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REVIEW

# Spatial memory, navigation and dance behaviour in *Apis mellifera*

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**Abstract** Navigation and dance communication in *Apis mellifera* have been extensively studied on the level of sensory processing, but the structure and content of the spatial memory underlying such phenomena have yet to be addressed. Here we survey new findings indicating that the memory used by bees to navigate within the range of their orientation flights is much more complex than hitherto thought. It appears to allow them to decide between at least two goals in the field, and to steer towards them over considerable distances. Two models concerning the structure of bees' spatial memory are developed from new empirical evidence. The first one relies on the integration of at least two flight vectors, while the second assumes the existence of a 'functional' map based on the information available on-site. These findings also raise questions about the process of encoding and decoding information in the context of the waggle dance. We review published data and recent evidence indicating that memories of topographical features might also be involved in dance communication, and point out what needs to be addressed to elucidate the corresponding memory demands. The flight paths of recruited bees can now be traced by means of radar techniques, and thus tools are available to tackle these questions.

**Keywords** *Apismellifera* · Navigation · Waggle dance · Memory · Spatial learning

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## Introduction

Navigation allows animals to travel between locations without having direct sensory access to these locations. In this sense, it differs from close, secondary orientation and guidance (Fraenkel and Gunn 1961), which include all forms of spatial relationships between the animals' body positions and movement trajectories relative to the various sensory conditions. There are different conceptual frameworks in which research on navigation is usually discussed (e.g. Tolman 1948; von Frisch 1967; Wallraff 1974; Mittelstaedt and Mittelstaedt 1982; Thinus-Blanc 1987; Gallistel 1990; O'Keefe and Nadel 1978; Redish 1999), but the task of surveying theories of spatial behaviour lies beyond the scope of this article. Instead, we review recent research in the field of bee navigation and dance communication, and pose open questions related to the structure and demands of the spatial memory used by bees to guide their flights in the field and to control their dance manoeuvres.

Navigation involves processing information available 'en route', collected and stored during the outward journey, as well as information available 'on-site', derived from specific stimuli present at well-defined positions in the field (see Mittelstaedt and Mittelstaedt 1982). Both vertebrates and invertebrates are able to not only reliably follow routes by the exclusive use of information acquired and stored en route, a mechanism called path integration (Mittelstaedt and Mittelstaedt 1973, 1982), but they also benefit from the information available on-site (e.g. von Frisch 1967; Akesson and Wehner 2002; Wiltschko and Wiltschko 2003; Etienne et al. 2004; Menzel et al. 2005). Theoretical accounts of path integration in polar or Cartesian coordinates have long been developed (Mittelstaedt 1983). Furthermore, the study of spatial behaviour in certain invertebrate taxa has led to a remarkable understanding of the basic mechanisms used by the animals to determine their position relative to a reference site and for taking up a directional bearing (Wehner 2003a, b). In spite of these achievements, however, the interaction between the information available en route and the information available on-site is poorly understood. Following routes in the known territory, for instance, usually relies on associations between landmark-based information and directions of movements, a well-documented strategy in insects (von Frisch 1967; Menzel et al. 1998; Collett et al. 2002a), but the complexity underlying this type of strategy remains a mystery. Does it rely on piloting (Akesson and Wehner 2002)? How many landmark views can be processed and stored, how much do the animals 'know' about these external cues (Collett et al. 2002b) and how do they relate them? Are sequentially learned landmarks generalized in such a way that they can be 'categorized' (Collett et al. 2003), 'counted' (Chittka and Geiger 1995; Chittka et al. 1995a, b), or 'combined'?

Bees are able to associate their homing flights (i.e. hive-directed paths) with on-site information (Lindauer 1961; Menzel et al. 2005). For this performance to succeed, they need information about the location of the hive relative to their current position in the environment in order to control their goal-directed movements. Interestingly, if successful homing depends upon landmark-based information (at least partially), it is pertinent to ask whether bees are able to process information from two or more of such 'learned' homing flights, and 'compute' new routes on their journeys back to the hive. If that were the case, what appears to be a route strategy based on information available en route, supported by landmark views, may turn out to be a map-like navigation strategy. The latter strategy is thought to allow goal-directed decisions at any place and towards any intended location within the familiar terrain, thus resulting in 'novel' routes (Gallistel 1990). Such a strategy is the subject of lively debate (Bennet 1996; Collett and Collett 2002). The most straightforward test of this possibility is to ask whether bees relate the corresponding computational processes not only to the hive, but also to other locations in the field (e.g. a foraging spot).

Experiments that avoided route training proved that displaced bees are able to exhibit fast homing flights from different locations in the field within the range of the animals' initial orientation flights (Menzel et al. 2000). These experiments led to the conclusion that bees are able to use a rather complex route strategy based on some sort of landscape memory that relates landmark views to the hive's location. Until recently, it had not been possible to critically test whether this strategy reflects a form of map-like navigation or a complex route strategy, due to the fact that the bees' flight paths could not be monitored over distances beyond direct observation. However, the complete flight paths of the displaced bees, inexorably faced with the problem of returning home after being transported to unexpected locations, have recently been recorded using harmonic radar (Menzel et al. 2005). The first part of this article explores these flight trajectories, which have provided new insights into the way in which navigational memories are functionally organized in the bee brain.

Work by von Frisch (1967) and colleagues revealed that the honeybee waggle dance conveys to the researcher the location of well-defined targets in a two-dimensional system of coordinates. It has also been concluded that those colony members 'attending' the dance can first decode the direction of and distance to the indicated goal (von Frisch 1967), and then find it on the basis of these two pieces of information (von Frisch 1967; Lindauer 1967; Gould and Gould 1988; Esch et al. 2001; Riley et al. 2005; see also Towne and Kirchner 1998). These discoveries are among the most important achievements made in behavioural biology in the 20th century, and gave rise to a number of puzzling questions about sensory, physiological and cognitive components of insect behaviour. They have also influenced the development of ideas about insect navigation (von Frisch 1967; Gallistel 1998; Dyer 1998a, b).

