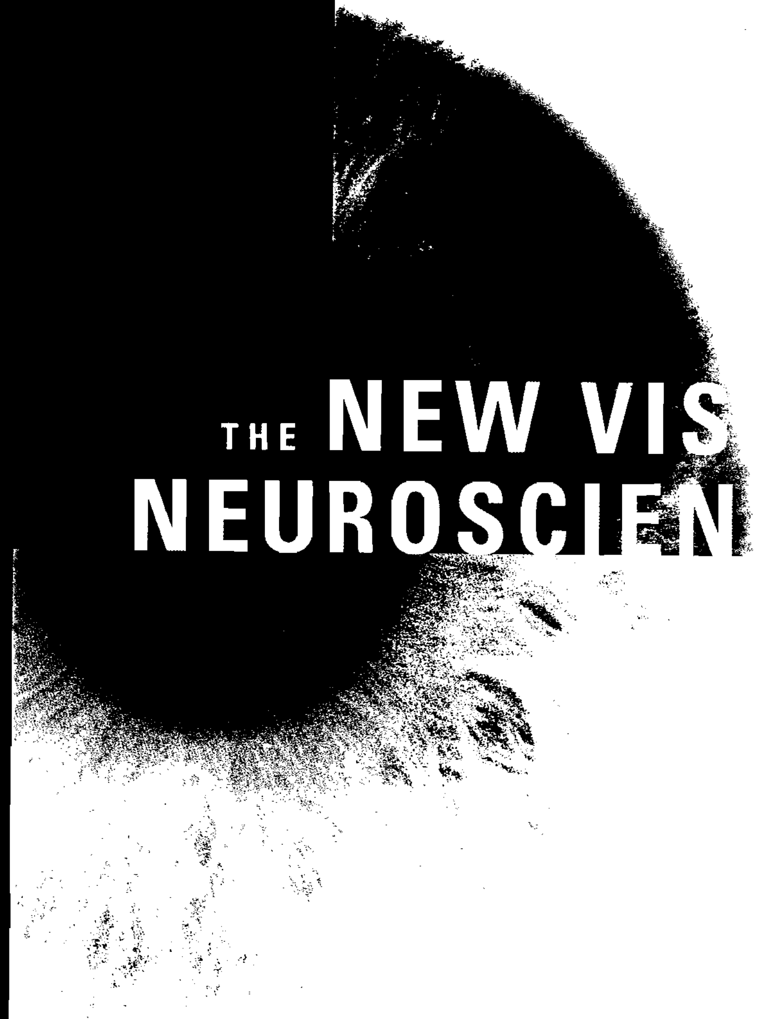

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82 The Cognitive Structure of Visual Navigation in Honeybees

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Animals use all their senses to explore the world, return to safe places, discover locations of importance, and travel between them. The phylogenetic history of the respective species equips it with information about the physics of the world, but locations need to be learned according to their relations to physical and chemical signals. Memory established by exploration and successful outcome of navigation links environmental cues and may lead to complex forms of neural representation of space. Cognitive levels of navigation range from guidance by predominantly innate stimulus–response connections to goal-directed planning based on highly integrated combinations of multisensory inputs. In this sense the study of navigation and its neural underpinnings presents a paradigmatic case of cognitive neuroscience.

Having accumulated a wide range of observations from "foraging" *Caenorhabditis* worms to human goal finding, behaviorists noticed that animals may apply rather simple strategies to head toward a goal or to return to a place. In an attempt to apply parsimony arguments strictly, behavioral biologists hesitate to assume any more complex forms of neural integration. Thus the assumption of a memory structure like a cognitive map is hotly debated and may even be entirely rejected (Bennett, 1996; Shettleworth, 2010). Neuroscientists, in contrast, refer to a cognitive map even for experimental settings in the lab where it cannot be excluded that the animal may have simply steered toward the goal by following a stimulus gradient, headed toward a beacon at the goal, or performed sequential matching procedures, gradually reducing the mismatch between an image learned close to the goal and that at the current position (O'Keefe & Nadel, 1978). Tolman's (1948) criterion of a novel shortcut as an indication for a cognitive map is indeed rather weak if other explanations like dead reckoning, beacon orientation, and image matching are not ruled out. Here I explore the cognitive levels of visual navigation in a flying insect, the honeybee, and present data and concepts that go beyond elementary forms of navigation. In so doing, I refer to the sophisticated form of social communication in honeybees, the waggle dance.

THE SPATIAL PRIMITIVES OF NAVIGATION

Elements of Spatial Primitives

The elements of spatial primitives are discussed at length in this volume, with many examples applying also to the honeybee. They belong to two groups: a basic visual recognition group and a more advanced group that integrates such elements in a performance-related way. Elements of the first group are, for example, various forms of taxes; object segmentation, discrimination, and learning; segmentation of celestial cues (sun, blue sky); odometry; detection of movement direction; associating flight vectors, objects, and circadian time to meaning (e.g., reward, expected outcome of own performance); and many more. Compositions of these basic elements control elements of navigation—for example, learning patterns of objects for the use of image matching (steering toward a goal by reducing the mismatch between the current and the learned pattern), learning the local time-compensated sun compass, relating the pattern of polarized light of the sky to the great circle of the sun, deriving sun compass directions from extended landmarks, estimating and learning sequences of objects, estimating a direct path by integrating partial vectors (dead reckoning and path integration), and many more. Here I dwell first on two of these components, path integration and image matching, because they are frequently thought to fully explain navigation performance in honeybees (Collett & Collett, 2002; Cruse & Wehner, 2011).

