1.25 Learning and Memory in Communication and Navigation in Insects

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1.25.1 Introduction

The distinction between instinctive and learned behavior is a fundamental issue in behavioral research. A major difficulty in addressing it relies on the fact that labeling behaviors as either instinctive or learned is in most cases a merely analytical approach to the problem. Behavior develops on the basis of the interplay between an animal's phylogenetic boundaries and the sources of external signals that belong to its specific sensory world (Tinbergen, 1963; Lorenz, 1981; Shettleworth, 1998; Macphail and Bolhuis, 2001). It follows that when an animal computes the differences between stimuli activating the same or different sensory modalities, its subsequent behavior will be the outcome of an unbroken succession of possible responses, whose particular boundaries have been modified by selection in the course of evolution. Learning is embedded into this continuousness, and its effects on the animal's instantaneous performance will be superimposed onto those of its specific phylogenetic boundaries. This is why it is so fundamental to focus on salient responses invariably linked to the animal's previous experience when

distinguishing between instinctive and learned behaviors. From a behavioral point of view, this leads to the search for the mechanisms underlying the animal's decision, a notion that denotes the process of parsing complexes of stimuli into equivalent options and the control of the subsequent responses that arise from the corresponding choices.

A central argument advanced in this chapter is that some invertebrate taxa constitute powerful model systems for the study of the teamwork between these two modes of behaviors, instinctive and learned, and for the analysis of basic principles of learning and memory, particularly within the context of communication and spatial cognition, where the possibility of revealing decisions might be within reach. Our focus is on social insects, animals that form societies and appear to have been exposed to higher cognitive demands during the course of evolution, perhaps due to their long lifetime, the diversity and complexity of the signals involved in their social interactions, and the development of counterresponses. In fact, "if Earth's social organisms are scored by complexity of communication, division of labor and intensity of group integration, three

pinnacles of evolution stand out: humanity, the jelly-fish-like siphonophores, and a select assemblage of social insect species" (Wilson, 2006). Within this insect group, emphasis is on the honeybee, *Apis mellifera*, simply because its communication and navigation skills are impressive (e.g., von Frisch, 1967; Seeley, 1995; Menzel et al., 2005). Furthermore, because their brains are small, bees appear to be suitable subjects for studying system-level neural correlates of learning and memory through robust behavioral approaches, both at the level of single neurons and neural networks.

1.25.2 Communication

Since its early days, ethology has nurtured the study of learning and memory phenomena, and a great deal of its classical ideas "emerged or crystallized from the study of animal communication" (Konishi, 1999). It follows, therefore, that communication in nonlinguistic animals has been at the center of many of the current behavioral approaches to learning and memory. The study of animal communication is concerned with the production of and the responses to signals, including adaptive advantages and mechanisms of central processing, motor coordination, and peripheral detection and filtering. In invertebrates, it is in the context of communication and navigation that learning transcends elementary forms of association in particularly clear ways (Menzel et al., 2006). The evaluating signal for storing experience must come from internal nervous system conditions at the time of learning, depends considerably on the motivational level, requires attention to a subset of stimuli, and is adjusted to the animal's own behavior in an intricate way. The signals learned are usually composed of multimodal inputs, which cannot be isolated from each other, and the motor performances involve sophisticated sequences of programs. Insects make use of all sensory channels for communication and evolved sophisticated sender–receiver systems serving mate recognition and sexual selection, predator–prey relationships, and complex social interactions. Although the sensory, ecological, and evolutionary aspects of these communication systems have long been studied in detail (see the following discussion), little is known about the cognitive dimensions of these communication systems (e.g., how innate mechanisms interact with experience-dependent developmental

processes, how these mechanisms depend on internal and external conditions, and how learning actually shapes a communication process). In the present context the neural mechanisms of insect communication will henceforth be eschewed altogether. We shall describe a few examples from several taxa illustrating the dominance of innate behaviors with regard to communication with conspecifics; these examples will be listed according to the sensory modalities involved in the processing of communicating signals. We will then focus on a few examples illustrating simple forms of learning in a selected group of insects, and finally, we will focus on the study case of the honeybee dance communication system, with special emphasis on the structure and content of the spatial memory underlying such complex phenomenon.

1.25.2.1 The Dominance of Innately Programmed Responses in Communication

1.25.2.1.1 Chemical
In highly eusocial species, the interplay between innate and learned behaviors becomes evident through group recognition, which greatly depends on smell and genetically programmed responses to information gathered in specific, innately recognized behavioral contexts (Lindauer, 1961; Wilson, 1971; Michener, 1974; Barrows et al., 1975; Oster and Wilson, 1978; Fletcher and Ross, 1985; Hölldobler and Wilson, 1990). Within an insect society, conspecific individuals respond differently to age, sex, and physiological groups, and the task of recognizing queens, males, workers (both egg-layers and infertile individuals), as well as intruders, strongly relies on volatile pheromones, variations in hydrocarbon cuticular profiles, and environmental odors (e.g., Eberhard, 1969; Bell, 1974; Franks and Scovell, 1983; Wagner et al., 1998; Liebig et al., 2000).

Individually distinctive or colony odors are frequent across highly eusocial insects and constitute the basis of colony integration and social organization (Hölldobler and Michener, 1980). Foragers from many ant species, for example, resume their field excursions by following trails chemically marked with colony-specific components (Hölldobler and Wilson, 1990; Billen and Morgan, 1998). Research on the harvesting ant *Pogonomyrmex*, for example, shows how context-dependent innate responses to olfactory stimuli lead to adaptive behavioral flexibility during foraging (Greene and Gordon, 2003). A colony of these ants consists of a single queen and

several thousand workers, including foragers and patrollers. Patrollers scout the foraging area before foragers leave the nest; if they do not return from their early excursions, the foragers will not begin to work. Recently, Greene and Gordon (2003) first blocked a *Pogonomyrmex* colony's foraging activity by removing its patrollers and then presented the foragers with glass beads at the nest's entrance. These beads had previously been coated with cuticular lipids from patrollers, hydrocarbon profiles from either patrollers or within-the-nest ants, and plain solvent; they also used live patrollers as a positive control. The authors thus found that task-specific cuticular hydrocarbons from patrollers were sufficient to rescue the colony's foraging activity, and that the foragers' responses depended not only on the patrollers' hydrocarbon profiles, but also on whether or not they were presented at the nest's entrance and at the right time of day (Greene and Gordon, 2003). The question remains of to what degree simple forms of learning, such as habituation (Barrows et al., 1975), underlie these responses to colony and individually distinctive odors.

1.25.2.1.2 Visual

Visual stimuli also control innate responses in communicating insects. Fireflies use luminescent signals for attracting mates (Lloyd, 1983). Butterflies use bright colors, iridescence, and polarized light in the context of long-range mate recognition and sexual selection (e.g., Vane-Wright and Boppre, 1993; Sweeney et al., 2003). Males of the hoverfly *Syritta pipiens* closely track the movements of conspecifics (Collett and Land, 1975), a skill that seemingly serves copulatory functions. Male flies of the genus *Lispe* perform a dancelike motion pattern during courtship that is seemingly perceived through vision (Frantsevich and Gorb, 2006). Visual cues enhance recruitment orientation to food sources in stingless bees (Nieh, 2004), that is, several species of these highly social insects exhibit local enhancement and orient toward the visual presence of foraging conspecifics (Slaa et al., 2003), a phenomenon also found in honeybees (Tautz and Sandeman, 2002) and wasps (D'Adamo and Lozada, 2005). Furthermore, stingless bees also appear to visually track the piloting flights of experienced conspecifics, and these movements can guide them for at least part of the distance to a food source (Esch et al., 1965; Esch, 1967; Kerr, 1969), although the role of learning in this intriguing form of recruitment has yet to be analyzed.

1.25.2.1.3 Mechanosensory

The use of air pressure waves, substrate-born vibrations, and touching is widespread in sexual selection, alarm and defensive behavior, and complex social interactions in insects (e.g., Webster et al., 1992; Fullard and Yack, 1993; Michelsen, 1999; Hölldobler and Roces, 2001; Virant-Doberlet and Cokl, 2004). Complex behaviors involving these types of signals vary considerably across species. Female crickets, for example, orient toward males by recognizing and localizing the sound signals they produce. Their auditory orientation emerges from mechanisms detecting species-specific temporal structures of the males' sound signals, as well as reactive motor responses to individual sound pulses (Webster et al., 1992; Stumpner and von Helversen, 2001; Hedwig and Poulet, 2004). Leaf-cutting ants are highly sensitive to substrate-borne vibrations (Markl, 1965) and possess stridulatory organs that produce such vibrations when the animals are engaged in leaf-cutting (Tautz et al., 1995; Hölldobler and Roces, 2001). It has been shown that these substrate-born stridulatory vibrations operate as short-range recruitment signals that enhance the effect of recruitment pheromones (Hölldobler and Roces, 2001).