Comprehensive reviews of research on dance behaviour have focused on different aspects of its sensory basis, its role in the context of social foraging strategies and the evolution of bee dances (Gould and Gould 1988; Seeley 1995; Dyer 2002; Michelsen 2003). In the present context, these aspects will henceforth be eschewed altogether. Our aim is to briefly describe the bee waggle dance, in order to pose open questions on the encoding and decoding processes involved in dance communication, i.e. the processing of spatial information underlying the dancer's manoeuvres and the seemingly use of the transmitted information by the dance followers, respectively. We decided on this approach because the information that the dancer uses to control its manoeuvres depends upon the same kind of information it uses to navigate its flights in the field.

## Displacement reveals a complex strategy

Research on navigation has been largely based on displacement experiments and the analysis of the homing abilities of various vertebrate (e.g. Mittelstaedt and Mittelstaedt 1980, 1982; Etienne et al. 2004; Wiltschko and Wiltschko 2003) as well as invertebrate species (e.g. Jander 1957; Mittelstaedt 1962; von Frisch 1967; Görner 1973; Collett and Collett 2002; Wehner 2003a, b; Menzel et al. 2005). Once bees learn the location of a foraging spot in the field, they usually follow straight flight trajectories to and from that spot and the hive (Beutler 1954; von Frisch 1967). If they are caught at the moment they depart from the hive, and are then released at a different location, they fly in the direction they would have taken if they had not been moved to the unexpected release spot. This means that they fly in the correct compass direction but along a false route relative to the goal towards which they were originally flying. They perform in a similar way when caught at the beginning of their way back to the colony (i.e. when, still at the foraging location, they are ready to return home). Once again, after displacement they fly in the correct compass direction, which might have connected the foraging location and the hive, but along a false route with respect to the actual hive's position (Wolf 1927; Gould 1986; Wehner and Menzel 1990; Menzel et al. 2005). Together with estimates of the flown distances, these compass bearings resemble vector flights and lead to the hypothesis that bees benefit from vector memories (Wehner 2003a, b), which develop on the basis of the repetitive flights they perform from the hive towards a given foraging location, and vice versa. Once trained along a fixed route, this type of vector memory will reliably guide them back to the hive or to their foraging goals unless they have been artificially displaced to a new, unexpected location. After flying according to their vector memories, displaced bees might have trouble finding their way back to the colony, particularly if their navigation strategy basically relies on internal cues. Bees, however, do return home when released at a new, unexpected location, and they do it reliably when released within the range of approximately 1 km from the hive (Capaldi and Dyer 1999; Menzel et al. 2000).

## Homing

The homing behaviour of displaced bees indicates that they store and retrieve allocentric cues while setting a compass direction in the field, and that they can 'feed' their working memory with navigational information previously associated with such external cues in order to control their motor commands. This poses the question how the animal's working memory about the information available on-site is finally organized, and what role its content actually plays during navigation. Path integration appears to be inexorably associated with computational errors, whose number depends upon the length of the animals' excursions (Benhamou et al. 1990). Thus, it controls navigation only as long as the animals combine it with learned strategies and environmental cues (Etienne et al. 2004). It is therefore reasonable to assume that, working alongside celestial cues (von Frisch 1967), visual information derived from landmark views provides a basis for rapid and accurate homing.

Consider the results of the experiment shown in Fig. 1, in which return flights were timed in two different groups of animals: (1) bees trained to forage on a stationary feeder placed 300 m away from the hive (see 'Fc' in Fig. 1a), and (2) bees trained to forage on a close feeder that rotated around the hive at a constant radius of 10 m several times a day (see 'Fv' in Fig. 1a), such that no route was learned (Menzel et al. 2000). These latter bees had never learned a flight vector connecting the hive and a fixed (and relatively far) foraging location. However, in spite of lacking experience of a direct homing flight, they returned home equally well from all possible directions, and as fast as the other bees that had experienced route training prior to displacement (Fig. 1b). This means that these bees did not find the hive by means of random flights. Furthermore, their return flights cannot be consistently explained by means of successful piloting, due to the lack of landmarks in the proximity of the hive (see Menzel et al. 2000). Therefore, they must have used orienting information available on-site in order to steer their movements towards the hive's location.

## Orientation flights

Allocentric cues are useful only if the navigating animals are able to learn the spatial relationships they define. In bees, most studies of large-scale spatial learning have focused on the contents of spatial memory in experienced animals (see Dyer 1996). With a few exceptions (Opfinger 1931; Becker 1958; Vollbehr 1975; Capaldi and Dyer 1999; Capaldi et al. 2000), the question of how spatial memory develops has received less attention. Intriguingly, young bees that leave the hive for the first time, as well as bees that start flying after the colony has been moved into a new location, perform 'orientation' flights (von Frisch 1967; Becker 1958; Vollbehr 1975; Winston 1987; Capaldi and Dyer 1999). Moreover, they begin foraging only after they have performed a series of such flights, normally on several consecutive days (von Frisch 1967). Using