Path Integration

Path integration in its basic form provides the information for an animal to return to a starting point—for example, the nest—by a memory of its own movements. From spiders to mammals, animals possess an accurate system for keeping track of relative spatial locations by integrating linear and angular motion even without access to external cues (Mittelstaedt & Mittelstaedt, 1982). Angular motion is extracted under daylight conditions from visual inputs like landmarks and celestial cues (see chapter 85, this volume) and from traveled distance from an odometer. The outcome of the path integration process provides a running estimate, leading the animal back to the starting point at any time during its excursion. Thus such home vectors can be computed solely on egocentric information and may include landmark information as an allocentric reference for the two components of path integration, namely, angular and translatory movement.

Formal descriptions distinguish between four cases (egocentric with polar or Cartesian coordinate systems, geocentric with polar or Cartesian coordinate systems) and conclude that the geocentric Cartesian system provides the most robust home vector information (Vickerstaff & Cheung, 2010). This latter finding is particularly relevant for the buildup of metric spatial representation by path integration, an idea first put forward by O'Keefe (1976). Location-dependent information may be used for corrections due to error accumulation in path integration and for estimates of spatial relations via single or multiple visits to these locations (Biegler, 2000; Gallistel, 1990; McNaughton et al., 2006).

Two fundamentally different learning situations need to be distinguished in path integration: the use of the running estimate of the home vector during exploratory movements in an unknown landscape and the movement along frequently traveled routes. I shall distinguish nonassociative dead reckoning, the basic form of path integration during exploration, from associative dead reckoning that requires traveling along a route multiple times. The latter strategy is most important for embedding egocentric into allocentric reference systems and is of particular interest here. Bees, for example, learn the sequence of objects experienced along a multiply flown path and use the sequence for distance estimation (Chittka & Geiger, 1995; Menzel et al., 2010). After training bees to two feeders and analyzing their straight flight components (SFCs) during homing behavior, we found multiple SFCs that resemble multiple vector memories (Menzel et al., 2012) (see figure 82.1). The vector memories belong to two forms: the experienced flight vectors reflecting the routes between the hive and each feeder (see figure 82.1a) and the vectors derived from vector integration. Two of these derived vectors connect the two feeders (see figure 82.1b); other flight vectors connect the release site or any location after some search flights and the hive (see figure 82.1c). We observed that all SFCs resembled the direct vectors between the feeders and were not performed at the feeder sites (feeders and all material were removed from the respective site during tests) but further away from the hive than the bee line between the feeders and the hive, suggesting that the animals related their choices to the overall spatial relations of the three sites—the hive and the two feeders.

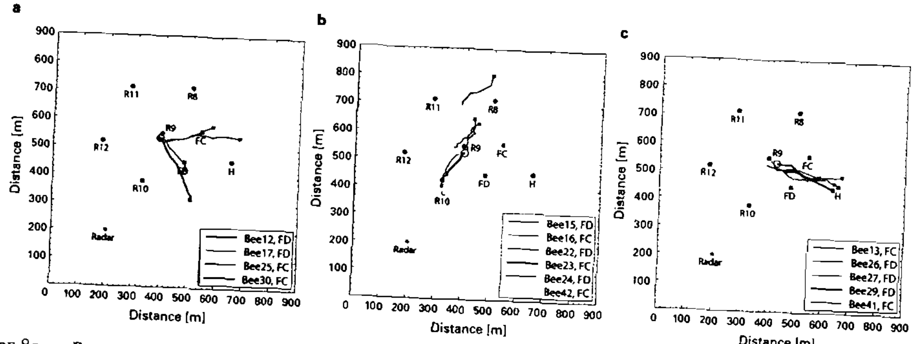


FIGURE 82.1 Representative examples of straight flight components (SFCs) of test bees released at the same release site (R9). The bees were trained from the hive (H) to two feeders (FC, FD). They did not experience the straight flight between FC and FD during training. The number of the test bee and the feeder from which it was collected is given in the respective inset. The two feeders are called FC and FD and form an approximately equal-sided triangle with the hive (length of side = 160 m). The circle gives the starting point of the respective SFC and the filled square its end point. The landmarks characterizing the feeding places and the release site are rather inconspicuous so that animals may not be able to notice at the release site that they have been moved to an unexpected location. (a) Animals flew along a path resembling homing flight vectors from the feeder from which they were collected. Thus the animals switched motivation from outbound to inbound flights. (b) Animals followed the vector components of the bee line between the two feeders. Two of the animals (bee 15 and bee 42) first performed extended search flights before the first SFC shown here. (c) Animals performed novel shortcut flights back to the hive. (After Menzel et al., 2012.)

The two kinds of derived vectors represent novel shortcut flights and may result from the integration of at least two associative dead reckoning vectors or from activation of site-specific memory. We observed that half of the first SFCs at release site R9 were directed toward the hive whereas none of the first SFCs from animals released at R7, R8, R10, and R12 belonged to this flight direction category, possibly indicating that the area around R9 more closely resembled the landmarks characterizing the two feeding sites. This would favor the activation of both home vectors from the two feeders leading to either a compromise flight vector or to vector integration of both vectors, an interpretation suggested by Menzel et al. (1998) for a similar constellation. An alternative interpretation assumes that the geometric relations between R9 and the hive favored the novel shortcut toward the hive, a behavior that would require knowledge of the geometric relations between the respective locations. As in the study by Menzel et al. (2005) these data do not allow one to distinguish between these two interpretations.

It has often been argued that the process of retrieving a vector memory on the basis of landmarks, switching motivation between outbound and inbound flights, and vector subtraction concepts are more parsimonious neural procedures than a geometric representation in spatial memory in ants and bees (Collett & Collett, 2002; see chapter 80, this volume). Indeed, a simple model of memory retrieval, motivational switch and path integration (Cruse & Wehner, 2011), formally meets the requirements for predicting the navigational performance of bees as tested in the study presented here and in the Menzel et al. (2005) study. Whether the model captures a more parsimonious neural implementation is a different question and must be kept open as long as we do not have any data on the neural processes in the insect brain allowing the animal to navigate over long distances in a highly flexible way. Running and flying insects may differ substantially in their capacity to relate the egocentric measures to an allocentric reference since the bird's eye view of flying insects offers a geometric layout as a primary visual source of information, whereas running insects are bound to multiple sequential views of cluttered objects whose geometric relations are only indirectly accessible and difficult to extract.

