's results (but see Menzel, Geiger, Jeorges, Müller, & Chittka, 1998).

Thus, the current thinking is that honeybees learn a number of routes that take them between their hive and foraging spots but that they do not compute new routes based on the trigonometry of known points within their territory. A route amounts to a vector, which specifies a direction and a distance from one's starting point to one's destination. Shettleworth (1998) comments, however, that a network of routes of sufficient complexity may be hard to distinguish empirically and conceptually from a "cognitive map." Nevertheless, that bees can fly vectors is not in doubt. A vector consists of a direction and a distance to a food source, the information communicated in the honeybee's famous dance (Seeley 1985, 1995; von Frisch, 1953). Evidence has accumulated on how bees determine the direction and distance flown en route.

Telling Direction:
Use of Sun Compass and Landmarks

The use of the sun compass by hymenopterans is well known. The strategy is to tell which direction is which by the position of the sun. The sun itself is not necessary for the job; in fact, any patch of blue sky will do. Ants and bees can perceive polarized light scattered by the atmosphere through which sunlight passes. The story of how insects perceive polarized light has been worked out in great detail, from the molecular to behavioral and computational levels (for review, see Wehner, 1994). I will mention only some highlights here. Special sensory machinery is devoted to the problem in bees and ants; receptors on the dorsal part of the eye are dedicated to perceiving polarized light. The system capitalizes on the angle of polarization, or e-vector orientation, which provides the most precise information. Because the system looks

at a pattern spread over the entire expanse of blue sky, it is more accurate than using only the sun itself, as has been demonstrated in behavioral experiments. Physiologically, an opponent process system has been identified in the cricket. Within the polarization sensitive area, photoreceptors sensitive to orthogonal directions of e-vector are found together, and polarization-opponent interneurons analyze direction channels of e-vectors (Labhart, 1988). This opponent process system, like other opponent process systems in vision, neutralizes the effect of overall light intensity. In this way, increasing or decreasing overall intensity will not bias the system to perceive one e-vector direction over another, and the system is more sensitive to the e-vector direction itself.

A little thought will reveal that perceiving the direction of the sun is hardly enough to figure out which direction is which. The sun changes position during the course of the day and is also at different positions at different times of year. The honeybee thus needs two more ingredients to use the sun compass: The bee has to have a circadian clock to tell what time of day it is and has to learn from experience where to expect the sun at different times of day. The function relating the azimuth of the sun to the time of day is called the *ephemeris* function. Recent research indicates that the honeybee has some innate assumptions about the course of the ephemeris function (Dyer, 1996; Dyer & Dickinson, 1994, 1996).

Dyer and Dickinson (1994) gave an experimental hive foraging experience only late in the afternoon for a number of days. To keep the hive attuned to the circadian cycle, the bees were exposed to diffuse light during the rest of the daylight hours but were kept from flying out of their hive. On the crucial test day, foragers were allowed to forage at a feeding station in the morning, under completely overcast conditions. The dances of these foragers were used to assay where they "thought" the position of the invisible sun should be during the course of the day.

The researchers found a step function. During the morning, the foragers indicated east, or 180° opposite the position of the sun that they experienced late in the afternoon. During the afternoon, the foragers indicated west. Similar results have been found for desert ants of the genus *Cataglyphis* (Wehner & Müller, 1993). This step-function ephemeris is roughly the course of the sun at the equator. With some experience of the sun throughout the course of the day, however, the insects do learn the entire course of the ephemeris (Dyer & Dickinson, 1994). How much and what kind of experience is needed to learn the entire ephemeris is still an interesting question to be addressed.

The sun compass is not the only way that the honeybee tells direction. This is to the bee's advantage because completely overcast days do occur. Dyer and Gould (1983) found evidence that honeybees also use prominent landmarks to tell which direction is which. Their bees were trained to fly along a line of trees to a feeder. Overnight, the landmark array was transformed by moving the hive to a different location. The line of trees now ran almost in the opposite direction. Feeders were set up in the original sun-compass direction and at the new landmark-based direction. Dyer and Gould reported that 80% of the foragers followed the line of trees rather than the learned compass direction on a sunny day and 100% followed the line of trees on an overcast day. Further evidence from overcast days also indicated that the bees remembered which direction was associated with the line of trees. After visiting the new feeder, the foragers' dance indicated the original direction in which the trees ran the day before. Dyer and Gould assumed that the bees had associated directions of the ephemeris with distant landmarks in the panorama about the hive.

The landmarks used to tell direction may have to be very prominent. Chittka and Geiger (1995) used a small number of tents as landmarks guiding honeybees to a feeder. If the direction of the line of tents from the hive were shifted by even 22.5°, however, the bees did not follow the tents but instead flew in the compass direction that they had learned to fly to the feeder. Presumably, a line of many trees is more prominent than a small number of tents. But more research is required to find out what landmarks honeybees will use to tell direction.

Measuring Distance Flown: Use of Visual Flow

A second component of a vector is distance. Honeybees communicate the distance to a food source by the duration of the waggle during their waggle dance (Seeley, 1985). Classic thinking was that bees measure the distance that they have traveled by the energy expended en route. One piece of evidence in favor of the energy hypothesis is what foragers communicate to their hive mates about food sources uphill versus downhill from the hive. At the same distance, an uphill site is communicated as farther than a downhill site. Recent evidence, however, has contradicted the energy hypothesis and instead found

that the honeybee uses mainly visual flow (Esch & Burns, 1995; Srinivasan, Zhang, & Bidwell, 1997; Srinivasan, Zhang, & Lehrer, 1998; Srinivasan, Zhang, Lehrer, & Collett, 1996). Visual flow is also used by desert ants, although not exclusively (Ronacher, Gallizzi, Wohlgemuth, & Wehner, in press; Ronacher & Wehner, 1995), and by walking bees (Schöne, 1996). We shall see shortly how the visual flow hypothesis accounts for the uphill/downhill results.

What is meant by using visual flow is integrating the velocity of the flow of visual texture over time as one flies. The integration of velocity over time delivers a measure of distance. What the hypothesis predicts is that the distance estimated depends a great deal on how near the objects are that are flowing by. Imagine using the flow of vertical objects, such as a line of trees to one's side. The closer one flies to the line of objects, the faster the velocity of visual flow for a given speed of flying, and, thus, the greater the distance estimate based on visual flow.