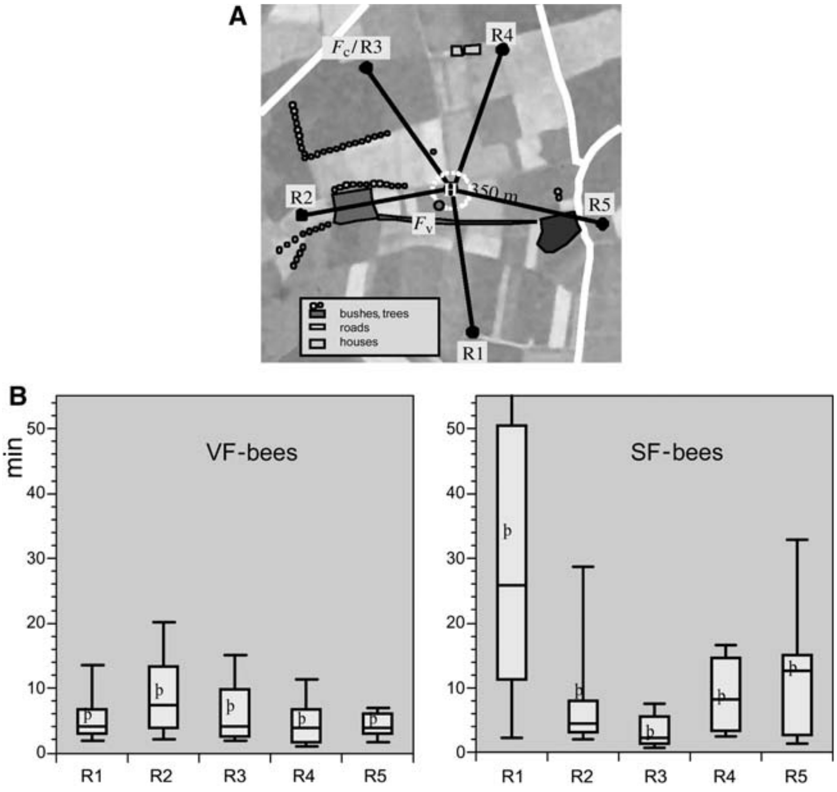


**Fig. 1** Experimental layout (**a**) and results (**b**) of an investigation of the flight times of bees released from five different locations around the hive (R1–R5). VF-bees foraged at a feeder (*Fv*) that moved around the hive, 10 m away from it; SF-bees were trained to a stationary feeder (*Fc*) 350 m away from the hive. SF-bees displayed vector flights. Thus, for example, when released at R1, they flew further away from the hive along the compass direction of their previous route training, thus having longer return times. VF-bees did not exhibit vector flights, due to the fact that they had not been trained to fly a fixed route. These bees returned home rather quickly, from all the five release sites, and their flight times did not differ significantly from those of the SF-bees released at R3 (Menzel et al. 2000)

harmonic radar, Capaldi et al. (2000) showed that orienting bees hold the trip duration constant but fly faster with increased experience of the terrain, so the later flights cover a larger area than the earlier flights. Moreover, each flight is typically restricted to a well-defined, narrow sector around the hive, and changes in orientation flights appear to be related to the number of previous flights. Taken together, these results indicate that the orientation flights provide honeybees with repeated opportunities to view different landscape features (including the position of the hive) from different viewpoints, suggesting that bees may learn the local landscape in a progressive fashion (Capaldi et al. 2000). At the individual level, however, the ontogeny of these orientation flights remains unknown, and the question of how bees may integrate external information collected (and stored) during sequential orientation flights into their navigation strategy is still open.

## Tracing full flight trajectories: new data lead to a new concept

Tracing the full flight trajectories of free-flying bees (over the range of a radius of ~1 km) allows evaluating the complexity of the animals' spatial memory. To this end, the bees are provided with electronic transponders that can receive and emit a modified radar beam. Once the transponder is attached to the animal, a radar system with two coupled, rotating antennae (one for the original pulse and one for detecting the signals emitted by the transponder) makes it possible to determine the bee's position in the field (Riley et al. 1996). More than 200 complete flight trajectories have recently been recorded using this method (Menzel et al. 2005). The flight paths of three different groups of animals were thus analysed: (1) bees that had been trained to a distant stationary feeder located 200 m east of the hive, henceforth: SF-bees—SF-bees thus established a route memory before being displaced; they were caught at the moment when they had finished feeding (and were ready to head back to the hive), transported in a lightproof container to a new location within 10–15 min, given a transponder and released; (2) bees trained to a moving feeder that circled around the hive within a short distance of 10 m, henceforth: VF-bees—VF-bees had not established a route memory before displacement; they were also caught after they had finished foraging, transported to a new location (as the SF-bees), given transponders and released; and (3) bees that lacked route training and that had followed a waggle dance which

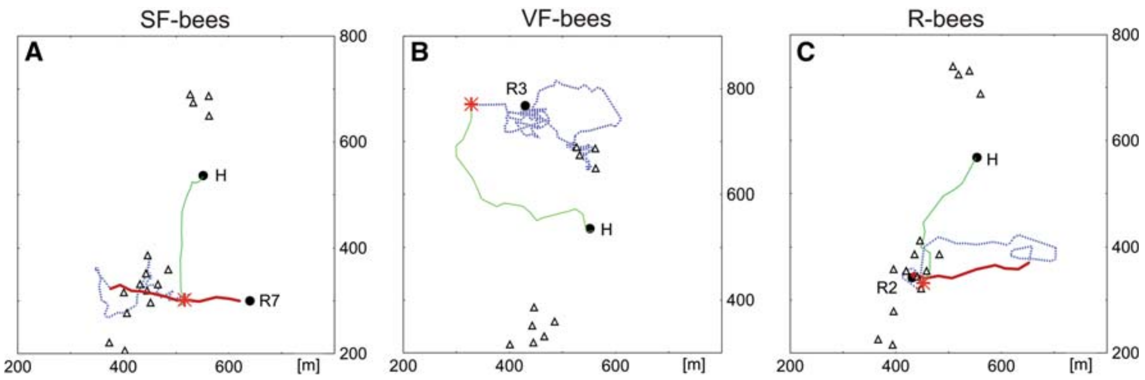


**Fig. 2** Typical flight paths of the displaced bees as shown by radar tracking (Menzel et al. 2005). **a** SF-bee released at location R7, south of the hive, after being trained to forage on a stationary feeder 200 m east of the hive (*H*). **b** VF-bee released at R3, northwest of the hive, after being trained to a feeder that rotated around the hive at a distance of 10 m. **c** R-bee (i.e. a dance follower) captured at its departure from the hive and released at R2. *Triangles* indicate the 3.5 m high tents used as artificial landmarks (see Menzel et al. 2005 for details). Three different flight phases can be distinguished in the SF- and R-bees: vector flights (*thick lines*), search flights (*dashed lines*) and homing flights (*thin lines*). VF-bees lacking route training show only the latter two phases

corresponded to a feeding station located 200 m east of the hive, henceforth: R-bees—R-bees were caught as they left the hive, transported (as the SF- and VF-bees), given a transponder and then released at different release sites (see Menzel et al. 2005 for details).

Three phases of navigation can be distinguished among these three groups of bees (Fig. 2; see also Menzel et al. 2005): (1) initial vector flights, (2) curved flights (henceforth: search flights), and (3) straight homeward flights, i.e. return flights. Vector flights were apparent in the SF- and R-bees, but not in VF-bees. The vector flights of the SF-bees showed compass directions and distances that matched those expected according to both the route training and the use of path integration information. Those of R-bees indicated that these animals used spatial information encoded in the waggle dances they had attended (Riley et al. 2005). Hence, whenever available, route memories (derived either from the bee's own experience in the field or from the waggle dance) are invariably applied first; vector flights are based on the heading and distance estimates related to those memories.