Moreover, the exchange of liquid food by mouth is widespread among highly eusocial species of insects (Wilson, 1971), and these social interactions depend strongly on intense antennal contacts that occur between donor and food-receivers (Free, 1956; Montagner and Galliot, 1982). In the honeybee, antennal interactions are also important in the transmission of waggle dance information (Rohrseitz and Tautz, 1999). Ants recruit nest-mates to newly discovered food sources as well as possible nest sites by means of tandem running (Hingston, 1928), a behavioral mechanism that strongly relies on mechanosensory cues (e.g., Wilson, 1959; Hölldobler et al., 1974; Möglich et al., 1974; Traniello and Hölldobler, 1984). Camponotus ants returning from successful field excursions stimulate nest-mates through fast directed movements of their front legs or even their entire bodies, as well as food samples; they then present the nest-mates with their gasters, and tandem running begins between pairs of leaders and followers (Hingston, 1928; Hölldobler et al., 1974; Hölldobler and Wilson, 1990). Hölldobler (1974) and colleagues demonstrated that tactile signals from the follower's antennae are sufficient to trigger an ant's leadership behavior, and that the subsequent following behavior relies on mechanical stimulation based on contact with a leader's gaster. Tandem running is especially

interesting in the context of genetically programmed mechanosensory communication because it clearly exposes the bidirectionality of the communication process. It has recently been shown through the behaviors of both the leader and the follower in a pair of tandemly running *Temnothorax* ants how they depend on each other (Franks and Richardson, 2006), that is, there is an evident feedback between both ants that relies on mechanical stimuli and helps in maximizing the speed at which the two of them can travel their path. It remains open whether and how the follower gathers path-related information during tandem running that might subsequently be used in solitary excursions.

1.25.2.2   Learning in Communication

1.25.2.2.1   Chemical
Some animals imprint on salient aspects of their sensory world pre- and postnatally. Slave-making ants provide an interesting example of imprinting. These ants invade colonies of other ant species and transport the pupae back to their own nest. Adults emerging from these pupae behave and work for the slave-making species as if it were its own species (Isingrini et al., 1985; Carlin and Schwartz, 1989). Evidence indicates that this phenomenon depends on a process of imprinting, by which the slave ants learn to recognize the slave-makers as members of their own species. This process involves learning about the slave-makers' hydrocarbon cuticular profiles, a distinctive olfactory mark of the species. Apparently, imprinting is successfully accomplished when the hydrocarbon cuticular profiles of both ant species, the slave-makers and the slaves, do not differ markedly (Lenoir et al., 2001; D'Ettorre et al., 2002).

Communicating insects also benefit from anticipatory behavior based on simple associative principles. In the honeybee, for example, and probably also in many other social species, the exchange of liquid food by mouth, called trophallaxis, allows individuals to assign nectar odors with predictive values. Animals associate the odor (as the conditioned stimulus or CS) and the sucrose (as the unconditioned stimulus or US) present in the nectar they receive through these social interactions. This form of learning leads to long-term olfactory memories after a single learning trial – even when trophallaxis is brief – and the strength of association depends on CS and US intensity, as well as on the animals' past foraging experience (Gil and De Marco, 2005). Olfactory memories established in this manner may have important implications in the organization of foraging (Gil and De Marco, 2006): First, foragers and food-receivers may benefit from learned odors in searching for a transfer partner, eliciting trophallaxis, or even avoiding it; second, currently unemployed foragers as well as nonexperienced foragers may benefit from a highly prevalent CS available within the colony to resume their subsequent foraging flights (e.g., the higher the rate of encounter with a rewarding olfactory CS the higher the probability of flying out to search for the prospective nectar source).

1.25.2.2.2   Visual
Polistes wasps provide an example of selective learning, which develops around innate responsiveness to simple sign stimuli: the yellow-black patterns of the wasps' faces and abdomens (Tibbetts, 2002). These patterns vary across individuals and correlate well with a wasp's ranking in a colony's hierarchy based on body size and dominance. Manipulating them induces aggressive responses in staged contests between pairs of unfamiliar individuals, and subordinate wasps with experimentally altered facial color patterns are targets of considerably more aggression from the dominant individuals than sham controls (Tibbetts and Dale, 2004). The question of whether these observations reveal individual recognition in insects remains open, but the wasps' behavior in the staged contests indicates that these animals learn about visual signals of quality that convey information on conspecifics on the basis of a colony's inherent hierarchy. Another interesting example of visual learning involved in communication may arise from the dance behavior of the Asian honeybee, *Apis florea*. In contrast to *Apis mellifera* bees, these animals do not dance on a vertical plane, but on the flattened tops of their open combs, which are directly exposed to a view of the sky (Lindauer, 1956; Koeniger et al., 1982; Dyer, 1985). These bees orient their dances on the horizontal plane according to both celestial cues and landmarks (Dyer, 1985), and the bees that closely follow these communicating dances might use their vision to collect information from them.

1.25.2.2.3   Mechanosensory and combined modalities
The seemingly ritualized movements or dances that honeybees use to recruit nest-mates from the colony – or the swarm – to the location of a desirable resource involve multiple signals, including mechanosensory stimuli (von Frisch, 1967). The role of learning in the context of dance communication was initially

dismissed (Lindauer, 1952), but we shall see that this system's functioning may depend strongly on the structure and content of the honeybees' spatial memory.

Karl von Frisch (1946) revealed that a highly stereotyped, still variable motion pattern that honeybees perform on the comb surface conveys to the human observer the position of a well-defined target at the endpoint of an average vector in a two-dimensional egocentric system of coordinates. Since its early days, von Frisch's (1946) discovery was recognized as one of the most impressive achievements of twentieth-century behavioral biology. This motion pattern involves finely controlled repetitive movements and can therefore be described on the basis of its inherent, well-defined features: orientation in space and tempo. The term waggle dance denotes a form of this pattern that conveys information about targets located fairly far from the hive, whereas the term round dance refers to a slightly different form that the animals perform after returning from nearby locations (von Frisch, 1967). Honeybees also use other stereotyped motion patterns when engaged in cooperative work that have also been called dances (von Frisch, 1967; Seeley, 1998). For example, a honeybee may shake its body back and forth, also rotating its body axis every second or so, and walk slowly in all directions across the comb (Seeley 1992). This type of motion pattern has been called tremble dance (von Frisch, 1923), and it helps the colony members to coordinate their activities while handling the collected nectar, both outside and inside the nest (Seeley, 1992). When a forager returns from a highly desirable nectar source and has problems searching for a food receiver (a younger bee that receives its load and eventually stores it in the honeycombs) (Doolittle, 1907; Lindauer, 1952), it usually performs a tremble dance, which may last several tens of minutes. These dances are followed by a rise in the number of available food-receivers and a drop in recruitment of additional foragers to nectar sources, thereby helping the colony to maintain its rate of nectar processing matched with its rate of nectar gathering (Seeley, 1992). In another intriguing example of these dances, a honeybee remains stationary and briefly vibrates its body laterally at a frequency of 4–9 Hz, sometimes alternating brief periods of self-grooming. This pattern has been called the grooming invitation dance (Haydak, 1945) and increases the workers' chances of being rapidly groomed by a nest-mate (Bozic and Valentincic, 1995; Land and Seeley, 2004). These two later forms of dances,

however, do not convey spatial information. Our focus is therefore on the waggle dance, which does convey spatial information and is perhaps the most intriguing form of these complex, iterative movements.

The homeostasis of a honeybee colony greatly depends on cooperative work and efficient communication (e.g., Lindauer, 1961). Compelling evidence indicates that the waggle dance is embedded in a series of communication systems that enables the colony to coordinate the activity of its members during foraging and nest-site selection (e.g., Seeley, 1995). Hence dancing honeybees have their own spectators. The colony members that keep close contact with a dancing bee, usually called dance followers or recruits, appear to detect a variety of signals emitted by the dancer and process them in such a way that their ensuing behaviors may greatly vary due to the content of these signals (von Frisch, 1967). Nevertheless, the way in which the followers detect the dance signals is not yet well understood, but the diversity of these signals indicates that multiple sensory modalities are involved in dance communication (Michelsen, 1999). Mechanical stimuli derived from the body contacts between dancers and followers are certainly involved, as well as environmental chemical cues brought into the colony by the dancers, and most likely also semiochemicals coupled to the dancer's wagging movements. Three-dimensional fields of air currents surrounding the body of the dancing bees and substrate-borne vibrations caused by the wagging movements of the abdomen also seem to play a role in dance communication (Esch, 1961; Wenner, 1962; von Frisch, 1967; Michelsen et al., 1987, 1992; Bozic and Valentincic, 1991; Kirchner and Towne, 1994; Tautz, 1996; Rohrseitz and Tautz, 1999). In addition to these external stimuli, propioceptive signals enable both dancers and followers to process mechanosensory information derived from the position of their body relative to the direction of gravity (von Frisch, 1967). Because the dance in *Apis mellifera* takes place on the vertical surface of the comb, the dancers have to transfer visual information gathered during their foraging flights to a reference system primarily defined by mechanosensory stimulation, a process called transposition also found in other insects (von Frisch, 1967). We shall focus on a few selected features of the waggle dance because they illustrate how learning may be involved in this form of social communication and also pose the question of how space is represented in the honeybee brain. Obviously, both

sides of the communication process, those from dancers and followers, must be taken into account if one is to understand what a successful follower actually learns from a dancing bee and how it combines the information available via the dance signals with that of its own spatial memory.