Esch and Burns (1995) used this logic in a clever experiment that pitted the energy hypothesis against the visual flow hypothesis. They trained foraging bees to obtain food from a feeder on a hot-air balloon. They measured what distance the foragers communicated to their hive mates. Then, gradually, they lifted the balloon off the ground, forcing the bees to fly higher and higher to get to the food source. According to the energy hypothesis, the higher the balloon, the greater the energy needed to get to the food, and the greater should be the distance estimate. According to the visual flow hypothesis, however, the prediction is the opposite: the higher the food source, the higher the bees fly, the less the visual flow, and, thus, the less the distance estimate. The results clearly supported the counterintuitive predictions of the visual flow hypothesis: Foragers communicated a shorter distance to their hive mates when the food source was lifted off the ground. The same visual flow hypothesis can explain the results of flying uphill versus downhill. When flying uphill, foraging bees tend to fly closer to the ground than when flying downhill. This increases the visual flow and, thus, their distance estimates.

The most detailed and careful studies on distance estimation, or odometry, come from the "tunnel" experiments of Srinivasan and colleagues (Srinivasan et al., 1997; Srinivasan et al., 1998; Srinivasan et al., 1996). A photograph of the tunnel is shown in Figure 2. The top of the tunnel was covered with clear Perspex. The bees' task was to enter the tunnel and fly a specified distance to find their food reward. The distance to be estimated remained constant from trial to trial, but the tunnel was shifted about the climate-controlled greenhouse serving as the lab in order to prevent the bees from using landmarks in the lab to do the task. Visual texture (e.g., the random patterns of black and white squares shown in Figure 2) or vertical stripes on the walls of the tunnel provided stimulus for estimating visual flow. After training, the bees were occasionally tested individually with the feeder absent in a
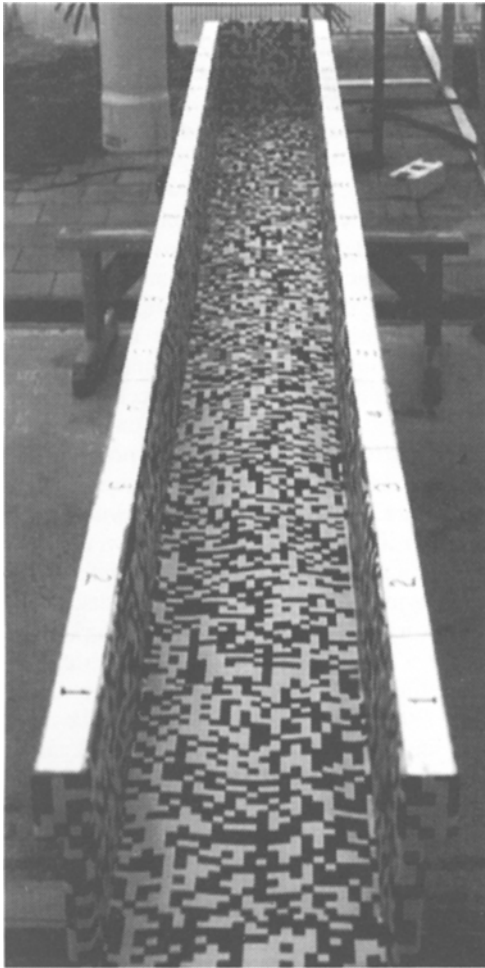
Figure 2. Photograph of tunnel used by Srinivasan and colleagues (Srinivasan et al., 1997; Srinivasan et al., 1998; Srinivasan et al., 1996) for experiments on how honeybees estimate distance traveled. Photograph courtesy of M. V. Srinivasan.

the tunnel. The bees showed dramatic failure to estimate distance: They flew back and forth from end to end under such conditions.

Two other points about the tunnel experiments are of interest. If we consider just the positions of the first two turns made by the searching bees, the standard deviation (across trials) of the positions of the turns are proportional to the means across different training distances (Cheng, Srinivasan, & Zhang, 1999). The same is true of the average of the first two turns (middle) and difference between the first two turns (spread): For each variable, the standard deviation is a proportion of the mean. Thus, error in estimating distance is proportional to the distance traveled. In other words, honeybee odometry obeys Weber's law. The same law is found in the peak procedure used to study interval timing in vertebrates, such as pigeons (Cheng & Miceli, 1996), rats (Church, Meck, & Gibbon, 1994), and humans (Rakitin et al., 1998). Weber's law is also found in the human perception of a number of sensations, such as the intensity of light, sound, pressure, and warmth (Schmidt, 1981, pp. 15–21).

Another inspiration from interval timing was the bisection task (Srinivasan, Zhang, Berry, Cheng, & Zhu, 1999). In a bisection task, the subject has to make one response to a long stimulus and make a different response to a short stimulus. In our task, the distance that the honeybees had to fly down the tunnel provided long and short stimuli. They flew either a long distance or a short distance before they met two potential feeders, one on the right and one on the left. If the bees flew a short distance down the tunnel, they had to visit the feeder on the left (the right one being blocked off); if they flew a long distance, they had to visit the feeder on the right. After training the bees, we tested them at a number of intermediate distances, with both response choices unrewarded. Analogous tasks have been conducted on vertebrates with durations of time serving as stimuli (e.g., Meck, 1983; Platt & Davis, 1983; Wearden, 1991). An interesting question is what the bees perceive as exactly midway, the "point of subjective equality," at which they choose equally between the right and left choices. In our experiment, the bees' percentage of "long" choices varied linearly as a function of distance with the subjective midpoint at the arithmetic average of the long and short training distances. This indicates that the honeybees measure distance flown on a linear scale. A similar linear relation is found between distance and waggle duration in the waggle dance (Seeley, 1985), so that it appears that distance is also communicated on a linear scale.

BEACONING

Beaconing is also known as *telotaxis*. The term *telo* means goal, and the strategy is one of zeroing in on a recognized landmark. Some examples from my lab are shown in Figure 3. Honeybees were trained to find a cap full of sugar water at a constant distance and direction

fresh tunnel. On such tests, the bees would fly down the tunnel for about the distance of the expected food source and then turn back. The bees would turn back and forth a number of times. Srinivasan and colleagues estimated searching distance from the positions of the first four turns. Manipulations were made on tests to figure out what cues the bees were using to estimate distance (Srinivasan et al., 1997).