Beacon Orientation and Image Matching

When leaving the hive or a food patch, honeybees perform a characteristic scanning behavior and learn the immediate surroundings in spatial relation to the hive entrance (see chapter 85, this volume). Whether bees use the same kind of image learning for close and far distance landmarks (panorama) is not clear as image matching experiments have only tested bees for close landmarks (Cartwright & Collett, 1987). The panorama is learned during exploratory orientation flights and route flights. Such forms of learning differ substantially from image learning at a vantage point. Furthermore, a flying insect like the bee will have access to the geometric layout around the hive and at further distances soon after it is in air. It is therefore questionable whether bees follow homing strategies similar to those of ants that travel in a visually cluttered environment and appear to follow the image-matching strategy even along multiply traveled routes further away from the nest (Philippides et al., 2011; see chapter 80, this volume). It is more likely that bees use different spatial learning strategies than do ants, and an extension of concepts developed for close-up image matching may not be adequate.

Mapping to Compass Values

Animals are innately prepared to relate their movements to one or several compass systems. Evidence in favor of spatial mapping comes from free-ranging animals under natural conditions both for far distance navigation and navigation within the home range. Analysis of a large database on bird navigation has led to the concept that intersecting stimulus gradients form a multicoordinate system by which any point in space is characterized by a unique combination of coordinates (Wallraff, 2005; Wiltschko & Wiltschko, 2003). These coordinate values appear to provide a global allocentric reference frame with respect to which items in spatial long-term memory (places, landmarks, home) could be represented. Pigeon homing has been conceptualized by a "mosaic map" that stores gradients associated with compass directions (Wallraff, 1974, 2005; Wiltschko & Wiltschko, 2003). Lipp et al. (2004) tracked many homing flights of pigeons carrying global positioning system devices and found that they followed highways, performed turns on intersections, and accepted detours if they were marked by such gradients.

Bees associate gradients (e.g., forest edges, roads) with sun compass directions and read the sun compass direction from these gradients when the sky is overcast (Dyer & Gould, 1981; von Frisch &

Lindauer, 1954). In their waggle dances bees report distance and direction of a feeding site or a nest site referring to celestial cues or cues derived from landmarks. They then transform the directional information into a code relative to gravity and encode the distance estimated by the outbound flight via their visual odometer. Thus waggle dance communication can be used to read the structure of their spatial memory (see below).

Beyond the Primitives of Navigation

The cognitive building blocks of navigation can be considered as letters and words arranged by rules to become a meaningful text. It is the search for the rules that characterizes the cognitive approach. Does the honeybee solve a navigational task that cannot be explained by a set of primitives and requires a higher level of integration? The basic design of experiments performed to address this question is the catch-and-release paradigm under natural conditions. An animal whose knowledge about the environment is known as much as possible by prior training is caught in a defined motivational state (e.g., when leaving a feeding place to return to the hive, when leaving the hive after following a waggle dance) and transported to an unexpected release site within its explored area. After being released its full flight path is recorded by harmonic radar. The test conditions require excluding beacon orientation and image matching as a navigation strategy. If the animal is able to return to the hive or steer toward any other important place (feeding place or dance-directed place) directly along a novel path (novel shortcut), one needs to conclude that it uses a strategy beyond navigation primitives. However, the structure of the spatial reference is not elucidated by such a result. One still needs to ask which landmark features guided the animal and what the structure of its navigation memory is. Experiments under natural conditions make it difficult to address these questions, but resorting to the lab or to simpler test conditions is not an option because reducing the environment may not allow the animal to apply its cognitive capacities. Furthermore, the question about the cognitive dimensions of navigation is not limited to path finding. It also includes motivational components, decision making, planning, and in the case of the honeybee, social communication. Do bees communicate primitives of flight vectors or places that are associated with meaning and create expectancy about a particular place both in the transmitting and the receiving bee?

NOVEL SHORTCUTTING

Experience from Route Flights Is Not Required for Novel Shortcuts

The method of training individually marked bees to a feeding site has been a major source of discoveries since its introduction into behavioral biology by the Nobel Laureate Karl von Frisch more than 100 years ago (von Frisch, 1967). Bees learn the distance and direction of their route flights between hive and feeder and report the outbound flight vector in the waggle dance. This vector is stored in memory and dominates the behavior of bees in catch-and-release experiments (Menzel et al., 2005). As long as only the vanishing bearings of released bees could be recorded, the stereotypic perpetuation of the sun compass–related direction of this vector gave the impression that bees' navigation is bound to an egocentric frame of reference and relies solely on the information gathered during route training (Wehner & Menzel, 1990). If this were true, bees would be lost if they were trained such that they did not learn a route vector. But bees are not lost. Figure 82.2 shows the flight time of two groups of bees under similar test conditions. One group was trained along a route, the other to a feeder close to the hive that was rotated around the hive. It took animals without route training no longer to return to the hive from five release sites around the hive than it took route-trained animals when they were released at their training site. Thus bees must be able to refer to a different spatial memory than that formed during route training, and this kind of memory cannot come from earlier foraging activities since the areas around the release sites differed considerably with respect to potential forage. Furthermore, beacon orientation toward the hive and image matching with the panorama were not possible because the view toward the hive was blocked either from R2 or R5.