In the waggle dance (von Frisch, 1946, 1948, 1967), the dancer moves forward on the comb surface while moving its abdomen from side to side at about 15 times per second. This straight portion of the dance is called waggle-run. Without interruption, it then moves in a semicircular trajectory and returns to the starting point of its recent waggle-run; this portion is called return-phase. Once at this position, it repeats the forward, wagging portion of the dance. The dancer also tends to alternate clockwise and counterclockwise throughout successive return-phases. The followers tend to approach the dancer's body during the return-phase, which indirectly restricts the area on the comb in which the dance takes place, and if they begin following the dance maneuvers, their movements during a given return-phase will determine their subsequent position with respect to the dancer's body during the following waggle-run. Moreover, during the return-phase, dancers and followers interact repeatedly with their antennae and mouthparts, allowing mutual stimulation through chemical and mechanical signals. Finally, consecutive waggle-runs are performed with some directional scatter, which decreases when the distance to the indicated goal increases.

A major feature of the dance is that it can be triggered by different constellations of external stimuli, thereby conveying information about different types of goals. Honeybees dance for desirable sources of nectar and pollen (von Frisch, 1967), thus improving the colony's food collection (Sherman and Visscher, 2002), and also for water, essential to downregulate the nest's temperature when the hive gets overheated (Lindauer, 1954). This undoubtedly speaks about how versatile the dance communication system is. But perhaps the most striking example of this versatility relies on its role during swarming (Lindauer, 1951, 1953, 1955). Upon leaving their old nest during a colony's seasonal division, honeybees rely on a complex group decision-making process for selecting a new nest site. Their ultimate success depends on an accurate, fast, and unified collective decision (Seeley and Visscher, 2004). During this process, numerous colony members locate and dance on the surface of the swarm for potential nest sites. The decision process thus relies on several groups of dancers indicating different sites and recruiting uncommitted bees to follow their own dancing; most of the swarm's members remain in place until all dancers achieve unanimity by indicating the same goal, then the swarm lifts off (Seeley and Visscher, 2004).

The number of dancing events varies across dances, thereby revealing the regulatory responses and amplification phenomena that operate on the signal production side of the communication process. The strength of the dance depends on the flow rate (Núñez, 1970) and sugar content (von Frisch, 1967) of the nectar that the dancers bring into the colony; the flown distance (Seeley, 1986) and the nature of the indicated goal, that is, either a nest site or a food source (Seeley and Buhrman, 2001); the colony's nectar influx (Lindauer, 1948; Núñez, 1970; Seeley, 1995; De Marco, 2006); the dancer's past foraging experience (Raveret-Richter and Waddington, 1993; De Marco and Farina, 2001; De Marco et al., 2005); and even weather conditions (Lindauer, 1948; Boch, 1956). Honeybees also adjust the rate of waggle-run production by modifying the duration of the return-phase based on specific properties of the indicated goal (Seeley et al., 2000; Seeley and Buhrman, 2001) and by means of signals derived from their interactions with their fellow mates (Lindauer, 1948, 1954; Núñez, 1970; Seeley, 1986; De Marco, 2006) and time-based cues coupled to the current foraging status of the colony as a whole (Lindauer, 1948, 1954; Seeley, 1995). These relations enable the dance communication system to be tuned according to both colony demands and availability of resource opportunities.

1.25.2.2.4   What is the information content of the honeybee waggle dance?

So far, we have briefly described the waggle dance as an intriguing example of multisensory convergence, central processing, and motor coordination. We shall now focus on how it relates to navigation. Flying bees are able to use the sun as a reference to maintain a course, a mechanism referred to as the sun-compass (von Frisch, 1967), and also recognize the sun's azimuth by the pattern of polarized light in the blue sky (von Frisch, 1949, 1967; Rossel and Wehner, 1984). They also compensate for the sun's time-dependent movement, even when neither the sun nor the pattern of polarized light is visible (Lindauer 1957, 1959). For this task to be accomplished, they must learn the sun's azimuth as a function of the time of

the day during their initial orientation flights (Dyer and Dickinson, 1996).

A waggle dance encodes the direction and distance of a goal. First, the average orientation of the successive waggle-runs relative to the direction of gravity approximates the angle between the direction toward the goal and toward the sun (von Frisch, 1949, 1967; Lindauer, 1963). Second, the average length of the waggle-runs increases together with the distance from the hive to the goal (von Frisch and Jander, 1957). Early studies suggested that a honeybee's estimate of the flight length depends on gauging the amount of energy expended while flying (Heran, 1956; Scholze et al., 1964). Cumulating evidence now suggests that honeybees gauge and control the distance that they travel by integrating self-induced optic flow during flight (i.e., the net amount of image motion over the retina accumulated during movement) (Esch et al., 1994; Esch and Burns, 1996; Srinivasan et al., 1996, 2000; Tautz et al., 2004; De Marco and Menzel, 2005). The functioning of this mechanism is not yet fully understood, but it seems to depend on flight height and initial calibration based on landscape features (Esch and Burns, 1996; Esch et al., 2001). These two correlations convey to a human observer the circular coordinates of specific locations in a two-dimensional space and also provide a direct access into the dancer's perceptual world.

Evidence indicates that some of the followers that keep close contact with a dancing bee subsequently fly the approximate direction and distance that the dance conveys to the researcher (Lindauer, 1967; Esch and Bastian, 1970; Gould, 1975; Judd, 1995; Riley et al., 2005). They also use additional cues (i.e., semiochemicals and visual cues provided by other colony members, as well as environmental odors) to pinpoint the location of the targeted goal (e.g., von Frisch, 1967; Tautz and Sandeman, 2002). Six decades after von Frisch's (1946) original discovery, however, the process of decoding information in the dance still remains obscure (Michelsen, 1999). Some reasons are probably to be found in the striking variability of the multiple dance signals (e.g., von Frisch and Lindauer, 1961; Esch, 1978), the rather suboptimal methods that have been used so far to record the movements of both dancers and followers, and the lack of suitable tools to track the behavior of the followers after they depart from the hive. Improvements arise along with new methods (see the following discussion).

However, it is also worthwhile to consider a general aspect of the dance communication system that has received little attention, namely, the interaction between two different sources of spatial information that the followers might be able to access simultaneously: (1) the actual dance signals and (2) their own spatial memory store, as derived from their previous flights and reward experience; we shall refer to this putative store as the animal's spatial knowledge. The interaction between these two sources of information refers to a fundamental question in any process of communication. Communication depends on reproducing at one point an abstract entity selected at and sent from another point, but the entity that is finally reproduced on the receiver's side also depends on stored variants of this entity, which the receiver computes together with the signals it receives from the sender. In other words, one needs to ask whether a follower recollects stored information while decoding information in the dance.