The bees' search flight phase showed highly variable curves and multiple returns to the release site (and also to the end of the vector flights in the case of SF- and R-bees). During the search phase, the flight speed was significantly lower than during the straight flight phases (vector and return flights). Moreover, search flights were 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 flight motion might not only underly re-orientation (necessary after displacement) but also some sort of exploratory behaviour through which bees may obtain information about external navigational cues if they do not run short of energy supply.

The third phase of navigation consisted of homeward flights, i.e. bees from all the three groups flew back to the hive along straight and relatively fast paths. Detailed analysis of the straightness of these homing flights led to a clear distinction between the search and return phases, which, in turn, revealed the precise locations in the field where the homing flights began (Menzel et al. 2005). Figure 3 shows these homeward flights, which originated along different directions relative to the hive's position, and which usually began outside the hive-centred area (radius 60 m) where the bees could have used visual cues to find their way back to the colony by means of piloting. Moreover, homeward flights began not only at locations in which conspicuous, artificial landmarks were present; when these landmarks were either displaced or removed, the bees were equally able to cover quite long distances during homing. These straight flights, in addition, were performed equally well under an overcast sky, and cannot be consistently explained on the basis of beacons present in the proximity of the hive. Moreover, since data had been reported indicating that navigating bees may use horizon landmarks to determine the direction of their homing flights (Southwick and Buchmann 1995), an area was chosen for these experiments that provided a homogeneous horizon (see Menzel et al. 2005 for further details). Taken together, these results indicate that the ground structure itself provided the displaced bees with reliable information for successful homing.

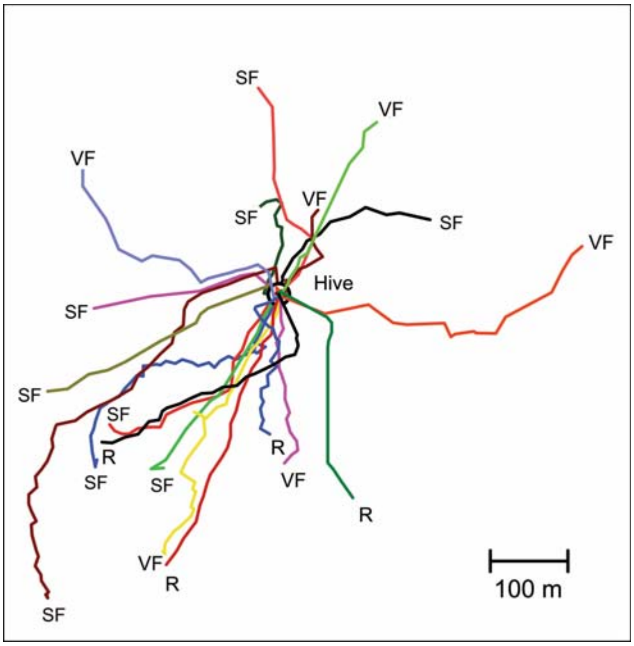


**Fig. 3** Homing flights directly to the hive made by the three different groups of bees: SF-, VF- and R-bees. Bees were displaced and released under conditions (1) where the artificial landmarks (3.5 m high tents) were arranged as during the animals' orientation flights; (2) where the arrangement of these tents was rotated by 120° around the hive; and (3) where the artificial landmarks were removed. The beginning of the homing flight component of the full trace was detected by using an algorithm specifically developed for this purpose (see Menzel et al. 2005)

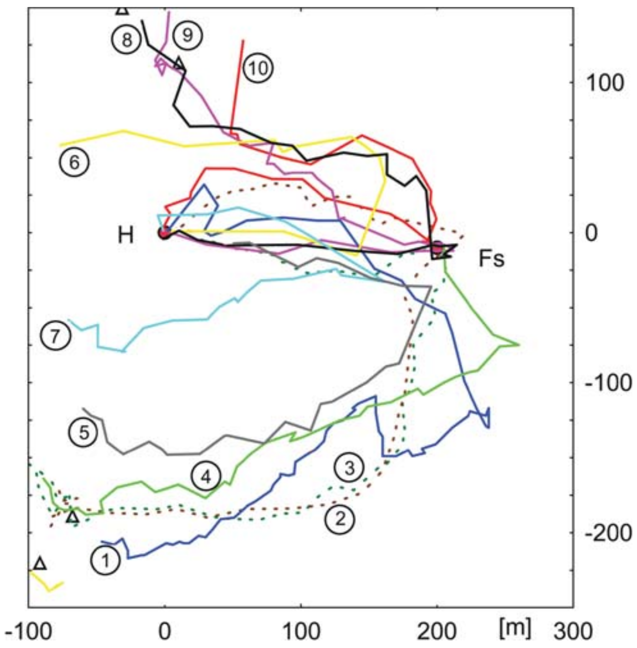


**Fig. 4** Homing flights via the feeder. Ten SF-bees (of the 29 bees tested under similar conditions) performed their homing flights via the feeder. Bees released at release site 2, south of the hive, are shown by flight paths 1–5, and those released at release site 3, north of the hive, are indicated 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 (see Menzel et al. 2005 for details)

## SF-bees' homing flights via the feeder's position

The ability to set a course from one location to another in a known territory is taken as evidence of a map-like spatial memory. Intriguingly, radar traces of SF-bees also showed that, upon being displaced, these animals made straight and fast flights directed not only to the hive but also first to the feeder and then to the hive (Fig. 4). Indeed, a third of these bees first headed towards the feeder, and then flew the route (from the feeder to the hive) that they had previously learned during route training.

## Two models

Two mutually related hypotheses might explain the homeward flights that the SF-bees performed via the feeder; both rely on spatial memories organized in such a way that they may represent spatial relationships between landmark-based information and specific coordinates (e.g. those of the hive and the feeder) in an allocentric, metric fashion. According to the first account, homing bees might integrate at least two vector memories. Let us assume that (1) they are able to associate homeward vectors with specific landmark views, not only during route training but also during previous exploratory flights, including their initial orientation flights (see above), and (2) when exposed to familiar landmark views, already linked to motor commands controlling large-scale flight motion, the corresponding homeward vectors are retrieved from the animals' spatial memory store. On the basis of this hypothesis, one might also assume that the vector memory derived from the route training is retrieved together with a stored homeward vector. Next, both vectors, which now reside in the animal's active working memory, are combined in order to steer the flight towards the feeder. (This interpretation is partially supported by the fact that, during the search phase of their flights, SF-bees frequently exhibited flight segments corresponding to the flight direction previously experienced during route training, an observation that is currently under further analysis.) Earlier experiments in which the bees had been trained to forage on two different locations suggested that they are able to integrate two different homeward flight directions (one from each location) when released at a spot located halfway between the two training locations (Menzel et al. 1998). If bees can indeed integrate two or more vector memories, thus being able to navigate along a new, 'computed' flight path in the field, then they might have a 'calculable' metric representation of their navigation space based on computations of stored vector memories.