Route-trained animals and animals without route training were also compared with respect to their homing flights using harmonic radar for tracking (Menzel et al., 2005) (see figure 82.3). The test area did not provide any panorama cues, and the animals relied on local ground structures for navigation. The initiation points of direct homing flights (homing points marked with a red star in figure 82.3 a and b) lie outside the visual catchment area around the hive excluding the possibility of beacon orientation. The distribution of homing points does not differ between V- and C-bees, indicating that they refer to a spatial memory not derived from route training. Accumulation of homing points in both groups of bees south of the hive overlaps with a long-ranging landmark (a border line between two differently cut pastures stretching north–east to south–west) and a patch of local landmarks (tents). Obviously these two landmarks have been learned by the bees in spatial relation to the hive, independently of route flights. Since the experiments were performed when no natural forage was available, the novel shortcuts to the hive from more or less all directions could not have been learned during foraging flights.

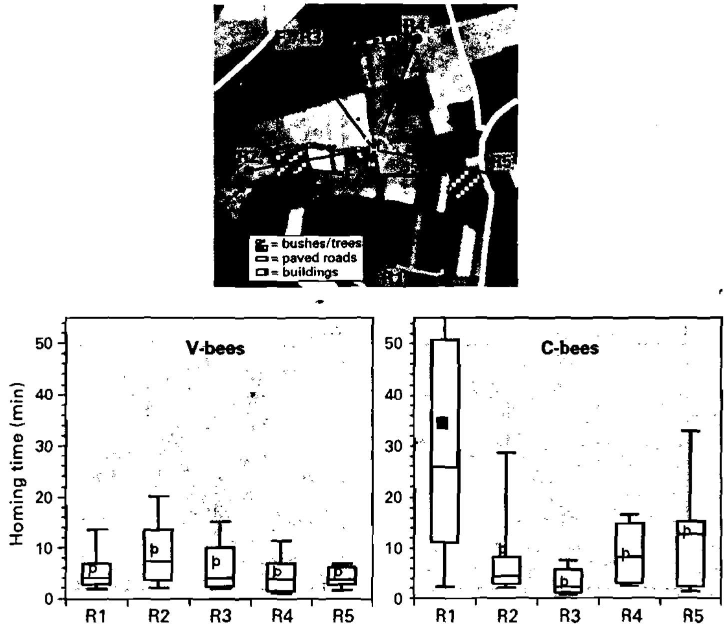


FIGURE 82.2 Catch-and-release experiment with two groups of bees. V-bees were trained to a variable feeder close to the hive (H) that rotated around the hive (white dotted line around the hive in the upper figure). C-bees were trained along a route to a stationary feeder (Fc/R3 in the upper figure). Fc and the 5 release sites (R1–R5) had a distance to the hive of 350 m. The two lower figures give the flight times between the respective release sites and the hive for both groups of bees. In both cases the bees were collected individually at one of the two feeders once they had sucked their fill and prepared for departure to the hive. Only the red marked bar (R1 of C-bees) is statistically significantly different from that of all other bars. C-bees released at R1 take longer to return to the hive because they first fly further away from the hive as they first apply their home bound vector memory from Fc/R3 to the hive (Menzel et al., 2000).

Shortcutting and Learning during Orientation Flights

A social animal and central place forager like the bee needs to return safely to its colony. Bees also need to learn a range of properties of the environment before initiating foraging flights. These properties relate to the sun compass, the time of the day and the local ephemeris function, and possibly also to the calibration of the visual odometer. In one of the most fascinating series of experiments Karl von Frisch and Martin Lindauer (1954) showed that bees use extended landmarks (such as straight forest boundaries) as guides for sun compass orientation. Later Dyer and Gould (1981) called the same phenomenon a backup system for cloudy days and related the connection between sun compass orientation and landmark orientation to a safety system. However, it is more likely that the tight connections between extended landmarks and sun compass need to be seen in the context of calibrating the properties of the sun compass. In any case, extended landmarks are obviously of special importance for the bee.

Exploratory orientation flights bring the bee in narrow loops into the surrounding environment (Capaldi & Dyer, 1999; Capaldi et al., 2000). One component of these orientation flights is nonassociative dead reckoning (see above). The other component is associative dead reckoning during which bees learn about the spatial relations of extended and local

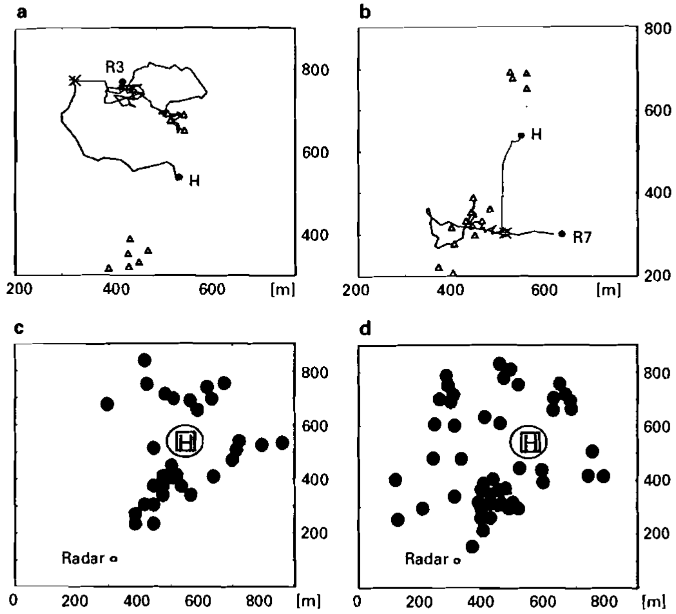


FIGURE 82.3 Homing behavior of V-bees and C-bees in a catch-and-release experiment where flight paths were recorded by harmonic radar (Menzel et al., 2005). The two upper figures (a, b) show representative examples of full flight paths of a V-bee (a) and a C-bee (b). (a) V-bees lack the vector flight, and start with a search flight at the release site (here at R3). The homing flight is shown in green starting at the red star (homing point) (b) The red line shows the vector flight of a route-trained bee whose feeder was 200 m east of the hive after it was released at R7. The vector flight is followed by a search flight component (in blue). Frequently bees return to the release site before commencing the homing flight. (c and d) The homing points for V-bees (c) and C-bees (d). The triangles in a and b mark tents in an otherwise rather homogeneous landscape. The circle around the hive (H) in c and d indicates the visual catchment area of the hive. Note the different scales in the upper and lower figures.