Manipulations included changing the size of the entrance, adding tailwind or headwind, changing the width of the vertical stripes on the wall, and changing the width of the tunnel. Only changing the width of the tunnel significantly affected the search distance. In concordance with the visual flow hypothesis, the narrower the tunnel, the shorter the distance that the bees flew.

A further manipulation tested whether visual flow was necessary for doing the task. The authors removed visual flow by making the stripes run axially down the length of
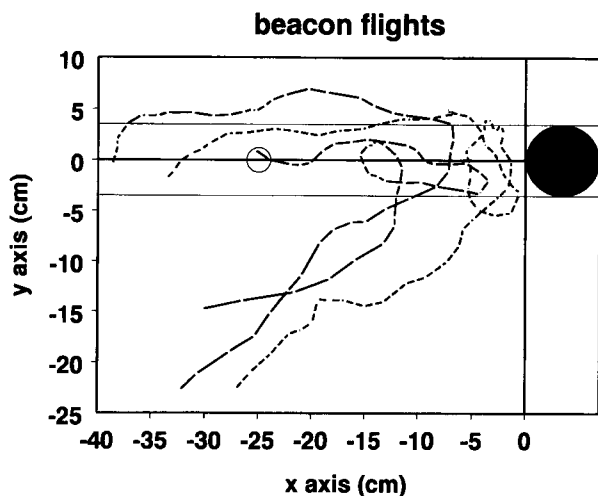
beacon flights

Figure 3. Beaconing followed by sensorimotor vectors, from 3 honeybees in my lab. The bees were trained to find food at the location marked by the small circle. The food dish stood on a strip of yellow cardboard running the length of the table. The dish was at a constant distance and direction from a blue cylinder serving as a landmark (large filled circle). The position of the landmark–target array changed from trial to trial during training. In searching for food, the honeybees typically first approached the landmark (beaconing) and then veered away from it toward the target (sensorimotor vector).

from a cylinder serving as a landmark. The direction of the food from the landmark was indicated by a strip of colored cardboard. The location of the entire array, however, varied from trial to trial, making the cylinder the only valid predictor of the exact location of the reward. In searching for the sugar water, the honeybees often flew first toward the landmark (beaconing) and then, turning near the landmark, flew toward the feeder (sensorimotor vector, described in the next section).

Collett and Rees (1997) set a feeder near some landmarks (e.g., a cylinder and a cone) outdoors and attracted nearby wasps and bees to it. The hymenopterans can be observed heading toward one or the other of the landmarks in one stage of their search for food. In their study as well, the array of landmark and target was moved about a small area from trial to trial. Collett and Rees noted that the approach was stereotypical. The insects tended to approach from a stereotypical direction and to be facing a stereotypical direction when doing so. This is perhaps not surprising because the nests of the animals were at roughly a constant direction and distance from the food source, the distance over which the array was moved being small in comparison with the distance from nest to food. Under different test conditions, however, this stereotypicality is lost (Cheng, 1999b). The bees entering my lab first had to go through a small opening to get into the lab. The table that served as the arena was then a meter or so away, and the food location could vary over the surface of the table. Thus, the location of food varied a good deal from the vantage point of the entrance to the lab. The

bees in my lab did not take a stereotypical approach. They tended to loop around over the table and approach from various directions from trial to trial.

How Landmarks are Identified

Beaconing means approaching a recognized object. The object must be recognized on some sensory basis. It appears that color cues are prominent for landmark identification and that different cues are used at different distances to the landmark, with distance defined not by physical distance but by the retinal angle projected by the landmark. But context cues also play a role in landmark identification: Sometimes, the correct landmark is some object in approximately the right place.

Cheng, Collett, and Wehner (1986) trained bees to distinguish two arrays of landmarks composed of the same elements in different arrangements. For example, when a blue cylinder was north of a yellow cylinder, the food was between the two landmarks. But when the yellow cylinder was north of the blue cylinder, the food was to the east of the array. The bees solved these discriminations.

The sensory characteristics of landmarks, however, are not the whole story. The region in which the landmarks are found, the context, also matters. Collett and Kelber (1988) trained honeybees to search at two different locations with respect to two different landmark arrays: one composed of blue triangles on end, and the other composed of yellow cylinders. During training, each array was always found in one context. On crucial tests, a training array was placed in the "wrong" context, putting the dictates of the context in conflict with the dictates of the perceptual characteristics of the landmarks. When the two contexts were inside identical-looking huts, presumably indistinguishable to the bees, the bees followed the dictates of the landmarks. If the yellow landmarks were put in the wrong hut, they still searched in the appropriate location for the yellow landmarks. But if the contexts were two open platforms outside, clearly distinguishable to the bees, the bees followed the dictates of the context. If the yellow landmarks were on the wrong platform, they were treated as if they were blue triangles. Thus, landmarks may be identified by context, as those that belong in a particular region, irrespective of their perceptual characteristics. That the context primes the landmark memory to be retrieved is supported by more recent research (Collett, Fauria, Dale, & Baron, 1997). Many questions about the role of the context, however, require further research. Such questions include the following: What exactly constitutes a context for the bee? What aspects of the context trigger memory retrieval? How is memory triggered?

Chromatic and Achromatic Cues at Different Distances

Recent work by Giurfa and colleagues shows that honeybees use different cues at different distances as defined by the retinal size projected by the stimulus (Giurfa & Vorobyev, 1998; Giurfa, Vorobyev, Brandt, Posner, &

Menzel, 1997; Giurfa, Vorobyev, Kevan, & Menzel, 1996). Giurfa and colleagues used a two-choice discrimination procedure in a Y-maze. The bees entered one arm of the maze to the center, from which they could view one stimulus down each arm of the maze. One stimulus, the S+, was always rewarded, and the other stimulus, the S−, was never rewarded. S+ and S− changed positions from trial to trial. The characteristics of the stimuli were carefully chosen to provide differences only in certain respects.