The extent to which individual honeybees are exposed to the waggle dance throughout their foraging life has been addressed only recently (Biesmeijer and Seeley, 2005). In their study, Biesmeijer and Seeley (2005) reported that no more than a quarter of an average bee's lifetime field excursions was preceded by dance following, and in most of the instances in which the bees did follow dances before resuming their field excursions, they did so by following those that appeared to be indicating the goals that they were already familiar with. These findings are in close agreement with previous results by von Frisch (1968), who reported that the followers' response to the dance depends on their background of experience with the indicated goal, and that dances for familiar goals lead to more effective recruitment. Biesmeijer and Seeley (2005) also reported that the honeybees with field experience followed an average of only two to four dance circuits before resuming their new flights to the target. This small number of dance circuits provides spatial information only roughly to a human observer (**Figure 1**) and poses the question how informative this sample can be to the followers (Haldane and Spurway, 1954). Taken together, the results of this study suggest that the most advantageous functioning of the dance communication system will depend not only on the dancer's ability to keep record and derive spatial features of its recent field excursion, but also on the follower's ability to acquire, store, and recall specific navigational memories in the dance context (Menzel et al., 2006).
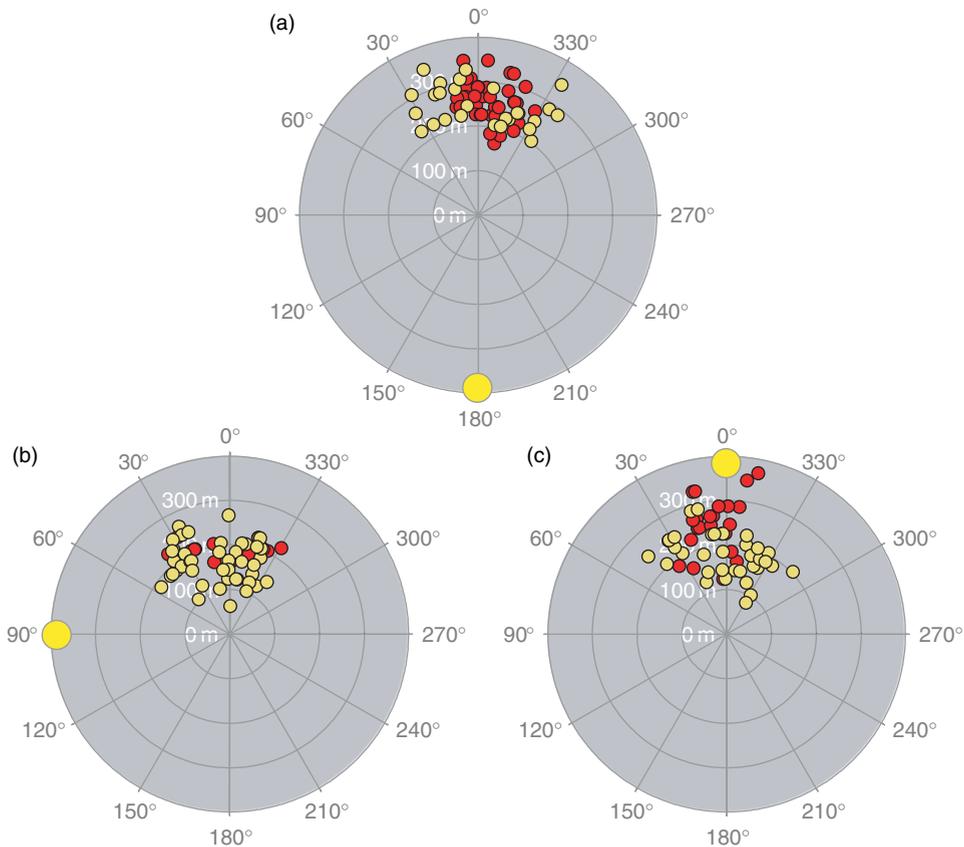
Figure 1 A waggle dance encodes the direction and distance of a goal: First, the average orientation of the successive waggle-runs relative to the direction of gravity approximates the angle between the directions toward the goal and toward the sun. Second, the average length of the waggle-runs increases together with the distance from the hive to the goal. These two correlations convey to a human observer the circular coordinates of specific locations in a two-dimensional space. The figure depicts radial maps indicating vectors' endpoints (in yellow and red) from waggle-runs performed by two dancing bees during single dances. These bees foraged regularly on a feeder placed 225 m west of an observation hive (52° 27′ 25″ N, 13° 17′ 46″ E) whose entrance pointed toward the north. In the radial maps, the direction of the feeder corresponds to 0°. Dances were video-recorded (at 88 frames s^{-1}) on the same day, in the morning (a), and the early (b) and late (c) afternoon, meaning that the sun (indicated by a yellow circle) was behind (a), to the side (b), or in front of the bees (c) during their flights toward the feeder, respectively. The coordinates indicated by the single waggle-runs are widely scattered around the actual position of the goal.

But is there any indication of some form of persisting spatial memory available to transitorily uncommitted honeybees (either dancers or followers)? Sometimes the waggle dance occurs in the absence of foraging. Under these conditions, it is performed in accordance with the current position of the sun and without any view of the sky, even during the night. These dances encode spatial information about goals that the dancers would have visited if they were guided by their sense of time (Lindauer, 1957, 1960; von Frisch, 1967). Furthermore, dancers seem to recall information related to goals visited several weeks earlier and estimate, at night, the closest goal in time after being trained to two different feeding places at two different times during the day (von Frisch, 1967). It follows, therefore, that honeybees use persisting memories to control their dances, which can be retrieved by specific stimuli (e.g., odors associated with the prospective goal) and whose content is appropriately combined with the time of day and complexes of signals that determine the animal's overall motivational state. The retrieval of long-term spatial memories has been observed in navigating bees (e.g., Menzel et al., 1998, 2000), but its appropriate incorporation into the dance context

poses additional questions. One of these questions is whether the waggle dance conveys to a follower only the approximate direction of and distance to the goal, or whether it also encodes a constellation of signals embedded in the follower's spatial knowledge, built throughout its previous flights and organized by reference to topographical features of the hive's surroundings. The structure of the spatial memory in honeybees will be addressed in the section titled 'Memory Structure'; we shall see that there is convincing evidence indicating that navigating bees may benefit from a topological representation of the environment, or a maplike spatial memory. It is thus conceivable that if honeybees are able to store spatial memories linked to specific locations in the field, and perhaps memories on specific features of their targets (e.g., food availability at a certain time of the day), the dance followers might also be able to combine information available through the dance with information from their own spatial memory, either already associated with the goals being indicated or in spatial relation to landmarks embedded in the seemingly topological structure of their spatial memory. What kind of spatial memory may be necessary for the waggle dance to encode information on past goals? How do these memories develop throughout the dancer's foraging life? These questions refer to the cognitive complexity underlying dance communication in honeybees. Future research on dance communication will certainly profit from the analysis of the interplay between the process of encoding and decoding spatial information in the dance and the structure and content of the honeybees' spatial memory.

1.25.3 Navigation

The term navigation denotes an animal's ability to efficiently travel between at least two specific distributions of concurrent signals (locations), even without having sensory access to the signals that define its targeted location. This notion removes any reference to the sensory modalities involved in gauging compass directions and distances and the control of the motor programs underlying the subject's locomotion. For the location to be reached, therefore, a navigating subject must be able to detect whether or not the immediate distribution of signals available within its current sensory horizon corresponds to the location it has been traveling to, a process that, in principle, only depends on innately

stored information and programmed responses. In most animal species, however, survival involves moving regularly from and to several locations. It follows that to cope with such a complex navigational task, the single distributions of signals defining these locations (available from either idiothetic or allothetic sources or from both) must be stored in specific forms of persistent memories. Differences in the content and the organization of these complexes of memories may arise as long as task complexity varies across taxa.

1.25.3.1 Typology

Different classification schemes are used in the analysis of spatial behavior. Kühn's (1919) attempt to conceptualize orientation mechanisms on the basis of the relationship between sensory stimuli and an animal's response to them is an early example of these schemes. In recent decades, research on spatial behavior has also nurtured the development of biologically inspired artificial navigation systems. This gave researchers an opportunity to classify several theoretical accounts of spatial behavior within a single unifying framework centered on the structure and content of the information used by the navigating agents. The ensuing classification schemes are based on task complexity and experimentally tested features of an agent's spatial behavior (Trullier et al., 1997; Franz and Mallot, 2000); they tend to be purposely broad, ignore endogenously coordinated performances, and dissect complex behaviors found in nature into motor programs that can be reliably implemented in artificial systems. Although somewhat crude, these typologies provide a suitable basis for analyzing basic strategies of spatial behavior, feature detectors, and navigation learning. Their most salient characteristic is that they account for complex navigational tasks by means of hierarchically organized, interacting strategies. For example, Trullier et al. (1997) conceive taxes (Kühn, 1919; Fraenkel and Gunn, 1961) as the basic machinery of all navigating agents and then distinguish between local navigation and way-finding. Local navigation accounts for orientation in the immediate environment, where the agent acts based on information available within its perceptual range, whereas wayfinding involves moving in a large-scale environment, where relevant cues lie beyond the perception range, and the goal is not in the immediate environment. Technically speaking, each of these categories can still be divided into several levels: search,

direction-following, aiming and guidance for local navigation, and recognition-triggered responses, topological, and survey navigation for way-finding (Franz and Mallot, 2000). Due to their hierarchical organization, way-finding relies on local navigation, but it is not yet clear how these strategies may interact in the brain, or how animals recognize specific locations, let alone how they may assign specific identities to these locations, a prerequisite of some high-level navigational tasks. Evidence indicates, however, that a hierarchical array of seemingly different, interacting strategies underlies the spatial behavior of some species of navigating insects (Wehner et al., 1996; Menzel et al., 2005). In the present context, we will use this basic typology to survey the structure and content of the spatial memory used by desert ants and honeybees, because data from these two navigating insects are frequently discussed using different terminologies and approached from different conceptual frameworks.