landmarks. Recently we found that bees return home faster after a single orientation flight when released in the explored sector as compared to releases in the unexplored sector. We also saw that multiple sequential orientation flights of the same animal are directed into different sectors with increasing range of exploration, suggesting that the surrounding environment is systematically explored. These data indicate that allocentric relations are learned during orientation flights.

Decision Making in Novel Shortcuts

Most interestingly, bees trained to a distant feeder returned home not only by direct flights to the hive but also via the feeder (see figure 82.4). The ability to decide between the hive and the feeder as the destination for a homing flight requires some form of relational representation of the two locations. Given that neither of these two locations could be approached with the help of a beacon or the panorama, it is tempting to conclude that bees made decisions between potential goals by referring to a map-like structure of their spatial memory. However, one can also argue they may have learned to associate home-directed vectors with local landmarks. This would explain the direct home flights, but an additional process would be required to explain the results shown in figure 82.4. This additional process may be based on the integration of memory of far-ranging vectors, one that leads to the hive from a particular location and one that was learned during multiple route flights from the hive to the feeder. Two motivations would have to be active at the same time, homing toward the hive and outbound flight from the hive to the feeder. A single motivation as claimed by Cruse and Wehner (2011) would not suffice. All these vector operations would have to be made on the level of a form of working memory in

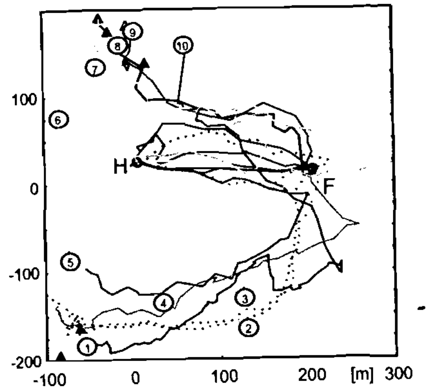


FIGURE 82.4 Final part of nine flight tracks of bees that flew back to the hive (H) via an area close to the feeder (F) (Menzel et al., 2005). One of these bees landed at the feeder.

which representations of these vectors are available for integration.

In the context of the data shown in figure 82.1 it may be argued that such operations on the level of working memory are basically not different from a map-like representation.

SOCIAL COMMUNICATION AND SPATIAL LOCATION

Social Communication in Honeybees

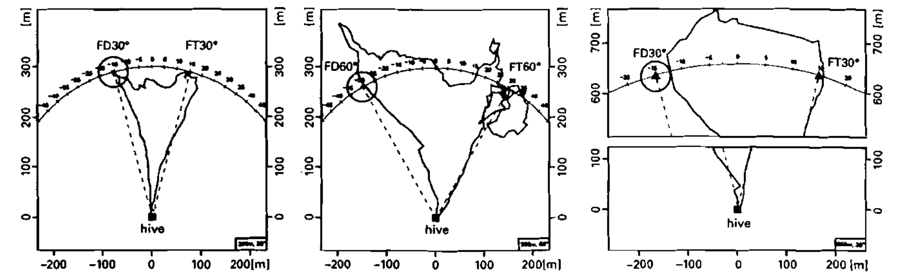
Honeybees use various kinds of stereotyped motion patterns for social communication (Seeley, 1995; von Frisch, 1967). The round and waggle dance communicates spatial relations to the hive. In the waggle dance, a dancing bee executes fast and short forward movements straight ahead on the comb surface, returns in a semicircle in the opposite direction, and starts the cycle again in regular alternation (each waggle dance involves several of these cycles). The straight portion of this course, called the waggle-run, is emphasized by lateral waggling motions of the abdomen. The length of single waggle-runs and the number of sound pulses increase with the distance flown to reach the source, and their angles relative to gravity correlate with the direction of the foraging flights relative to the sun's azimuth in the field and sun-linked patterns of polarized skylight. Thus by encoding the visually measured distance and the direction toward the goal, the waggle dance provides vector information toward a desirable goal. But what does the dancer really indicate? This will depend on both the transmitter (dancer) and the receiver (recruit).

Early detour experiments by von Frisch and colleagues (reviewed in von Frisch, 1967) indicated that the bees' odometer is primarily decoupled from directional information processing, indicating that no global flight vector is reported in the context of the waggle dance. These early findings were recently confirmed by manipulating the navigational information provided to a dancing bee (De Marco & Menzel, 2005). Thus one might ask whether the waggle dance encodes spatial information provided only by the actual flight path. The detour experiments by von Frisch and the results of von Frisch and Lindauer (1954) cited above suggest that the directional component reported in the waggle dance may also be derived from landmarks. This idea is not without precursors. Early experiments showed that with increasing experience of the terrain, directional information available during the inbound flight (and not only the outbound flight) may be computed for the purpose of directional indication in the waggle dance (Otto, 1959). It thus appears that bees may rely on some form of geocentric reference system.

Is there a symbolic component in the bee dance? To answer this question, we need to know what kind of neural or mental state the dancing bee refers to when it communicates a location of particular properties. Does she transmit only the motor performances to be applied by the recruit, or does she express her memory of the location of the site in the same geometric reference frame as the recruit? Does she read out the memory of the experience made with the site, or does she just convert a stereotypical measure of quality (of the food source, of the potential nest site) into a dance parameter? We do not know (yet?).