The second account can be thought of as an extended and more complex form of the first one. It assumes that the bees' orientation flights, together with their initial successful foraging bouts, lead to a memory of a network of homeward vectors that create a surface of relational connections between specific landmark views, the hive's location and a variable number of specific foraging spots in the field. These relational connections would be the substrate for a geometrically organized memory, a 'functional' map. In this case, bees would analyse their current location based on flight paths previously associated with the information available on-site, and then choose a given spot that may be flown to (even along a new flight path) according to expected goals. Such a navigation mechanism is believed to be true in mammals and birds (Gallistel 1989; O'Keefe and Nadel 1978). On the basis of this interpretation, it would be also interesting to investigate whether the bees attending the waggle dance only decode information about direction and distance, or if they also recall navigational memories that have been associated with specific foraging spots (von Frisch 1946, 1948, 1967).

## Three different navigational memories

It appears that honeybees develop spatial memories in three different contexts: (1) during their initial orientation flights (we call the memory achievable via these flights the 'general landscape memory', a descriptive term that makes no assumptions about its specific structure); (2) during flights between the hive and specific goals in the field, which are often performed and during which the sequential order of landmarks might be stored (we call the type of memories achievable via these flights the 'route memory'); and (3) while attending dancing displays, when the spatial information encoded in the dancer's movements seems to be decoded and stored (we call the memory available via the waggle dance the 'dance memory'). These three memories might have different properties.

Route and dance memories provide information about direction and distance. They are kept in the active working memory, are applied first, and, once used, lose their influence on behaviour. These two forms of memory also include a directional component that can be updated according to changes in the animal's motivation (see below). When multiple route memories are stored, it becomes feasible to recognize that they have been linked to landmark-based information. This leads to the concept that bees use their route memories to estimate the sun's azimuth (von Frisch 1967; Dyer and Gould 1981), and that vector integration takes place under specific circumstances (Menzel et al. 1998). The route memory alone, however, does not allow a targeted, purposeful discovery of a spot to which the animal has yet not flown. The general landscape memory resembles a map-like structure that may arise through either internal operations based on one or more vector memories, or by a process in which the locations are distinguished and remembered according to the information available on-site (see above). On the basis of this interpretation, bees may benefit from their landscape memory only when their active working memory is completely free of route or dance memories. Therefore, if available after displacement, route memories will overshadow the general landscape memory (see Wehner and Menzel 1990).

The concept of multiple memories hierarchically organized reflects a generally accepted mindset in neurosciences. Implicit and explicit knowledge, or declarative or non-declarative 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, which has been intensively studied regarding the role of the hippocampus and striatum, can be embedded in a convincing theoretical framework, in which hippocampal 'place cells' are responsible for orientation according to the relational connections among landmarks and sequential experiences in the sense of a geometric map, whereas the striatum is responsible for those forms of learning that use a signal sent out from the goal (O'Keefe and Nadel 1978; Moser and Paulsen 2001). It might be interesting to ask whether navigational memories showing different properties (as those described above) also correspond to the various neuronal structures in the bee brain. What can be behaviourally tested in the near future, in addition, is whether and how the dance memory is coupled to the general landscape memory, i.e. whether dance followers collect only 'an instruction on how to act' based on the information on distance and direction, or whether they (also) use information from their own experience in the field in order to control their ensuing responses.

## Dance behaviour

In the waggle dance, a dancing bee executes fast forward movements straight ahead on the comb surface, returns in a semicircle in the opposite direction and starts the cycle again in regular alternation. This means that waggle dance has the form of figure eight, with the straight portion of the dance constituting the segment common to the two loops. Each waggle dance involves several of these cycles (von Frisch 1967). The straight portion of the dance, called a waggle-run, consists of a single stride (Tautz et al. 1996) emphasized by the lateral waggling motions of the abdomen (von Frisch 1967). Intriguingly, the length of the waggle-run increases with the distance flown to reach the signalled goal (von Frisch and Jander 1957), and its angle relative to gravity correlates with the direction of the foraging flight relative to the sun's azimuth in the field and sun-linked patterns of polarized skylight (Lindauer 1963; von Frisch 1967; Gould and Gould 1988). Thus, by encoding distances and directions, the waggle dance conveys to the researcher the circular coordinates of specific locations in a two-dimensional space. The body movements of a dancing bee are followed by a variable number of colony members (von Frisch 1957, 1967; Bozic and Valentincic 1991; Tautz and Rohrseitz 1998; Judd 1995; Michelsen 2003), usually called dance followers or recruits. Although the mechanisms through which these followers may perceive the spatial information encoded in the waggle dance are still unknown (Michelsen 2003), evidence has shown that they actually fly the distance and direction encoded in the dance (Lindauer 1967; Esch and Bastian 1970; Riley et al. 2005; see also Towne and Kirchner 1998).

A distinctive property of the waggle dance is that it encodes spatial information about different types of goals, which indicates that it can be triggered by different constellations of both external and internal stimuli. Bees dance for highly desirable sources of nectar, water and pollen (Lindauer 1948, 1954; von Frisch 1967), as well as for potential nest sites during swarming (Lindauer 1955). Moreover, it also has been reported that the waggle dance encodes information associated with seasonal migrations (Koeniger and Koeniger 1980; Dyer and Seeley 1994; Schneider and McNally 1994). A single waggle dance, in addition, may consist of anywhere from just a few to a hundred waggle-runs. The regulation of the dance manoeuvres appears to depend on a variety of factors, ranging from the sugar concentration (von Frisch 1967) and the flow rate (Núñez 1970) of the nectar being collected, to the distance to the goal (Seeley 1986), the type of goal being signalled (e.g. a nest site usually triggers a high number of waggle-runs that gradually diminish with the successive dances, Lindauer 1955; Seeley and Buhrman 2001), the colony's nectar influx (e.g. the lower the colony's nectar influx the higher the probability and duration of the motor display, 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). These context-dependent variations illustrate the role of multimodal convergence in regulating the motor display according to the dancer's general motivational level. In the present context, the most salient feature of the waggle dance is that it provides us with a direct access into the dancer's perceptual world, and, more specifically, into the cognitive aspects underlying long-range navigation.