1.25.3.2   Navigation in Desert Ants

Desert ants of the genus *Cataglyphis* live in subterranean nests surrounded by relatively flat and featureless areas. They forage individually and travel over distances of hundreds of meters along circuitous paths during their foraging excursions. After grasping a food item, they quickly return in a straight line to the proximity of the starting point of their journey, where they finally break off their homeward runs and start a systematic search aimed at pinpointing the entrance of the nest; avoiding overheating is crucial in their environment. These ants primarily benefit from path integration (Mittelstaedt and Mittelstaedt, 1980), also referred as to dead-reckoning (*See* Chapter 1.12), to accomplish their remarkable homing performances (Wehner, 1992; Collett and Collett, 2000). This means that a navigating ant iteratively computes all its rotational and translational motion components, integrating them into a sort of global vector (Wehner, 2003) that connects, at any time, its current location and that of the starting point of the excursion. This navigation strategy can easily be revealed by displacing the animal over some distance; after being released, it chooses a compass direction and walks an approximate distance that brings it to a predictable, virtual reference point (Pièron, 1904; Santschi, 1911).

Desert ants appear to inexorably compute this type of vectorial information and are incapable of using more than one vector simultaneously. They benefit from inverse forms of these home vectors and efficiently move from the nest to previously visited field locations. Global vectors also appear to be stored and recalled in accordance with specific contexts, meaning, for instance, that when a returned ant is moved back to a recently visited location, it does not apply its recent home vector to once again navigate its way to the nest. Instead, it uses a systematic, time-consuming search strategy to find the nest's entrance (unless it navigates in familiar terrain offering conspicuous landmarks, as we will see). Under these circumstances, however, the information about its recent home vector does not disappear, and the ant is able to subsequently use an inverse form of it to quickly find its way to the previously visited location. This indicates, in turn, that path integration information is transferred from some form of working memory into a different, more persisting memory stage, from which it can be later recalled on the basis of context-dependent signals (Wehner, 2003).

In order to use path integration, a desert ant must be able to align its trajectory with a locally available compass direction and to reliably acquire distance information. *Cataglyphis* ants do not acquire directional information by means of idiothetic sources, such as an inertial compass or proprioreceptive signals; they do it using a celestial compass based on a specialized set of polarization-sensitive ultraviolet receptors located within a particular portion of the retina (Wehner, 1994, 1997), which detect the pattern of polarized light in the blue sky (Wehner and Müller, 2006). The functioning of this celestial compass involves an internal ephemeris function (Wehner and Müller, 1993) and demands recalibrations due to the inexorable changes in the pattern of polarized skylight that take place during the day. Desert ants do use idiothetic sources to compute translational motion: Distance information appears to be gauged by means of a step integrator (Wittlinger et al., 2006), and the control of distance by self-induced optic flow seems to be only slightly modified under specific test procedures (Ronacher and Wehner, 1995). These two path-related components – distances and directions – are combined via some sort of accumulator, the state of which encodes the ant's current coordinates relative to the reference point. The task of surveying the possible computational boundaries of this hardwired accumulator lies beyond the scope of this chapter (for comprehensive accounts of this issue, see Wehner 1997, 1999, 2003). In the present context, let us simply say that its functioning directly depends on locomotion (Seidl

et al., 2006), that it must process distance and compass information simultaneously (Sommer and Wehner, 2004), and that it allows an ant to gauge the ground distance while traveling undulating paths (Wohlgemuth et al., 2001; Grah et al., 2005). Its output can also be combined with external, sensory cues, thereby reducing search costs and improving the ants' general foraging strategy (Wolf and Wehner, 2000, 2005). This accumulator or path integrator also appears to continuously process information, that is, when homing ants are captured at the nest's entrance and displaced several times in a row to the initial position of their homeward runs, they move away from their reference location (the proximity of a virtual nest) when transferred to a featureless test channel (Andel and Wehner, 2004).

The findings described earlier illustrate how path integration, a basic local navigation strategy, enables *Cataglyphis* ants to reliably find the proximity of a virtual nest in unfamiliar terrain. Things are different in familiar terrain, however. The use of landmark-based information improves the efficiency of an ant's path integrator because the number of inaccurate alignments increases together with the length of the animal's excursion (Wehner and Wehner, 1986). Due to these unavoidable computational errors, a cross talk between path integration and guidance decreases the chance of missing the goal (Collett and Collett, 2000). Provided with an irregular environment, homing ants use landmarks while on their way to the nest's immediate surroundings (Bregy and Wehner, 2003; Knaden and Wehner, 2005), thus following well-defined paths or routes (Collett et al., 1992; Wehner et al., 1996; Kohler and Wehner, 2005). Moreover, it has recently been shown that they can also use memories of minute ground features to pinpoint the entrance of the nest (Seidl and Wehner, 2006). Guidance, therefore, leads navigating ants to locations where they have acquired a certain egocentric relationship with respect to a specific configuration of external signals (Wehner et al., 1996; Collett and Collett, 2000). They thus take advantage of a store of reliable landmark-based memories, which can be associated with specific motor routines and recalled in the appropriate context, and exhibit goal-directed movements at different locations (Collett et al., 1998; Collett and Collett, 2000, 2002; Åkesson and Wehner, 2002). Research on other ant species (e.g., Jander, 1957; Graham and Collett, 2002; Wehner et al., 2006) also provides evidence of local navigation and even more complex navigation strategies based on (1) the recognition of a catchment area from which a configuration of landmarks is perceived to be identical, (2) successful orientation within this area, and (3) the subsequent selection of a goal-directed movement. These strategies, therefore, rely on the combination of several recognizable areas associated with specific goals and directed actions (Barto and Sutton, 1981; Trullier et al., 1997; Collett and Collett, 2000).

The study of navigation in desert ants has led to a remarkable understanding of the basic mechanisms that these animals use for setting a directional bearing in the field (Wehner, 2003). Experience-dependent behavioral flexibility is conceived as a calibration process of path integration computations. Next, a context-dependent recollection of path integration coordinates may eventually lead to the ants' seemingly idiosyncratic routes. Landmarks provide information about turns to make and distances to travel next (Collett, 1996, 1998; Collett and Collett, 2000; Kohler and Wehner, 2005), such that seemingly complex performances might be based on simple rules that depend on learning sensory-motor routines. This is frequently referred to as procedural learning. Traditional thinking on ant navigation therefore conceives a toolbox of sensorimotor routines, whose stepwise application enables the animals to solve seemingly complex navigational tasks. Moreover, the recollection of single vectors does not require an overall representation of multiple locations, and the selection of goal-directed actions may exclusively depend on innately stored, calibrating information. This corresponds to the fact that ants do not appear to make decisions involving equivalent options. The question remains how ants use external signals to map several recognizable places. None of the current approaches to navigation in several ant species has yet reached the level of analysis achieved in the study of homing by desert ants, let alone the principles of navigation learning in walking insects.

Honeybees also exhibit procedural learning. They learn to negotiate complex mazes of adjacent boxes by associating colored disks with right or left turns, for example (Zhang et al., 2000; Srinivasan and Zhang, 2004), and also refer to compass directions in their dances on overcast days (von Frisch, 1967; Dyer and Gould, 1981). The latter result reveals that landmarks serve as a backup system, which conveys direction information to navigating bees and poses the question of how external signals are actually incorporated into the bees' representation of space (Gallistel, 1990). Interpretations from the study of ant navigation have often been transferred to bees. In

contrast to ants, however, bees fly over distances of a few kilometers, cruising well aboveground; they also use depth information extracted from motion parallax (Lehrer, 1996) and learn about the absolute size of landmarks (Horridge et al., 1992). Furthermore, honeybee foraging behavior involves a remarkable diversity of responses, including those underlying cooperative work during food gathering (see earlier discussion). When an experienced worker forages on a given flower species, for example, it leaves the colony and flies toward its targeted location for a certain amount of time, without interrupting its flight even when alternative flowers of the same species might be within reach. Once this motor program is extinguished, it begins searching for the flowers it recognizes according to their odors, colors, and shapes and inspects them by means of specific motor commands that allow it to efficiently find and collect the offered nectar (von Frisch, 1967). Meanwhile, it adjusts its estimate of how much nectar ought to be collected (Núñez, 1966). Finally, it initiates its return flight to the hive. Although exaggeratedly simplistic, this scheme illustrates an intriguing feature of the honeybee foraging strategy: each animal leaves the colony with a large – and diverse – amount of information, which is used in context-specific ways and involves expected outcomes of particular behaviors. The contexts are defined by both time and space, a fact that becomes strikingly evident when bees forage on multiple locations throughout the same day. Furthermore, there is a cross talk between navigation and collective foraging (see earlier discussion), which involves specific responses to numerous features and dynamic components of the animal's sensory world. As we shall see next, the repertoire of navigational performances in honeybees is far from simple. Together with complex modulatory processes, learning is at the heart of the animals' navigation skills.