A Common Frame of Spatial Memory in Navigation and Communication

How do recruits deal with the information they receive from the dancer? Do they treat this information for their sensorimotor performance during the outbound flight, or do they integrate the spatial components of this information into their memory about the landscape? We addressed these questions in experiments in which a group of bees foraged at a feeding site (the trained food site FT) and later experienced that FT did not provide any food anymore (Menzel et al., 2011). As a consequence they gave up foraging at FT and became recruits to two other bees performing dances for a food site (the dance-indicated food site FD) at the same distance as FT but at either 30° or 60° to FT (see figure 82.5). As in all other experiments with the harmonic radar we did not use any odor at the food site and the two locations could not be seen by the animals over



300 m, 30° *300 m, 60°* *650 m, 30°*

FIGURE 82.5 The figure shows three conditions under which recruits performed shortcuts between the dance-indicated location (FD 60°, FD 30°) and a location the animal had learned before (FT 60°, FT 30°). The distance between hive and FD or FT was either 300 m or 650 m, and the angle between the directions from hive to FD and that to FT was either 30° (FD 30°, FT 30°) or 60° (FD 60°, FT 60°). Test bees did not fly shortcuts between FD and FT (or FT and FD) for distances of 650 m and an angle of 60° (not shown). These findings indicate a common frame of reference for experienced and communicated locations. Recruits perform shortcuts according to the absolute and relative distance between the respective locations (Menzel et al., 2011).

distances greater than 50 m and without the help of the panorama. We found that recruits performed differently depending on the difference between their own foraging experience and the information transmitted in dance communication. The number of outbound flights to either FT or FD depended on the angular difference between FT and FD. Furthermore, recruits performed a range of novel flight behaviors. In the 30° arrangement some of them deviated from the course toward FD during their outbound flights and crossed over to FT. Most importantly, after arriving at either FD or FT some of them performed cross flights to the respective other location (see figure 82.5). From these observations we conclude that locations FD and FT are both stored in spatial memory in such a way that bees are able to fly directly from one location to the other following a novel shortcut.

We asked whether the decision for FD or FT depends on the number of waggle-runs followed by the recruited bee and found that more information is needed by recruits to fly to FD, the dance-indicated location. Bees that followed fewer waggle-runs either flew to their experienced feeding site, returned to the hive after a short excursion, or did not leave the hive. Following more waggle-runs (in our experiment on average 25 runs) resulted in FD flights indicating that the motivation to apply the information collected about FD is enhanced after longer dance following. However, the information about FD has been learned also during shorter dance following since animals that flew first to FT performed shortcut flights from FT to FD (see figure 82.5). Obviously dance communication involves two separate components, a motivational and an instructive component, the former requiring less information transfer. The motivational component appears to remind a recruit about its own foraging experience.

Given the bees' rich navigational memory, one may ask what exactly is communicated by the waggle dance: just the outbound vector or the location of the goal? In the first case the amount of vector information accumulated by the recruit may have to pass a certain threshold before new vector information can be applied. In the latter case the recruit would compare the expected properties of the indicated location with its own knowledge of this location and other potential foraging options from its own experience before reaching a decision about where to fly. Since we interpret our radar tracking data to document a rich form of a common allocentric memory as the structure of navigational working memory, it is tempting to conclude that vector information from the waggle dance is incorporated into such a common memory, and thus it too has an allocentric structure.

HOW COGNITIVE IS THE COGNITIVE MAP?

Arguments against a Cognitive Map in Bees

The structure of a cognitive map should allow the animal to localize itself within the explored environment irrespective of how it reached the current location and to perform novel paths to an intended goal along a short route (novel shortcut). Such a behavior requires the capacity to spot the current location and to estimate the direction and distance of the intended goal. Additional properties of a cognitive map can be assumed. The animal may be able to decide between two or more goals on the basis of the expected outcome when arriving at the goal, it may qualify these goals (nest, feeding sites, higher or lower ranking feeding or nest sites), and it may make its decision dependent on its own motivational state.

Five arguments have been put forward against the hypothesis that bees navigate with reference to a memory structure best described as a "cognitive map" as introduced by Tolman (1948) for rats and humans:

1. *The cognitive map is not the most parsimonious explanation* Parsimony is a strong argument in the interpretation of experimental data (Bennett, 1996). Although it should not be overlooked that radical forms of parsimony as applied to behavioral science were and may still, at least partially, be a historical burden (Menzel & Fischer, 2011), it is essential that "simpler" explanations be excluded in the experimental design. Parsimony can be understood as a formal criterion and, in the case of behavioral biology, as an argument for the simplest implementation in neural structures. Both aspects depend on what needs to be explained. Even if we ignore the evidence that bees make decisions according to the expected outcome (see below) and do not take into account any qualitative evaluation of the intended goal, we are left with the conclusion that bees either perform some sort of long-distance vector integration with at least three vectors to be considered or they refer to geometric relations of landmarks, best conceptualized as a cognitive map. The former is a geometric map, too, so the difference lies only in the procedure by which spatial relations are established and used.

2. *Small brains like that of the bee do not support a memory structure like that of a cognitive map* The parsimony argument is often combined with the statement that brains as small as those of bees cannot support such a memory structure. Furthermore, it is argued (Collett & Collett, 2002) that small brains need to solve their tasks with less "cognition," meaning with a toolbox of loosely interrelated elementary functions rather than an integrated, allocentric level of spatial representation. It should be recognized that we simply do not know whether the integration of multiple and complex sensory and procedural neural processes into a common spatial memory with geometric organization (a map) may not be a more economical and thus simpler way of representing sequential experiences during navigation (Griffin, 1984). It is likely that the mushroom bodies with their 360,000 neurons, each equipped with thousands of synapses, receive highly processed visual information (Gronenberg, 2001), freeing it from low-level processing. Are these neurons too few to encode geometric relations between identified objects? We simply do not know.