## How the waggle dance depends upon spatial information

For the waggle dance to encode directional information, a foraging bee must record the angle formed by the position of the hive, the sun's azimuth (i.e. its compass direction) and the position of the goal to be signalled. This angle equals the mean direction, relative to gravity, of the dancer's successive waggle-runs. The mechanism that enables a flying bee to hold a course by reference to the sun is called the 'sun-compass' (von Frisch 1967). In addition to the sun-compass, bees also acquire compass information from the patterns of polarized light in the blue sky, and can orient both their flights and dances according to either the sun or polarized skylight (von Frisch 1949, 1967; Rossel and Wehner 1984). An intriguing feature of the sun-compass lies in the fact that the bee brain compensates for the time-dependent variation in the compass direction of the sun, even during periods when it is not possible to directly view the sun and when the pattern of polarized light is not available (Lindauer 1957, 1959). This feature of the sun-compass depends on both an internal clock and the processing of information about the local solar ephemeris function, i.e. a record of the sun's compass direction as a function of the time of the day indicated by the internal clock (Dyer and Dickinson 1996).

Interestingly, the memory content involved in setting a flight course in the field is thought to be the same as that involved in setting the directional information encoded in the waggle dance (von Frisch 1967). In addition to the sun-compass, an accurate encoding of the flown distance presupposes that the dancer has correctly measured the flight length. Early studies suggested that bees primarily estimate flight distance by gauging the amount of energy they expend to reach the goal (Heran 1956; Scholze et al. 1964). These early studies appeared to be controversial, however (Neese 1988; Esch and Burns 1996). Accumulating evidence now suggests that flight distance is visually gauged (Esch et al. 1994; Esch and Burns 1996; Srinivasan et al. 1996, 2000; Si et al. 2003; Tautz et al. 2004; De Marco and Menzel 2005), and the functioning of this visually driven odometer seems to depend upon initial calibration based on landscape features as well as flight height (Esch and Burns 1996; Esch et al. 2001). Although the mechanism involved in distance estimation is not yet understood, navigating bees seem to gauge distances primarily during their outbound flights, even though they monitor travelled distances on the way back to the colony (Srinivasan et al. 1997). However, experiments by Otto (1959) showed that bees use both their outbound (hive-to-goal) and inbound (goal-to-hive) flights to gauge the distance that is finally encoded. Furthermore, experiments aimed to evaluate whether bees encode in their dances detours such as trips between flowers showed that the waggle dance does not encode the distance separating two different goals that have been sequentially visited during a single foraging trip (Edrich and Scheske 1988). In the case of a single artificial food source, recent detour experiments (see below) support the interpretation that the length of the waggle-run mainly refers to the distance gauged on the way to the goal (De Marco and Menzel 2005).

## 'Marathon dances'

An intriguing feature of the waggle dance is that it may occur in the complete absence of foraging. Under this condition, it is performed in accordance with the current position of the sun and without any view of the sky, even during the night (Chalifman 1950; Lindauer 1954; Wittekindt 1955). These spontaneous dances, called 'marathon dances', appear to encode spatial information about the goal that the dancers would have visited if they were guided by their time sense (Lindauer 1957, 1960; von Frisch 1967), and pose stringent questions about the corresponding memory demands. How does the dancer recruit from its memory information related to the goal last visited 1.5 months ago? Or, how does the dancer estimate, at night, the closest goal in time after being trained to two different feeding places at two different times during the day? (Lindauer 1960; von Frisch 1967) These and the other observations (see von Frisch 1967) lend support to the concept that bees benefit from long-term memories to encode spatial information in their waggle dances. Indeed, the occurrence of spontaneous dances for past goals clearly suggests that bees store navigational information in the form of persisting memories, which can be retrieved by specific stimuli (such as those triggering the waggle dance), and whose content is appropriately integrated (once retrieved) with a number of current conditions such as the time of day, the animal's general motivational state and recent learning. 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. 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? Or, still, do dancers and followers have similar memories?

## The memory content 'expressed' in the waggle dance

Path integration (Mittelstaedt and Mittelstaedt 1973) has long been considered to provide spiders (Görner 1973), ants (Jander 1957; Mittelstaedt 1962; Wehner 2003a, b), birds and mammals (Mittelstaedt and Mittelstaedt 1980, 1982, respectively), and most likely also bees (von Frisch 1967; Wehner and Menzel 1990; Collett and Collett 2002), with 'global' vectors at the ends of their outbound paths (see above). Although these global vectors appear to be emptied each time the animals return home, desert ants can store a short-lived 180°-reversed form of a recently experienced homing path, and use it to guide their next outbound paths towards the recently visited locations (Schmid-Hempel 1984; Wehner 1992). Moreover, when trained bees arriving at a foraging target are held captive for several hours, they subsequently fly farther outward from the hive along the same hive–target direction (Dyer et al. 2002). Accordingly, it is reasonable to assume that vector memories derived from recent flights may provide bees with the necessary information to control their dance manoeuvres. But does the waggle dance encode a global vector?