1.25.3.3   Navigation in Honeybees

Foraging honeybees usually follow straight flight trajectories between specific locations and the hive (Beutler, 1954; von Frisch, 1967). If they are caught at the moment they depart from the hive and then released at a different spot in the field, they fly in the direction they would have taken if they had not been moved to the release site, meaning that they fly in the correct compass direction but along a false route relative to the goal they were originally traveling to. They perform in a similar manner when caught at the beginning of their homeward flight. Once again, they fly in the predisplacement compass direction which might have connected their foraging location and the hive, but along a false route with respect to the actual location of the colony (Wolf, 1927; Menzel et al., 2005). The bees' flown distances and compass bearings in this type of experiment resemble the global vectors observed in desert ants (see the section titled 'Navigation in desert ants'), supporting the view that honeybees also use vector memories that develop through their regular flights. Furthermore, when bees arriving at a foraging spot are held captive for several hours, they subsequently fly farther outward from the hive along the same hive-target direction (Dyer et al., 2002). After being trained along a fixed route, therefore, vector memories will reliably guide honeybees back to the hive and toward specific field locations; unless they have been artificially displaced.

In fact, navigation research in flying hymenoptera has long been based on displacement experiments and the analysis of the animals' homing abilities (Tinbergen and Kruyt, 1938; Thorpe, 1950; von Frisch, 1967; Tinbergen, 1972; Menzel et al., 2000, 2005). If navigating bees only rely on global vectors and random searches, displaced foragers might have trouble rapidly finding their way back to the colony. They do return home when released at a new, unexpected location, however, and they do it reliably and relatively fast when released within the range of approximately 1 km from the hive (Capaldi and Dyer, 1999; Menzel et al., 2000). Consider the following experiment: One group of bees was trained to forage on a stationary feeder placed 300 m away from the hive, and another group was trained to forage on a close feeder that rotated around the hive at a constant radius of only 10 m. Hence, the foragers from the latter group had not experienced a flight vector connecting the hive and a fixed, distant foraging location. However, despite lacking this experience, they returned home equally well from various possible directions and as quickly as the animals from the former group, which had experienced a predisplacement route training (Menzel et al., 2000). Furthermore, the results of this experiment could not be explained by reference to local navigation strategies, due to the lack of landmarks in the vicinity of the hive and the actual distance to the different released sites (Menzel et al., 2000). This indicates that successful homing in honeybees does not necessarily depend on a random, time-consuming search strategy. Recently, radar traces of the full flight

trajectories of displaced honeybees revealed that the last phase of homing is eventually accomplished by straight, goal-directed flights toward the hive (Menzel et al., 2005), supporting the view that honeybees are able to store and retrieve allocentric cues that help in defining compass directions in the field (Menzel et al., 1998).

The results described, in addition, pose the question of how the forager's working memory is organized and what role its content actually plays during navigation. Path integration is the subject of computational errors (Benhamou et al., 1990) and controls navigation as long as the animal combines it with multiple environmental cues. It is therefore reasonable to ask how landmarks provide honeybees with a basis for accurate homing. The complexity underlying such a strategy still remains open. How does it rely on guidance? How many configurations of landmarks can be processed and stored? How much does the animal perceive about these configurations, and how does it relate them? Are sequentially learned configurations generalized in such a way that they can be categorized, or counted, or even embedded into a more general, combined representation of space (Menzel et al., 2006; *see also* Chapter 1.12)? These questions are also at the heart of a long-lasting controversy (Wehner and Menzel, 1990), namely, whether navigating insects have at their disposal only minimal cognitive modules enabling them to store and retrieve ordered sequences of context-dependent actions (Wehner, 1999), or whether they also store and retrieve relations among points, lines, and surfaces somehow embedded in an internal representation of space (Menzel et al., 2006; *see also* Chapter 1.12 for a detailed account of this issue). Answering these questions, however, would only be possible after revealing the mechanisms underlying what we now merely label as specific responses to specific configurations of external signals, such as the response of a navigating bee to a familiar visual scene. Consider the term snapshot (Cartwright and Collett, 1983), for example; it denotes an insect's memory of visual landmarks, and it helps in formulating hypotheses based on matching algorithms and behavioral data, but its neurobiological basis is yet to be established. Similarly, we simply do not know how multiple and complex procedures might be combined in a common spatial memory store.

One of the reasons that led to differences in conceptualizing navigation in flying insects lies in the fact that most experiments were performed with animals trained along fixed, predisplacement routes and subsequently observed only during their initial postdisplacement flight paths. Most likely, only the motor routines based on the actual content of the animals' working memory can be revealed in this manner. The bees' exploration of the environment, however, does not begin with flights along fixed routes, which develop relatively late in the animals' foraging careers, and it is the spatial memory that develops during the bees' exploratory flights that might supply the animals with information for successful homing when vector memories fail. Therefore, an important aspect related to the questions listed earlier might be at stake – how spatial behavior develops.

Honeybees begin foraging only after executing a series of exploratory flights of increasing lengths (Becker, 1958; Vollbehr, 1975; Winston, 1987; Capaldi and Dyer, 1999), normally on several consecutive days (von Frisch, 1967). Using harmonic radar, Capaldi et al. (2000) showed that when honeybees are engaged in these exploratory flights, they keep the trip duration constant, but fly faster with increased experience of the terrain, so that the later flights cover a larger area than the earlier flights. Each flight, in addition, is typically restricted to a well-defined, narrow sector around the hive, and changes in this respect appear to be related to the number of previous flights. Taken together, these results indicate that early flights provide honeybees with repeated opportunities to become exposed to different landscape features (including the hive's position) from different viewpoints, supporting the view that they may store landscape information in a progressive fashion (Capaldi et al., 2000). At the individual level, however, the ontogeny of these flights remains a mystery, and the question of how the animals use information available throughout successive flights is still unanswered.

Tracing the full flight trajectories of free-flying bees allows evaluation of the complexity of the animals' spatial memory, and this is now possible using harmonic radar techniques (Riley et al., 1996). Menzel (2005) and colleagues recorded more than 200 flight trajectories in this manner (Menzel et al., 2005) and analyzed the flight paths of three different groups of animals: (1) honeybees that had been trained to forage on a stationary feeder located 200 m east of the hive, thereby repeatedly following a well-defined predisplacement route; we shall call them SF-bees; (2) honeybees trained to forage on a feeder that circled around the hive within a distance of 10 m, thereby experiencing no route prior to

displacement; here we call them VF-bees; and (3) honeybees that lacked training and had closely followed a waggle dance for the feeder placed 200 m east of the hive; we shall call these bees R-bees. Three phases of navigation can be distinguished among these groups of honeybees (Menzel et al., 2005): (1) vector flights, (2) circuitous flights, and (3) straight homeward flights. Vector flights were apparent in the SF- and R-bees, but not in VF-bees. Those from SF-bees showed compass directions and distances that matched the predisplacement route, and those from R-bees matched the spatial information that the waggle dances conveyed to a human observer (Riley et al., 2005). Hence, it follows that, when accessible, route memories are invariably applied first, and vector flights are based on directions and distances from these memories. The circuitous flights showed multiple returns to the release site and to the end of the vector flights in the case of SF- and R-bees. During this phase, the flight speed was significantly lower than during phases of straight flights. These flights were also considerably longer for the SF- and VF-bees (carrying full crops) and shorter for R-bees (captured before getting in contact with any sugar reward), suggesting that this type of motion might not only underlie a process of reorientation (necessary after displacement), but also some sort of exploratory behavior (Menzel et al., 2005).