Giurfa et al. (1997) took advantage of the fact that the bee's visual system contains two subsystems: one color system based on two pairs of opponent processes (Backhaus, 1991), and another achromatic system based on just one receptor type, the "green receptor" with maximum sensitivity in the green range (green to human eyes). The color opponent system functions much like the opponent processes system in human color vision. The green receptor comprises ~75% of the visual receptors and is used as a color-blind system, independently of the other two receptor types, for some tasks of spatial vision (see Lehrer, 1994, 1996). What Giurfa et al. (1997) constructed were pairs of stimuli that differed only for one of the subsystems (the color system or the green receptors). In this fashion, they could test which system was doing the job of discrimination at different retinal sizes.

Their results showed that, below ~5° retinal size, the bees could not discriminate S+ from S− at all. Between ~5° and ~15°, it was the green receptor system that worked. Stimuli that differed only for the color system were discriminated at chance levels. Above ~15°, the green receptor system drops out, except under conditions in which the green contrast is particularly high (Hempel de Ibarra, Brandt, Giurfa, & Vorobyev, 1998), and the color system takes over the job of discrimination: Stimuli that differed only for the green receptor system were discriminated at chance levels. Thus, object detection is first done with the green receptors at a distance. Closer to the target, the object is detected by the color system. This makes functional sense, since, at a distance, it is best to use the system with the most receptors to increase sensitivity, whereas, at close range, the color of the object being approached takes on importance.

Giurfa et al.'s (1997) results suggest that the object being approached may be, in a strong sense, more than one object to the bee. The object may be encoded as multiple views. Recent evidence on wood ants also supports a multiplicity of stored views (Judd & Collett, 1998). In a simple and elegant experiment, the ants approached a cone, standing upright or inverted. At the base of the cone, food was provided. Occasionally, the ants were tested with a slanted black-and-white edge that mimicked one side of the cone. Suppose that the ant remembered a series of views of the cone, "snapshots" taken at different distances from the cone. En route to the cone, it first attempts to match one snapshot and then the next, in sequence. The behavior of ants approaching the inverted and upright cones should differ on the single-edge tests.

The snapshots of the inverted cone would always have the bottom straight ahead, at the location to which the ant is approaching. The ant should always keep the bottom of the edge straight ahead during approach. With an upright cone, on the other hand, the bottom part of the edge would appear more and more eccentrically on the eye as the ant approached. If the ant really uses a series of snapshots, it should attempt to place the single edge at a constant location on the eye, followed at some point (when the next snapshot is retrieved) by a rapid shift to place the edge on a different part of the eye. Such step functions of the location of the edge on the approaching ant's eye were precisely what Judd and Collett found.

In short, beaconing (approaching a recognized object) is multifaceted. The process could entail recognition by a monochromatic system followed by recognition by a chromatic system, the object to approach could be identified by the context surrounding the object, rather than features of the object itself, and a series of views of the object might be used to guide approach.

SENSORIMOTOR VECTOR

Approaching a landmark near one's target takes one closer to the goal, but one does not want to approach it indefinitely. At some point, this servomechanism of beaconing must give way to another servomechanism that heads one toward the goal rather than the landmark. Sometimes, but not always, this takes the form of a sensorimotor vector. This vector is much shorter than the first one that took the forager to the vicinity of the target. The sensorimotor vector is stimulus–response (S–R) behavior. It is called sensorimotor because a particular sensory view of the landmark being approached (S) triggers the vector (R), which is a particular motor trajectory that heads one toward the precise location of the target.

Honeybees can be trained to execute sensorimotor vectors. Collett and Baron (1995; Collett, Baron, & Sellen, 1996) required honeybees to fly in a particular direction for a short distance after entering an arena, in order to go through a hole leading to the next compartment. The honeybees executed the learned trajectory even on tests in which the hole was absent. This indicates that the trajectory was a vector, defined by a direction and distance from the starting point, and not by characteristics at or near the end of the trajectory. It is thought that the same kind of trajectory underlies search behavior in other experimental situations.

Collett and Rees (1997), in their setup outdoors, reported some of these sensorimotor vectors, although they did not report the extent or frequency of the behavior. The bee or wasp was usually facing a landmark head-on at the start of a sensorimotor vector. In the course of executing the vector, the view of the landmark swept from a frontal view to a lateral view.

Figure 3 illustrates examples of sensorimotor vectors. After beaconing toward the landmark used in training, the honeybees turned away from the landmark and flew toward the target. In this case, it is unclear how the vector
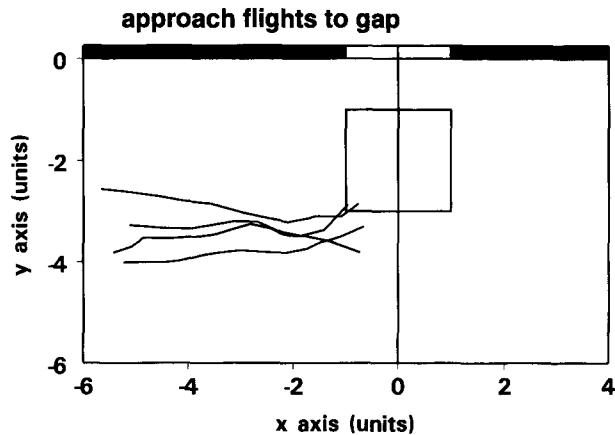
approach flights to gap

Figure 4. Characteristic approach flights of honeybees to an absent target in front of a gap in a wall 11 cm high. Target location in training was the middle of the square shown. The square was not marked. The bees would fly toward the wall and then turn and fly parallel to the wall. Only the last part of the approaches were captured on camera and translated to graphic representation. Each unit was 5.2 cm. Research reported in Cheng (1999b).

was defined. For example, the direction might be determined as a particular compass direction from the landmark or by the colored cardboard strip on the table, with the bees simply following the strip.