3. *Bees should fly directly home from the release site* Indeed they don't. They first perform a flight according to the active state of their working memory. This behavior is not an argument against a cognitive map because the spatial memory bees need to refer to has been learned during orientation flights, and this memory is obviously not active when they follow their route flights or fly according to the dance information; it has to be recruited from remote memory.

4. *Bees should not fly into a region they have not explored—for example, out on a lake* Gould and Gould (1982) reported that bees reject dance information which would have brought them out on a lake. Wray et al. (2008) interpreted their data as showing that bees have no problem flying out on a lake after following a dance; however they had to use odor marking of the feeding station on a boat, and although they tried to downgrade an odor effect, they still could not eliminate the possibility that bees flew out on the lake because they were attracted by the odor. In our view, the topic of bees not accepting dance information into a white spot of their navigational memory is not yet resolved and requires testing with the harmonic radar. Let's assume for the moment that bees do not hesitate to fly into an unknown area. Does this mean they do not have a cognitive map? Certainly not, because white spots are surrounded by known area, and why should bees (like humans) not explore the unknown?

5. *As long as you cannot rotate the landmarks used by bees relative to their sun compass one cannot believe in the cognitive map concept* We all know from our discussions in science that sometimes abstruse arguments are put forward that ask for something impossible. This is such an argument. It has its roots in a tradition of experimentation in which the experimenter controls for all possible parameters, varies just one, and finds that the animal performs according to the hypothesis behind just that variable. It is then concluded that the animal can do only what was just tested. Navigation does not deal with close-up object recognition. Navigation in bees cannot be tested in a white 1×1-m box with three black stripes on the wall. Navigation occurs in the natural environment when bees fly over many hundreds of meters.

The Structure of a Cognitive Map in Bees

What could be the structure of such an overarching memory? Vectors are formally the most efficient way of specifying a location (Biegler, 2000; Gallistel & Cramer, 1996; Vickerstaff & Cheung, 2010). If these vectors are anchored to landmarks, they provide a geocentric reference frame. Vectors are reported in the waggle dance. Thus bees appear to take advantage of the formal applicability of such a spatial measure and need to encode only two parameters. This does not have to mean that all they are communicating is the vector. The directional component of the communicated vector may be retrieved from the memory of spatial relations to extended landmarks (gradients) because these are also defined by their relations to compass directions. Such gradients could compose a memory for a rather simple "bearing map" as proposed by Jacobs and Schenk (2003). Such a rough bearing map does not require a large amount of neural encoding and storage but would provide a geometric representation of the whole experienced environment at a coarse resolution. Picture memories ("sketch maps," in the terminology of Jacobs and Schenk) could exist loosely distributed and only partially connected to each other, leaving white spots in between. Way finding (and possibly communication about ways) could therefore consist first in identifying the sketch map of current location, the spotting of that sketch map in the bearing map, and then the creation of a novel shortcut flight according to the compass direction to the goal as derived from the sketch map. The bee would travel through "unknown" territory (white spots) whenever she leaves a sketch map memory and has not yet reached another one, but she would not be lost because at any point she has access to the bearing map. If such a scenario applies, bees would dance for a location in a bearing map, and recruits would interpret the message according to such a map. The finding by von Frisch and Lindauer (1954) that extended landmarks can replace access to the sun compass on overcast days could in fact indicate the use of such "gradients" providing a primary source of information for navigation. The link to the compass may just be a side effect of learning about such gradients. Since there is no vocabulary for particular gradients in the dance, the flight direction has to be encoded into a compass direction.

What We Need to Ask Next

The kinds of questions to be asked in the future in navigation and communication studies in honeybees differ from those addressed so far. The sensorimotor routines involved are well understood, and they have een analyzed by asking "What can the animal do?" ow we need to ask what kind and how the information stored in their working memory, how this information is processed, and how decisions are made. We will thus have to analyze the structure of internal representations. Dance communication provides us with a window into these processes, and carefully designed experiments will allow access to processes beyond behavioral acts. These operations are far from simple and transcend elemental forms of associations (Menzel & Giurfa, 2001; Menzel, 2012). The richness of these operations is accessible only in animals behaving in their natural environment, and the methods for collecting the relevant data are now available. Ultimately we want to know how and where the bee's small brain performs these operations; the answers lie in the future.