The honeybees from all these three groups returned to the hive by means of fast, straight homeward flights, and a detailed analysis of the straightness of these flights led to a clear distinction between the second and third navigation phases, thereby revealing the field locations where the straight homeward flights began (Menzel et al., 2005). They originated along different directions relative to the hive's position and usually began far outside a radius of 60 m, where the animals might have used visual cues to find their way back to the colony by means of aiming or guidance or both. Furthermore, they also began at locations with conspicuous, artificial landmarks, and when these landmarks were either displaced or removed, the animals were equally successful during homing. The most consistent hypothesis that accounts for these homing performances is that the ground structure itself provided the displaced honeybees with reliable information to find their way back to the hive (Menzel et al., 2000, 2005). Most significant is this: A third of the SF-bees made straight and fast flights directed not only to the hive but also first to the feeder and then to the hive (Figure 2). This latter result fits well with a
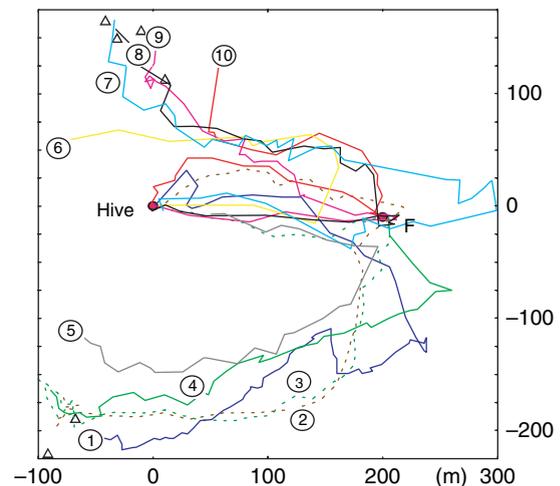
Figure 2 The homing flights via the feeder. Ten SF-bees (of the 29 bees tested under similar conditions) performed their homing flights via the feeder. Bees released south of the hive are shown by flight paths 1–5, and those released north of the hive are indicated by flight paths 6–10. The bee from flight path 4 landed at the feeder and flew to the hive after filling its crop. All bees were tested with the normal arrangement of tents under sunny weather conditions (for details see Menzel R, Greggers U, Smith A, et al. (2005) Honeybees navigate according to a map-like spatial memory. *Proc. Natl. Acad. Sci. USA* 102: 3040–3045).

topological representation of the environment (Trullier et al., 1997) and can also be explained by two mutually related hypotheses. First, homing bees might be able to integrate at least two vector memories. Assume the following premises: (I) they are able to associate vector memories defining homeward flights with specific configurations of external signals, and (II) when exposed to these signals, the corresponding vector memories can be recollected from a memory store. Next, if two of these memories are simultaneously recollected and transferred to the animal's active working memory, they might be combined to steer a seemingly new flight trajectory. The second hypothesis can be thought of as a more complex form of the first one. It assumes that the bees' orientation flights, together with their initial foraging excursions, lead to a memory of a network of several homeward vectors connecting specific distributions of external signals, including the hive's location. Such a process is believed to be possible in mammals and birds (Gallistel, 1989; O'Keefe and Nadel, 1978).

These concepts are closely interconnected to several issues about the honeybee dance communication

system, somehow embedded in the following question: Do dancers and followers have analogous memories? When von Frisch (1967) compelled honeybees to fly a two-legged detour path to reach an artificial feeder, the trained animals indicated in their dances the direction of a straight line toward the goal. They might have computed this compass direction from the two legs of the detour, but they also indicated the actual flown distance, and not the distance of the segment connecting the feeder and the hive. Thus the bees encoded in their dances the direction of a virtual flight vector, but not its length (von Frisch, 1967). This poses the question whether it is the outbound or the inbound flight or both that provides the dancer with the spatial information that is finally conveyed to the human observer. If spatial information available during the homeward flight (a directional bearing, for example) can successfully be incorporated into the dancer's maneuvers, the waggle dance might also be capable of conveying information that the dancer (and probably also a follower) has already linked to a specific spot in the field. It follows, therefore, that the efficiency of the dance communication system would greatly depend on the way in which both dancers and followers acquire, store, and retrieve navigational memories.

Behavioral studies of self-induced optic flow in honeybees (e.g., Srinivasan et al., 1997) take advantage of the following fact: Flying a short distance close to a surface gives the same integrated optic flow as flying a longer distance further from the surface. As a result, when honeybees fly through narrow tunnels with visually textured walls, they experience a subjectively flown distance that is greater than that actually flown (Srinivasan et al., 1996), also indicating a longer distance in their dances (Srinivasan et al., 2000). This allows manipulation of a bee's navigational experience of a subjective flight path (De Marco and Menzel, 2005). Honeybees perform longer waggle phases when they fly through a visually patterned tunnel on their outbound flight (**Figure 3(a)–(c)**). Thus, when the tunnel is set perpendicular to the straight line connecting its entrance and that of the hive, a mismatch arises between the animals' estimate of the goal's location (derived from path integration information from the outbound flight) and its actual location in the field. Under such conditions, the bees' waggle dances indicate a direction close to that of the straight line connecting the hive and the actual goal's location (**Figure 3(d)– (i)**), and the virtual detour has no significant effect on

the duration of the bees' homeward flights, indicating that they fly directly back to the hive after leaving the tunnel through its far end. Moreover, path integration coordinates appear to be more strongly weighted in the dance maneuvers only with increasing experience of the terrain (**Figure 3(j)–(l)**), thus supporting previous interpretations (Otto, 1959; Edrich and Scheske, 1988) of the relationship between information available on-site and the encoding of direction in the dance. These results indicate that (1) a discrepancy between subjective measures of distances and directions and path integration coordinates already linked to visual scenes has no significant effect on the triggering of the waggle dance, and (2) the process of encoding spatial information in the dance involves detecting and processing such a discrepancy (De Marco and Menzel, 2005). It is not yet clear to what degree honeybees might refer in their dances to the inbound component of their journeys, or whether they embed the encoding spatial information in the dance into their maplike spatial memory.

1.25.3.3.1 Memory structure

It appears that honeybees develop spatial memories in three different contexts: (1) during their initial orientation flights, (2) while flying repeatedly from and to a specific field location, and (3) while following dances. We refer to these memories as (1) the general landscape memory, (2) the route memory, and (3) the dance memory, respectively. Note that the term general landscape memory makes no assumptions about the structure of the spatial information accessible through it, and that route memories may involve vector memories as well as procedures based on sequences of context-dependent actions. This typology, therefore, denotes processes not yet understood, but accounts for predictable actions. These memories might have different properties. Route memories provide information about directions and distances, and the same may be true for a dance memory, although the extent to which the latter may be combined with spatial information accessible from the bees' memory store remains an open question. Honeybees seem to transfer these two memory forms into their active working memory and apply them first. Once applied, however, they lose their influence on behavior. The directional component of these memories, in addition, is susceptible to updates according to changes in the animal's motivation. When at least two route memories are accessible, it becomes feasible to recognize that they have been linked to landmark-based information.

This led to the concept that honeybees use their route memories to estimate the sun's azimuth (von Frisch, 1967; Dyer and Gould, 1981), and that they may integrate at least two of them under specific circumstances (Menzel et al., 1998, 2005). The general landscape memory might be thought of as a structure of several recognizable locations within the range of the animals' orientation flights. It might arise through the integration of information provided by two or more route memories (Menzel et al., 2005)

or by a process by which the bees innately store specific distributions of external signals and assign them specific identities based on idiothetic and allothetic cues. According to these hypotheses, honeybees may use their general landscape memory only when their active working memory has no access to route or dance memories.