In my lab, whether honeybees execute stereotypical sensorimotor vectors depends on training conditions (Cheng, 1999b). Different honeybees were tested with two different setups. For the block group, a single rectanguloid block standing on edge served as the sole landmark. The target was 10 cm in front of one face of the block. For the gap group, a whole wall of blocks running the length of the table served as landmarks. The wall had a gap in it of one block's width, and the target was 10 cm in front of the gap. The location of gap or block was moved about the table from trial to trial, thus forcing the foragers to use the block or gap for precise localization. The extent of using sensorimotor vectors differed for the two groups. The "block" bees hardly exhibited any behavior identifiable as sensorimotor vectors, but the "gap" bees did the majority of times. Some characteristic approaches are shown in Figure 4. What the bees typically did was to approach the wall, and not the gap. Because the table was to the right of the entrance to the lab, they approached most often from the left (as the examples shown in Figure 4), but they sometimes approached from the right as well. Having reached about the "correct" perpendicular distance from the wall, they then flew parallel to the wall until they reached the gap. They then would search in the vicinity of the gap for the absent food dish. In this case, the term vector is not quite an accurate description. The honeybees flew in a stereotypical direction defined by the wall, but the distance to be flown was probably unspecified; rather, the bees flew until a gap was encountered. It is clear that the type and the extent of this

behavior depend a good deal on stimulus conditions. More research is needed, however, to characterize the sensorimotor vector, to determine the conditions under which it is found and to specify how and when a beaconing approach gives way to it.

Vector Averaging

As already mentioned, Collett and Baron (1995) and Collett et al. (1996) trained honeybees to execute sensorimotor vectors. The forager entered a multicompartmentalized arena and had to strike a particular vector to get through a hole to the next compartment. The reward was found in the last compartment. Each vector to be executed was also cued by a pattern of stripes on the wall, thus making it a sensorimotor trajectory. The honeybees could be trained to fly in a particular direction, to fly a particular distance, and to execute a vector (particular distance and direction).

The sensory pattern had some control over behavior. This was demonstrated by varying the pattern on some tests. For example, suppose that the bees were trained to fly to the right with stripes oriented oblique right in one compartment and to fly to the left with stripes oriented oblique left in another compartment. On an interpolation test, they might be presented with vertical stripes. The bees flew in an intermediate direction, showing orderly interpolation.

An interesting question is how the honeybees interpolate or average vectors. They have two ways of doing this: vector averaging or independent averaging (Figure 5). A vector is composed of a distance and a directional component. The components may be separately averaged, or the entire vectors may be averaged. With vectors pointing in different directions, the vector averaging gives a shorter distance than independent averaging (see Figure 5). Interpolation experiments with bees trained to execute sensorimotor vectors clearly support the hypothesis of vector averaging (Collett et al., 1996). This makes functional sense. Averaging is a form of addition: the addition of weighted elements. If one is adding a number of vectors together to figure out how far one is from the starting point, one must compute distances and directions together. This amounts to vector addition. Adding distances of segments without consideration of direction gives the path length, which is, in general, different from the distance from the starting point. It is the distance from the starting point, and not the path length, that is of most interest in executing trajectories.

IMAGE MATCHING

After the sensorimotor vector, if the honeybee sees its goal (in laboratories, the food dish offered), the bee beacons in on its target. But, on tests, during which no food is offered, the insect then executes image matching. In this process, the bee attempts to place nearby landmarks at the correct positions. The correct position means at the correct distance and correct compass direction from

**averaging distance and direction
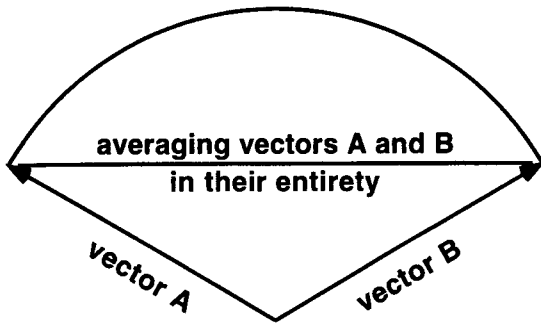components of A and B separately**

Figure 5. Logic of vector averaging versus independent averaging of distance and direction. Two possible ways to average two vectors, A and B, are to average the entire vectors using vector addition or to average the components of distance and direction separately. The weighted average must lie on the line segment connecting the endpoints with vector averaging and on the arc connecting the endpoints with independent averaging. Honeybees do vector averaging of trajectories but independent averaging of vectors to landmarks.

each nearby landmark. Gould (1987) determined the landmark resolution of honeybees to be 3.1° horizontally and 5.5° vertically. Image matching is using landmarks to specify an exact position and is perhaps most closely associated with the notion of using landmarks to find a place. The evidence comes from a large number of studies that have manipulated the landmark array (e.g., Cartwright & Collett, 1982, 1983; Cheng, 1999a, 1999b; Collett, 1992; Collett & Baron, 1994; Collett & Rees, 1997; Collett & Zeil, 1998). These manipulations show that honeybees rely on nearby landmarks to determine search location. Image matching refers to the theory that best explains the results of studies using landmark manipulations. Collett (1992) and Collett and Zeil (1998) provide summaries of the research.

The task of image matching comes down to placing each landmark element at the correct position. The correct position breaks down into the correct distance and the correct direction (from the viewpoint of the target location). Next, I provide brief descriptions of how direction and distance to a landmark are determined.

Determining Direction

Telling the direction to a landmark is more complicated than determining a direction to fly in for executing a vector. The direction to a landmark is registered on the eye, but its position on the eye depends on which way the forager is facing. The honeybee either needs a "rotatable image," (i.e., one whose retinal specifications change systematically with the direction in which the forager is facing) or must face a limited number of directions during search. The bee adopts the latter, simpler strategy, which bypasses the need to translate retinal coordinates to some other system. When the bee faces only one direction, one

position on the eye is always the correct one for a landmark. Collett and Baron (1994), studying bees outside, found that their subjects faced magnetic south except when the landmark was directly to the north of the target location, in which case they tended to face north. Collett and Baron manipulated the magnetic field about the target to verify that it was the magnetic south that the bees chose. The chosen direction is not always defined magnetically, however, nor always in the same direction from one situation to another. Often, it is defined by the stimulus setup. Frier, Edwards, Smith, Neal, and Collett (1996), for example, trained honeybees to enter a tube to collect a reward. Different bees had tubes facing different directions. When searching for the tube on tests, the foragers tended to face the direction appropriate for entering the absent tube. In the gap and block experiments in my lab (Cheng, 1999b), bees were trained to search in front of a gap along a wall of yellow blocks or in front of one yellow block. The gap or block ran east–west. I examined which way the insects were facing when near the target position on unrewarded tests. In both situations, the honeybees tended to face two directions almost parallel to the gap or block, facing east or west. In both directions, they were turned slightly (0° to 30°) toward the landmark.