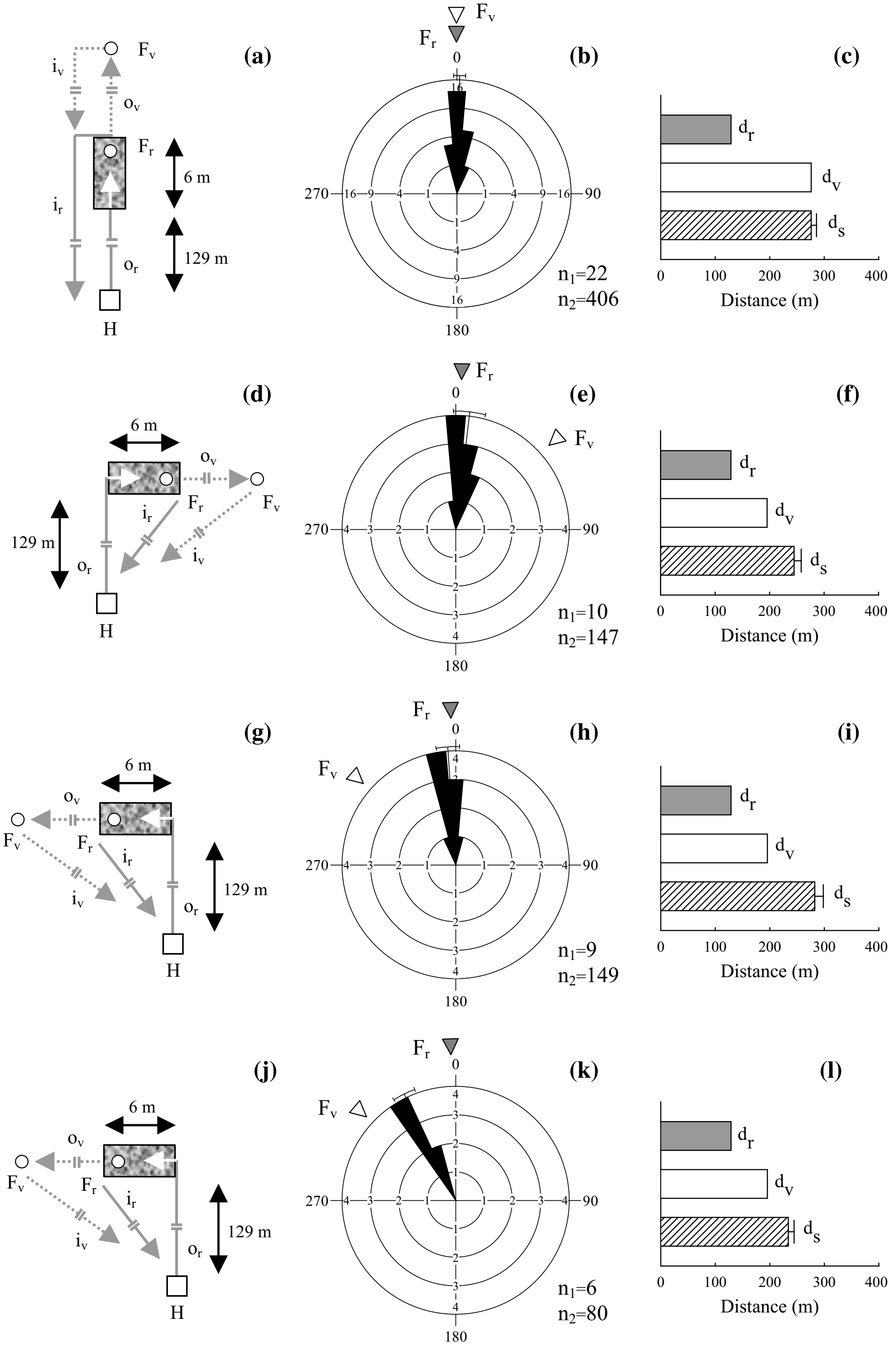
Early detour experiments by von Frisch and colleagues (reviewed in von Frisch 1967) indicated that the bees' odometer is primarily decoupled from the processing of directional information; which means, in turn, that no resulting 'flight vector' is necessarily encoded in the waggle dance. When von Frisch (1967) compelled the bees to fly a two-legged detour path to reach an artificial feeder, they did indicate in their dances the direction of the 'virtual' straight-line towards the goal (which might have been computed from the two legs of the detour), even when they had followed the detour on the way back to the colony, but they also indicated the 'actual' flown distance, and not the distance of the straight segment connecting the target and the hive's entrance. These bees thus encoded in their dances the 'direction' of a global vector, but not its 'length' (von Frisch 1967), indirectly posing the question whether it is the outbound or the inbound flight (or both) which provides the dancer with the spatial information that is finally encoded. At first glance, this question might appear to be exclusively related to dance communication. However, it becomes extremely important in the context of navigation. If the waggle dance encodes directional information which depends not only on path integration information, but also on the information that the dancer has already associated with a given position in the environment, e.g. local vectors associated with specific landmark views (Etienne et al. 2004), then one might assume that navigating bees critically rely on the information available on-site, which operates alongside internal references gained from a stored record of past movements. Under such conditions, in addition, dance communication would greatly depend upon the way in which dancers and followers acquire, store and retrieve navigational memories.

When bees fly through narrow tunnels, having walls lined with random visual textures, they indicate a distance in their waggle dances that is much greater than that actually flown (Srinivasan et al. 2000). This, in turn, allows manipulating the animal's navigational experience of the subjective goal it has flown to during its outbound flight. In a series of recent experiments, De Marco and Menzel (2005) used this type of patterned tunnels to create virtual detours, in order to examine how the dance manoeuvres encode the ensuing 'subjective' spatial information (Fig. 5). First, they asked whether the bees measure the distance to the goal on their outbound or on their inbound flight, and found that the bees only perform longer waggle phases when they fly through a visually patterned tunnel on their outbound flight (Fig. 5c). Next, they placed the tunnel perpendicular to the straight-line connecting the goal and the hive's entrance, and allowed the bees to fly through the tunnel only during the outbound flight, thus creating a mismatch between what the animals 'perceived' to be the goal location and its actual position in the field (Fig. 5d, g). Under such conditions, De Marco and Menzel (2005) found that the virtual detour has no significant effect on the inbound flight, and that the dances indicated a direction close to that of the straight-line connecting the hive and the actual location of the goal, i.e. the direction of the inbound flight (Fig. 5e, h). This means that, at the beginning of the inbound flight, the dancer's nervous system had to correct the directional information provided by its path integrator in order to take up the signalled direction, suggesting that the encoding of spatial information in the waggle dance includes a component that detects the deviation between the subjective measures of distance and direction and the information available on-site, which may, in turn, define the shortcut between the goal and the hive. Indeed, these results can only be explained if we assume that bees are able to use external information derived from their position in the environment in order to guide their flights back to the colony, and that this type of information can determine (either directly or indirectly) the direction that is finally encoded in the subsequent dance manoeuvres (De Marco and Menzel 2005). In this context, the role of landmarks is emphasized (indirectly) by the fact that the path integration coordinates were more strongly weighted in the dance manoeuvres only with increasing experience of the terrain (Fig. 5j, k).