The concept of multiple memories hierarchically organized is a generally accepted mind-set in neurosciences. Implicit and explicit knowledge, or
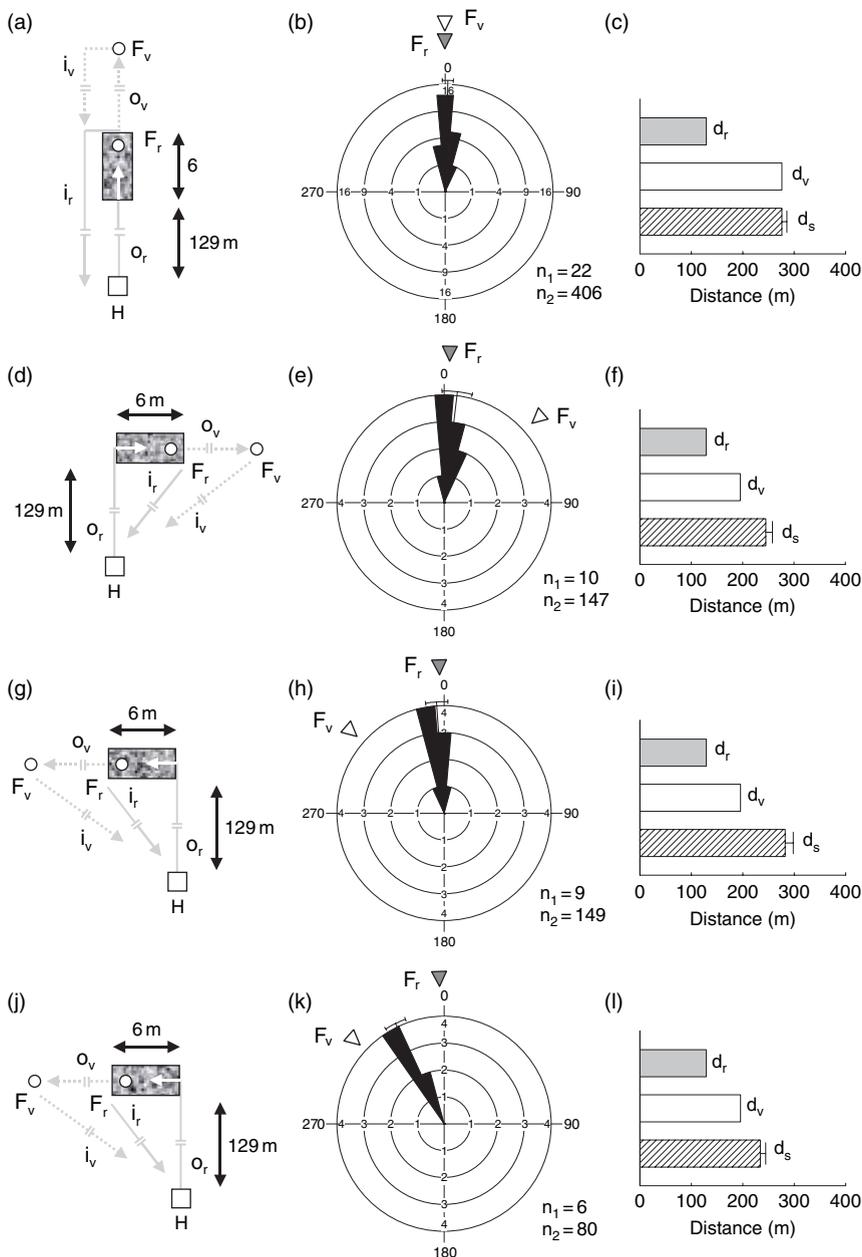
declarative and nondeclarative knowledge, develop from the various learning strategies, which involve various brain structures in mammals, including humans (Cohen and Squire, 1980; Packard and McGaugh, 1996; Schroeder et al., 2002; Chang and Gold, 2003). Navigation in mice and rats, intensively studied with respect to the role of the hippocampus and striatum, is actually embedded in a convincing theoretical framework, whereas hippocampal place cells are responsible for orientation based on specific distribution of signals and sequences of experiences that help in defining geometric relations among landmarks, and the striatum is responsible for those forms of learning based on signals sent by the goal (O'Keefe and Nadel, 1978; Moser and Paulsen, 2001; McNaughton et al., 2006; Witter and Moser, 2006). It might be interesting to evaluate whether and how the seemingly different navigational memories described earlier rely on the various neuronal structures in the bee brain. What can be behaviorally tested in the near future is whether dance memories are coupled to the general landscape memory.

1.25.3.4 Insect Migrations

Several insect orders exhibit far-distance movements referred to as migrations (Drake and Gatehouse,

1995). Populations of butterflies, moths, dragonflies, and locusts are seasonally engaged in far-distance migrations (e.g., Williams, 1958; Johnson, 1969; Holland et al., 2006). Costs and adaptations have long been addressed in migrating insects (e.g., Rankin and Burchsted, 1992), but the selective forces behind these movements are not yet fully understood. The distribution of offspring across a range of areas and conditions favorable for future reproduction might have played an important role in the evolutionary development of these movements (Wilson, 1995; Holland et al., 2006). At least two distinctive features of these far-distance movements distinguish them from the regular excursions of the central place (Orians and Pearson, 1979) foraging hymenopterans (i.e., bees, wasps, and ants). First, return migration has yet to be documented in insects (Holland et al., 2006), meaning that with a few exceptions (e.g., Urquhart and Urquhart, 1979), migrating individuals do not perform round-trip journeys that bring them into the areas from which they previously departed (Holland et al., 2006). In monarch butterflies, for example, several generations are produced during their northward migrations (Brower, 1995, 1996). Second, although migrating insects compensate for wind drift and maintain a heading using the sun compass (Srygley and Oliveira, 2001; Mouritsen

Figure 3 Experimental layout and results of an investigation of the encoding of spatial information in the waggle dance. A visually patterned tunnel was used to create a virtual detour. By compelling the bees to fly through such a tunnel, set up outdoors in various configurations, it is possible to add a virtual distance to the journey from the hive to the feeder – either straight ahead or to the right or left. Bees were trained to forage on a feeder placed at the far end of a 6-m-long, 30-cm-wide, and 30-cm-high tunnel. The tunnel's entrance was located 129 m away from the hive, and its walls and floor were decorated with a random visual pattern. (a) Experimental arrangements first had the tunnel oriented at $0°$ with respect to the direct line connecting its near entrance and the hive (h). The bees flew through the tunnel during their outbound flights (o_r) but not during their inbound flights (i_r). F_r and F_v correspond to the real and the virtual location of the feeder (white circle), respectively; whereas o_v and i_v correspond to the virtual outbound and inbound flights, respectively, as derived from the overestimated distance flown inside the tunnel. (b) Distribution of the individual mean directions signaled in the waggle dances recorded in the tunnel experiment described in (a), mean vector direction $\mu = 1.33°$, $r = 0.99$, $P < 0.001$, n_1 (number of animals analyzed) $= 22$, n_2 (number of waggle-runs analyzed) $= 406$. The frequencies within $10°$ class ranges are shown as the areas of the dark wedges. The dark spoke and segment indicate the mean vector μ and 95% confidence interval, respectively. The gray and white arrows indicate the directions toward the real (F_r) and the virtual (F_v) feeders shown in (a), respectively. (c) Shown are the flown distance (mean $\pm$ SE) signaled in the waggle dances recorded in the tunnel experiment described in (a) (d_s, striped bar), the distance to the virtual feeder (d_v, white bar, in this case equivalent to the signaled distance), and the real distance from the hive to the food site (d_r, gray bar). (d–f) Experimental arrangements and results as in (a–c) with the tunnel rotated $90°$ to the right. The distance flown inside the tunnel oriented at $0°$ (c) was used to compute the location to be signaled (F_v: direction and d_v: distance) if the global vector computed by the path integration of the outbound flight provides the dancers with the spatial information encoded in the waggle dance. In (e), mean vector direction $\mu = 6.77°$, $r = 0.98$, $P < 0.001$, $n_1 = 10$, $n_2 = 147$. (g–i) Experimental arrangements and results as in (d–f) with the tunnel rotated $90°$ to the left. In (h), mean vector direction $\mu = 356.1°$, $r = 0.99$, $P < 0.001$, $n_1 = 9$, $n_2 = 149$. (j–l) Experimental arrangements and results as in (g–i), obtained with the experienced bees. In (k), mean vector direction $\mu = 333.99°$, $r = 0.99$, $P < 0.001$, $n_1 = 6$, $n_2 = 80$. The reader will find a detailed description of this experiment in De Marco RJ and Menzel R (2005) Encoding spatial information in the waggle dance. *J. Exp. Biol.* 208: 3885–3894.

and Frost, 2002) and possibly also a magnetic compass (Etheredge et al., 1999), their flight routes depend strongly on atmospheric conditions and seasonal wind patterns (e.g., Rainey, 1951, 1976; Kanz, 1977; Drake and Farrow, 1988; Gatehouse, 1997; Chapman et al., 2002). It thus appears that insect migration is basically controlled by innate mechanisms and does not rely on learning, although the genetic control of flight direction in migrating insects has yet to be confirmed (Holland et al., 2006).

1.25.4   Conclusions and Future Prospects

We have argued that a distinction between instinctive and learned behaviors, a fundamental issue in behavioral research, is not possible without thoughtfully considering the interplay between an animal's possible phylogenetic boundaries and the sources of the external signals that belong to its specific sensory world, simply because the effects of learning on a subject's performance will always be superimposed onto those of its phylogenetic boundaries. We also claimed that it is in the context of communication and navigation that learning transcends elementary forms of association in particularly clear ways. Communication and navigation in insects have been extensively studied on the sensory processing level, but the structure and content of the spatial knowledge underlying such phenomena have yet to be addressed. This might be particularly feasible in honeybees, due to their extensive behavioral repertoire, which also seems to involve decisions, and their small, experimentally accessible brains, which allow the study of system-level neural correlates of learning and memory. In honeybees, in addition, these two behavioral domains appear strictly related to each other via the famous waggle dance, although their relation is not fully understood. We have explored new findings (Menzel et al., 2005) indicating that the spatial knowledge used by honeybees to navigate within the range of their orientation flights is much more complex than hitherto thought. Several interacting – and probably competing – memory systems seem to be at work. These findings also raise questions about the process of encoding and decoding information in the waggle dance (De Marco and Menzel, 2005). We reviewed published data (von Frisch, 1968) and recent evidence (Biesmeijer and Seeley, 2005) suggesting that the spatial knowledge available to followers is also involved in dance communication and that learning might be at the heart of this impressive communicating system. The flight paths of navigating bees can now be traced with radar techniques. Mechanical models of dancing bees and virtual environments allowing navigation experiments under controlled experimental situations can also be developed. Thus tools are available to tackle these questions.

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