In the section on following a route, I reviewed how a honeybee determines direction when flying outside. It is not clear what the animal is using to determine direction inside a lab, as they must do. The lab typically has a window, so that the direction of entering light is one cue. Labs usually have distal landmarks, which can provide another directional source. Systematic manipulations of directional cues within a lab, the kind done on some studies of spatial cognition in rodents (e.g., Cheng, 1986; Etienne, Joris-Lambert, Dahn-Hurni, & Reverdin, 1995; Etienne, Joris-Lambert, Maurer, Reverdin, & Sitbon, 1995; Etienne, Teroni, Hurni, & Portenier, 1990; Suzuki, Augerinos, & Black, 1980), have not been done for honeybees.

Determining Distance

The honeybee has two ways of telling the distance to a nearby landmark: motion parallax and object size. It is thought that their compound eyes, which do not focus, lack any other means of obtaining distance cues. Object size refers to the size that the object projects on the eyes. Motion parallax refers to how much the object appears to move as the bee moves a given unit of distance: The closer the object is, the more it would appear to move. It is now clear that the honeybee uses both these cues in landmark-based search (Cartwright & Collett, 1979, 1982, 1983; Cheng, 1999b; Cheng, Collett, Pickhard, & Wehner, 1987; Lehrer & Collett, 1994).

The use of the retinal size projected by an object has been demonstrated by changing the size of a landmark on crucial tests. Honeybees were trained to search at a particular distance and direction from a single landmark. After learning the task, the size of the landmark was changed on some tests (Cartwright & Collett, 1983; Cheng, 1999b).

The honeybees' search distance varied systematically with landmark size: The larger the landmark, the farther away from it they searched. In neither case, however, was control by landmark size complete. That is, if we make predictions of search distances based solely on retinal size, the bees did not vary their distance to the extent predicted. Much individual difference was also found in Cheng's (1999b) study, with some bees hardly changing their distance of peak searching with variations in landmark size. It is clear then that bees also use some other distance cue, and that cue must be motion parallax.

Evidence for the use of motion parallax has come from experiments in which the honeybee had the task of picking out a flower at a different depth from all other flowers (Lehrer, Srinivasan, Zhang, & Horridge, 1988; Srinivasan, Lehrer, Zhang, & Horridge, 1989). The flowers were positioned beneath a transparent Perspex plate, they varied in size, and the size of the target flower varied from trial to trial, rendering retinal size a useless cue. Nevertheless, the bees solved the task. Cheng et al. (1987) found that, in landmark-based search, honeybees put more weight on landmarks that were closer. The landmarks in that study projected the same retinal size, with farther landmarks being proportionally larger. Lehrer and Collett (1994) also found evidence that honeybees learned the distance to the landmark without using retinal size. It is reasonable to suppose that motion parallax is used in part to determine the distance to a nearby landmark in landmark-based search.

Servomechanistic Control by Landmark Direction and Distance

If landmark direction and distance are to control search in image matching, they ought to have an effect on the rate of change of direction and distance as the insect nears its target position. When the retinal position is nearly correct, the change in the retinal position of the landmark (retinal velocity) ought to slow down. When the distance to a landmark is nearly correct, the approach speed to a landmark ought to diminish. Collett and Rees (1997) examined such details in a small number of wasps and found the expected negative correlations between retinal position and retinal velocity and between landmark distance and approach speed. In both cases, the optimum correlation was found with a time lag of ~100 msec between the target position and the velocity or speed. The 100 msec might be interpreted as the lag of the system in processing and reacting to the incoming signal.

Distance and Direction Computed Separately

The correct position for a landmark comprises distance and direction, which together define a vector from the target to the landmark. The meaning of a vector here differs from that of a sensorimotor vector. In a sensorimotor vector, the distance is to be covered in travel. The direction specifies a motor instruction (e.g., fly north-east for 20 cm). In a vector to a landmark, the distance is a static target-to-landmark distance. The direction is the compass direction to the landmark. Different cues are used by honeybees in calculating the distance and direction to a landmark. Distance is calculated by retinal size and motion parallax, and direction is calculated by retinal position. The two kinds of computations may well go on independently. If the bee were to average the dictates of different landmarks near the target, nothing requires that averaging of entire vectors be done. Separate computation of distance and direction has the advantage of modularity. Different specialized subsystems may be devoted to each task. Only their final outputs need to be combined.

By using paradigms exploiting the logic illustrated in Figure 5, I have tested honeybees in landmark-based search. In contrast to the findings of Collett et al. (1996) on averaging sensorimotor vectors, in landmark-based search, evidence suggests that honeybees compute distance and direction to a landmark separately and independently (Cheng, 1998a). Similar experiments on pigeons have found that the birds also compute distance and direction separately (Cheng, 1994).

MULTIPLE MEMORIES

The foraging honeybee typically visits a number of flowers before it flies home with its load. One might suppose then that the honeybee can learn multiple landmark-based memories in experimentally contrived situations and can keep track of which locations it has visited. Some evidence supports both suppositions. Collett and colleagues (Collett & Baron, 1995; Collett et al., 1996; Collett et al., 1997) have found that honeybees can learn different sensorimotor trajectories to different patterns of stripes on the wall of an arena. Collett and Kelber (1988) showed that honeybees can learn to search at two different locations with respect to the same constellation of landmarks placed in two different rooms or to search at different locations with respect to two different constellations of landmarks in two different global locations (rooms or platforms). Cheng and colleagues (Cheng, 1998b; Cheng et al., 1986) showed that bees can learn to search at two different target locations with respect to two different arrangements of the same landmark elements within the same room. Honeybees solved such tasks on the basis of the hues but not the brightness level of the landmarks (Cheng et al., 1986). Use of brightness was also not evident in Backhaus's (1991) multidimensional scaling analysis of color vision in bees. Bees do not solve the task by combining the two constellations into one composite memory, but they have two separate memories of two constellations (Cheng, 1998b).