REFERENCES

Bennett, A. T. D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology, 199,* 219–224.
Biegler, R. (2000). Possible uses of path integration in animal navigation. *Animal Learning & Behavior, 28,* 257–277. doi:10.3758/BF03200260.
Capaldi, E. A., & Dyer, F. C. (1999). The role of orientation flights on homing performance in honeybees. *Journal of Experimental Biology, 202,* 1655–1666.
Capaldi, E. A., Smith, A. D., Osborne, J. L., Fahrbach, S. E., Farris, S. M., Reynolds, D. R., et al. (2000). Ontogeny of orientation flight in the honeybee revealed by harmonic radar. *Nature, 403,* 537–540.
Cartwright, B. A., & Collett, T. S. (1987). Landmark maps for honeybees. *Biological Cybernetics, 57,* 85–93.
Chittka, L., & Geiger, K. (1995). Can honeybees count landmarks? *Animal Behaviour, 49,* 159–164.
Collett, T. S., & Collett, M. (2002). Memory use in insect visual navigation. *Nature Reviews. Neuroscience, 3,* 542–552.
Cruse, H., & Wehner, R. (2011). No need for a cognitive map: Decentralized memory for insect navigation. *PLoS Computational Biology, 7,* e1002009. doi:10.1371/journal.pcbi.1002009.
De Marco, R. J., & Menzel, R. (2005). Encoding spatial information in the waggle dance. *Journal of Experimental Biology, 208,* 3885–3894. doi:10.1242/jeb.01832.
Dyer, F. C., & Gould, J. L. (1981). Honey bee orientation: A backup system for cloudy days. *Science, 214,* 1041–1042.
Gallistel, C. R. (1990). *The organization of learning.* Cambridge, MA: MIT Press.
Gallistel, C. R., & Cramer, A. E. (1996). Computations on metric maps in mammals: Getting oriented and choosing a multi-destination route. *Journal of Experimental Biology, 199,* 211–217.
Gould, J. L., & Gould, C. G. (1982). The insect mind: Physics or metaphysics? In D. R. Griffin (Ed.), *Animal mind–human mind* (pp. 269–298). New York: Springer.
Griffin, D. R. (1984). *Animal thinking.* Cambridge, MA: Harvard University Press.
Gronenberg, W. (2001). Subdivisions of hymenopteran mushroom body calyces by their afferent supply. *Journal of Comparative Neurology, 436,* 474–489.
Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review, 110,* 285–315.
Lipp, H. P., Vyssotski, A. L., Wolfer, D. P., Renaudineau, S., Savini, M., Troster, G., et al. (2004). Pigeon homing along highways and exits. *Current Biology, 14,* 1239–1249. doi:10.1016/j.cub.2004.07.024.
McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M. B. (2006). Path integration and the neural basis of the "cognitive map." *Nature Reviews. Neuroscience, 7,* 663–678.
Menzel, R. (2012). The honeybee as a model for understanding the basis of cognition. *Nature Reviews Neuroscience, 13,* 758–768. doi:10.1038/nrn3357.
Menzel, R., Brandt, R., Gumbert, A., Komischke, B., & Kunze, J. (2000). Two spatial memories for honeybee navigation. *Proceedings. Biological Sciences, 267,* 961–968.
Menzel, R., & Fischer, J. (Eds.). (2011). *Animal thinking: Contemporary issues in comparative cognition* (pp. 1–416). Cambridge, MA: MIT Press.
Menzel, R., Fuchs, J., Nadler, L., Weiss, B., Kumbischinski, N., Adebiyi, D., et al. (2010). Dominance of the odometer over serial landmark learning in honeybee navigation. *Naturwissenschaften, 97,* 763–767.
Menzel, R., Geiger, K., Müller, U., Joerges, J., & Chittka, L. (1998). Bees travel novel homeward routes by integrating separately acquired vector memories. *Animal Behaviour, 55,* 139–152.
Menzel, R., & Giurfa, M. (2001). Cognitive architecture of a mini-brain: The honeybee. *Trends in Cognitive Sciences, 5,* 62–71. doi:10.1016/S1364-6613(00)01601-6.
Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., et al. (2005). Honeybees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences of the United States of America, 102,* 3040–3045. doi:10.1073/pnas.0408550102.
Menzel, R., Kirbach, A., Haass, W. D., Fischer, B., Fuchs, J., Koblofsky, M., et al. (2011). A common frame of reference for learned and communicated vectors in honeybee navigation. *Current Biology, 21,* 645–650.
Menzel, R., Lehmann, K., Manz, G., Fuchs, J., Koblofsky, M., & Greggers, U. (2012). Vector integration and novel shortcutting in honeybee navigation. *Apidologie, 43,* 229–243. doi:10.1007/s13592-012-0127-z.
Mittelstaedt, H., & Mittelstaedt, M. L. (1982). Homing by path integration. In W. Papi (Ed.), *Avian navigation* (pp. 290–297). Berlin: Springer-Verlag.
O'Keefe, J. (1976). Place units in the hippocampus of the freely moving rat. *Experimental Neurology, 51,* 78–109.
O'Keefe, J., & Nadel, J. (1978). *The hippocampus as a cognitive map.* New York: Oxford University Press.
Otto, F. (1959). Die Bedeutung des Rückfluges für die Richtungs- und Entfernungsangabe der Bienen. *Zeitschrift fur Vergleichende Physiologie, 42,* 303–333.
Philippides, A., Baddeley, B., Cheng, K., & Graham, P. (2011). How might ants use panoramic views for route navigation? *Journal of Experimental Biology, 214,* 445–451.
Seeley, T. D. (1995). *The wisdom of the hive: The social physiology of honey bee colonies.* Cambridge, MA: Harvard University Press.
Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). New York: Oxford University Press.
Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55,* 189–208.
Vickerstaff, R. J., & Cheung, A. (2010). Which coordinate system for modeling path integration? *Journal of Theoretical Biology, 263,* 242–261.
von Frisch, K. (1967). *The dance language and orientation of bees.* Cambridge, MA: Harvard University Press.
von Frisch, K., & Lindauer, M. (1954). Himmel und Erde in Konkurrenz bei der Orientierung der Bienen. *Naturwiss, 41,* 245–253.
Wallraff, H. G. (1974). *Das Navigationssystem der Vögel.* Munich, Germany: R. Oldenbourg Verlag.
Wallraff, H. G. (2005). *Avian navigation: Pigeon homing as a paradigm.* Berlin: Springer.
Wehner, R., & Menzel, R. (1990). Do insects have cognitive maps? *Annual Review of Neuroscience, 13,* 403–414.
Wiltschko, R., & Wiltschko, W. (2003). Avian navigation: From historical to modern concepts. *Animal Behaviour, 65,* 257–272.
Wray, M. K., Klein, B. A., Mattila, H. R., & Seeley, T. D. (2008). Honeybees do not reject dances for "implausible" locations: Reconsidering the evidence for cognitive maps in insects. *Animal Behaviour, 76,* 261–279.