This interpretation is in close agreement with previous results (Otto 1959; Edrich and Scheske 1988), which showed that directional information available during the inbound flight is computed in the context of the waggle dance for the purpose of directional indication. However, it is not yet clear to what degree bees might refer in their dances to the inbound component of their flights, or whether they embed the process of encoding spatial information in the dance into their map-like spatial memory (see above).

## Learned vectors within a map-like spatial memory?

The ability to navigate by the exclusive use of information available en route can be directly revealed in unknown territory. However, in known territory, the use of information available on-site can never be entirely excluded from the store of navigational tools. Bees are central-place foragers in that they depart from and return to fixed locations. Moreover, they also exhibit orientation flights at the beginning of their foraging life (Becker 1958; Vollbehr 1975; Capaldi et al. 2000). Hence, it is reasonable to assume that landscape learning and the use of the sun-compass (possibly also the magnetic compass) are tightly interconnected. This interpretation is supported by the fact that bees learn extended landmarks in relation to the sun-compass,



which allows them to steer their flights and to encode directions in their dances without recent views of the sun or polarized skylight (von Frisch 1967; Dyer and Gould 1981). However, it is not yet known whether young bees may associate path integration coordinates and landmark-based information during their initial orientation flights, and whether and how these memories can be later recalled. The homing behaviour of displaced bees might be explained according to this ability. If that were the case, one might assume that at least two vector memories can be recalled and processed in such a way that new flight paths can be computed and followed. Since orientation flights occur at the very beginning of the foraging life, one also might

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**Fig. 5** 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 either straight ahead or to the right or left, to the journey from the hive to the feeder. 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 signalled 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 analysed) = 22, $n_2$ (number of waggle-runs analysed) = 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 $\mu$ and 95% confident interval, respectively. The *grey* and *white arrows* indicate the directions towards the real ($F_r$) and the virtual ($F_v$) feeders shown in **a**, respectively. **c** Shown are the flown distance (mean ± SE) signalled 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 signalled distance) and the real distance from the hive to the food site ($d_r$, *grey 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 signalled ($F_v$: 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 and Menzel (2005)

assume that bees attending a waggle dance may benefit from navigational memories. According to this hypothesis, neither the dance nor the flight path of a recruited bee would be exclusively guided by the two independent estimates of direction and distance, but would also be by some form of 'expectation' of arriving, at that time, at a particular location. A component of this expectation would be the route to be followed. Indeed, von Frisch (1968) stated that the success of the waggle dance in terms of recruitment depends upon the foraging experience of the dance followers. When two groups of fellow bees have visited two different (and currently exhausted) unscented feeding places, the contact with a dancer indicating the accustomed goal is much more effective than the contact with a dancer indicating the unfamiliar one (von Frisch 1946, 1948, 1967). In spite of these early findings, however, the role of stored navigational information on the decoding process involved in dance communication remains unknown.

## What, where, when: episodic-like memory in honeybees?

A foraging bee learns the place and the time of the day when a nectar source is productive. Since it also adjusts its foraging efforts to the quality and quantity of the available food, one might assume that it 'expects' a given quality and quantity at a particular location and at a particular time of day. However, it has not yet been proven whether foraging bees decide between multiple combinations of 'what, where and when'. Moreover, it is unknown whether bees evaluate and compare properties of simultaneous food sources. This type of evaluation has been demonstrated in food-storing birds, and its corresponding ability has been characterized as a form of 'episodic-like memory' (Clayton and Krebs 1994; Clayton et al. 2003).

Episodic-like memory provides an animal with the potential to relate specific features to a particular location, and to store many such compounds in such a way that the animal can decide between them without being exposed to any signal emitted from that location. What is required is the ability to retrieve multiple combinations of 'what, when and where attributes', such that they can be evaluated against each other on the basis of current needs. Since these attributes do not become explicit in animals, a characteristic of episodic memory in humans, it is necessary to refer to such cognitive capacities as 'episodic-like' memory. As in the case of navigation in general, it is rather difficult to dismiss explanations based on more elemental forms of cognition, e.g. chains of associations, procedural rather than the rule-based memories. However, dance communication may again provide an expedient tool to access the level of cognition involved in the multiple 'what, where and when-judgement'.

The current objects of interest on navigation and communication in bees differ from those that have been addressed so far. The corresponding sensory–motor routines are better understood, and now we need to ask how the information that animals access in their working memory is stored, processed and retrieved, in order to tackle the structure of internal representations. Particularly, since it is recognized that carefully designed experiments allow access to processes that lie beyond behavioural acts, processes which may be called operations at the level of the working memory, or operations based on representations. These operations are far from simple and transcend elemental forms of association (Menzel and Giurfa 2001). The richness of these operations, however, is accessible only in the animals' natural environments. In the case of honeybees, stringent methods are now available for collecting pertinent data. Ultimately, one would like to know how and where the bee's small brain performs these operations.

## Conclusion

We have reviewed two aspects of navigation in honeybees strictly related to each other, but whose relationship is not yet understood. The structure of the spatial memory in foraging bees is much more complex than hitherto thought. The homing flights of displaced bees point towards a map-like organization of their spatial memory; either composed of computations of at least two experienced vectors, or of processes allowing the bee to determine their position in the field relative to viewpoints and landmarks, and to steer to a different location.

In the traditional view of the waggle dance it has been frequently assumed that a global vector of the outbound flight is encoded in the dancer's movements. However, if the global direction and distance flown by a dancing bee are separately manipulated, it becomes obvious that they are not encoded as an integrated vector. The process of encoding direction appears to involve information available on-site. It is not clear yet whether bees refer to stimuli collected and stored during the inbound flight, or whether they embed the process of encoding spatial information in their dances into their map-like spatial memory. In the latter case, the encoded information would not be a vector, but rather a set of coordinates as defined by the flight path towards its corresponding position in the field. An answer to this question also presupposes the analysis of the process of decoding by recruited bees. Do bees interpret the information collected via the dance differently according to their own experience? Do they decide to take up a foraging trip depending on their former experience with the indicated location? Methods (radar tracking of full flights) are now available to tackle these questions.

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