Not surprisingly, in distance estimation as well, honeybees can associate two different distances to two different stimuli (Srinivasan et al., 1998). In this case, the two stimuli were each presented to one eye in the tunnel task. This

is accomplished by providing textured stimuli on only the right or left wall. Bees can learn to fly one distance with visual flow to the left eye and another distance with visual flow to the right eye.

Confusions in Multiple Memories

Some interesting results from some of the demonstrations of two memories are the confusions between the two memories that the bees sometimes exhibit. In Cheng's (1998b) landmark memory task, honeybees often searched in the correct location for the other constellation. In Srinivasan et al.'s (1998) task of multiple distance estimation, honeybees sometimes confused the distances. For example, bees trained with a single task of flying the single distance of 9 units (1 unit = 20 cm) rarely made their first turn at Units 5, 6, or 7 on tests. Bees trained to fly 9 units with input to one eye and 4 units with input to the other eye, when tested on the "9-unit eye," frequently made their first turns at Units 5, 6, or 7. In this case, it looks as if the bees had averaged the target distances of the two memories (in a weighted fashion) and used this derived intermediate distance as a target. Such confusions can reveal much about the organization of learning and memory and deserve far more study.

Working Memory

To keep track of locations it has visited, the forager must remember the characteristics of the feeder in one visit, exhibiting what is called *working memory*. In a typical study on working memory, the insect first visits one feeder and then, after a delay, must visit a feeder with the same or different characteristics for further reward. In studies by Brown et al. (1998) and Couvillon, Arincorayan, and Bitterman (1998), honeybees have shown working memory for color; however, interestingly, in both studies, the behavior was independent of reward conditions. Whether the bees were rewarded for choosing the same or a different color after the first visit, they showed a reliable tendency to revisit the feeder with the same color. Honeybees have also been tested on analogues of the radial maze task. On these tasks, the foragers had to avoid locations that they had already visited. On such tasks, Brown and colleagues (Brown & Demas, 1994; Brown, Moore, Brown, & Langheld, 1997; Demas & Brown, 1995) have consistently found positive results using a six-location maze. Burmeister, Couvillon, and Bitterman (1995) used only three locations and obtained negative results, whereas Isnec, Couvillon, and Bitterman (1997) found that the bees tended to revisit locations already visited no matter what the reward conditions. It is not clear what causes the discrepancy in results. Brown (personal communication, September 22, 1999) and I both think, however, that a pattern of spatial win-shift and color perseverance makes functional sense in the lives of foraging bees. Honeybees typically visit the same kind of flower from one visit to another, a phenomenon known as *flower constancy* (see Seeley, 1985, pp. 103–106), but they usually visit many individual flowers on one foraging trip. Color perseverance can serve the purpose of flower constancy, whereas spatial win-shift keeps the bee foraging at undepleted flowers.

THE LEARNING PROCESS

So far, I have described the servomechanisms by which the honeybee finds its way to a foraging spot. Each servomechanism has a target that the system aims for. Target specifications are inputs into the system that must be gathered from experience—that is, learned. A good example of a target specification is what a landmark near the target location looks like. This is required for beaconing in on the landmark. Honeybees and wasps take characteristic learning flights upon leaving a place they have to get back to (Collett, 1995; Collett & Zeil, 1996, 1998; Tinbergen, 1972; Zeil, 1993a, 1993b). In the lab, the behavior has been called "turn back and look" (Lehrer, 1993). The honeybee, upon leaving the dish of sugar water proffered, turns back a number of times upon its journey out. This behavior diminishes greatly after the first few trials. Outside, wasps take elaborate flights upon leaving a just-found foraging spot (Collett, 1995) or upon leaving their nest hole for the first time each morning (Zeil, 1993a, 1993b), turning and sweeping ever wider arcs while facing the target. The way the insect faces on such learning flights is closely correlated with the way they face upon approaching the target, making it likely that these orientation flights serve the purpose of learning the landmark characteristics near the target. Classic work by Becker (1958) has shown that foraging bees deprived of orientation flights around their hive failed to return to their hives after displacement, whereas those with the experience of orientation flights did return. An example of a learning flight from a wasp is shown in Figure 6.

The "learning flights" cannot be all there is to learning to find the foraging spot again. The learning flights may enable the insect to learn about views at various distances from the target. Yet, the forager must also learn what it looks like at the target. Presumably, this takes place at or near the target. By manipulating cues at a feeding site, Couvillon, Leiato, and Bitterman (1991) found evidence that honeybees learn about features of the feeding site both on arrival and on departure.

This review has concentrated on the products of learning, the servomechanisms that the honeybee learns to use to find a place. In each case, the process of learning—the topic of how a honeybee establishes a memory for a target foraging location—requires far more research. Working memory can clearly contribute to learning, and its role in this regard also requires further research.

DISCUSSION

"A bag of tricks, indeed, an almost bewildering bundle of special-purpose, tailor-made tricks, evolved through
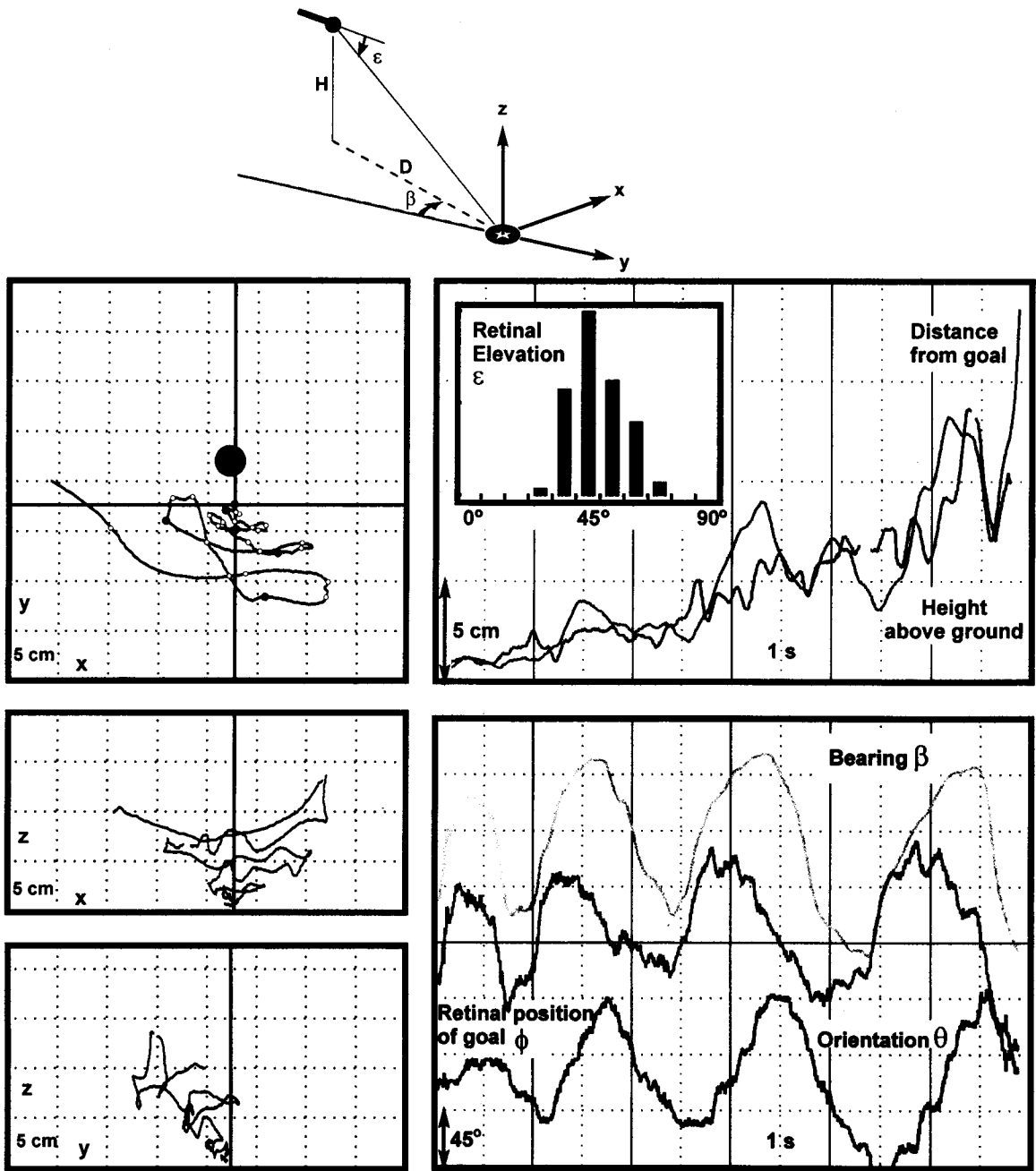
Figure 6. Positions (left panels), distance and height from the goal (top right), and the bearing, orientation, and retinal position of the goal (bottom right) of a typical learning flight of a *Cerceris* wasp. The wasp takes off from a nest hole in the ground and turns to face it. The wasp then backs away in a series of arcs that are roughly centered on the nest (top left). The wasp's horizontal distance and its height increase at the same rate, so that it views the nest at a constant angle below the horizon (top right). While flying around the nest, the wasp matches pivoting and turning velocity so that the image of the nest entrance is kept at retinal positions between 30° and 70° away from the midline (bottom right). Mean turning and pivoting rate are constant and independent of distance from the nest. Unpublished figure kindly supplied by J. Zeil.

natural selection to solve the various problems" (Seeley, 1995, p. 264).

This quote might be from a cognitive scientist speaking about the primate visual system or a neuroscientist speaking about the mammalian brain. But it is Seeley writing about a beehive's allocation of workers to tasks. The tasks include foraging for nectar, pollen, and water, unloading and storing food, and building combs. The special-purpose mechanisms are instantiated in individual worker bees, and foraging ability is part of that bundle.

The sequence of behaviors leading the forager from hive to food can be characterized as a sequence of place-

finding servomechanisms. Each servomechanism has a standard to aim for (Cheng, 1995). In executing a route, the standard is a vector to be covered. In beaconing, the standard is approaching a recognized object. In a sensorimotor vector, the standard is again a vector to be covered. In image matching, the standard consists of the positions of many landmark elements, with position divided into separate components of distance and direction. I propose that each servomechanism brings the animal to a position at which the next servomechanism may be run. None by itself is sufficient. Image matching, for example, cannot be run until the bee is near the target. The initial route to the vicinity of the target is not accurate enough to lead the animal right to the target. As a sequence, however, the routine brings the forager to its goal. It should be noted again that the nature of transitions in the sequence and the sequential nature of the servomechanisms need further empirical evidence and should form a theme for further research.

The navigational abilities encompass a range of special-purpose tools, including a sun compass and a landmark-based compass constructed from the sun compass, an "odometer" that measures distance flown, and a view-based image matching system. If the story is correct in basic outline, then the spatial cognition of bees consists of a number of special-purpose stereotypical routines to get the forager to a small number of foraging spots. The honeybee does not have a general-purpose solution to spatial problems, something embodied in the concept of a map. But the specific solutions supplied by the bee's navigational abilities suffice to get the forager to its food sources. And this serves the beehive well enough to have been preserved in evolution.

Special-purpose mechanisms are not peculiar to honeybee navigation but serve navigational purposes in other invertebrate and vertebrate species as well. Path integration is one such mechanism, especially well studied in rodents (Etienne, Berlie, Georgakopoulos, & Maurer, 1998) and ants (Müller & Wehner, 1988; Wehner, Michel, & Antonsen, 1996; Wehner & Wehner, 1990). The geometric module is another (Cheng, 1986; Gallistel, 1990, ch. 6; Hermer & Spelke, 1996). Learning in other realms, perhaps much of learning, may also rely on special-purpose modules. This theoretical view is represented by Gallistel (1990) and Shettleworth (1998).

Special-purpose devices do many jobs of navigation; however, it does not follow that spatial cognition has its own set of laws of learning. Many general laws of learning no doubt apply in the spatial realm for honeybees as for vertebrate animals (Cheng & Spetch, 1998). In honeybees, spatial generalization produces the typical generalization gradients, and the gradients obey Shepard's law (Cheng, 1999c, in press), much as vertebrate gradients (Shepard, 1987). Honeybees weight nearer and bigger landmarks more (Cheng et al., 1987), as do vertebrates (e.g., in birds, Bennett, 1993; Cheng, 1989). Thus, spatial

cognition has a mix of special-purpose devices and general laws of learning.

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