Dimensions of Cognition in an Insect, the Honeybee

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This review provides evidence for the enormous richness of insect behavior, its high flexibility, and the cross-talk between different behavioral routines. The memory structure established by multiple forms of learning represents sensory inputs and relates behaviors in such a way that representations of complex environmental conditions are formed. Navigation and communication in social hymenoptera are particularly telling examples in this respect, but it is fair to conclude that similar integrated forms of dealing with the environment will be found in other insects when they are studied more closely. In this sense, research addressing behavioral complexity and its underlying neural substrates is necessary to characterize the real potential of insect learning and memory. Usually, such an approach has been used to characterize behavioral simplicity rather than complexity. It seems therefore timely to focus on the latter by studying problem solving alongside and in addition to elemental forms of learning.

Key Words: learning and memory in the honeybee, navigation, comparative cognition, nonelemental forms of learning

One of the most important distinctions in conceptualizing cognition is that between implicit and explicit knowledge. Explicit knowledge may, in a strict sense, exist only in humans. Animals might possess only implicit knowledge, but this does not exclude the possibility that certain forms of knowledge might reach an explicit-like status specific for the animal species in question in the sense that internal operations on memories are performed without motor expression of such operations. A telling example of this form of knowledge is the choice behavior of food-storing birds, which make their choices depending on which kind of food they have stored and when and where they have stored it (Clayton, Bussey, Emery, & Dickinson, 2003; Emery, 2006; Güntürkün, 2005; Katz, 1950a). Thus, *expectation, attention, planning,* and *decision making* could be useful terms for animals, even if we assume that they possess only implicit knowledge. If such terms are used, we assume that the animal retrieves a memory whose structure allows two or more alternative outcomes to be evaluated and compared before any motor action is performed. In this article, we will address the question as to whether it is reasonable to assume such forms of internal processing in an insect, the honeybee. Specifically, we will ask whether these animals can recollect the contents of their memory without expression of sensory-motor routines and use them for internal operations and decision making. There are good reasons for rejecting this kind of questioning when it comes to understanding invertebrate behavior. On the other hand, searching for experimental conditions that would allow us to address the internal processing of the brain devoid of sensory-motor control, its spontaneity, and its creativity, even in such tiny brains as those of insects, may help to do better justice to the complexity of neural functions in bigger brains.

WHY USE BEES FOR STUDIES ON COGNITIVE COMPLEXITY?

Three main reasons justify the use of the honeybee as a model for studies on cognitive complexity: (a) behavioral richness, including complex learning and memory faculties; (b) experimental access in terms of controlled training and testing; and (c) accessibility of the central nervous system. With respect to the first characteristic, bees exhibit developed learning and memory capabilities

that apply to local cues characterizing the places of interest, which are essentially the hive and the food sources. At these places, honeybees learn, memorize, and discriminate colors, shapes, patterns, odors, and textures, among other characterstics (Menzel, 1985, 2001). These capacities allow enhanced foraging efficiency and, coupled with learning abilities for landmark constellations and for celestial cues (azimuthal position of the sun, polarized light pattern of the blue sky), ensure efficient navigation in a complex environment. The second characteristic is what makes honeybees useful for the experimenter: They are accessible for controlled training and testing. Different paradigms have been used to this end, two of which deserve special attention: (a) the olfactory conditioning of the proboscis extension response (PER) in harnessed bees and (b) the training of the approach flight toward a visual target in free-flying bees. In the former, harnessed bees are trained to associate an odor with a sucrose reward delivered to their antennae, which elicits the PER (Bitterman, Menzel, Fietz, & Schäfer, 1983; Takeda, 1961), and then to the proboscis; the association formed is of Pavlovian nature and enables the odor to release the PER in a subsequent test. In the latter, free-flying individually marked bees are pretrained to fly toward the training/test place and are rewarded with sucrose solution whenever they choose the appropriate visual target at that place (von Frisch, 1967). In this way, bees can be trained to visual stimuli such as colors, shapes, patterns, depth and motion contrast, among others. The associations built in this context link visual stimuli and reward but also the animal's response (e.g., landing) and the reward, thus representing an instrumental form of learning. Finally, the third characteristic that makes bees interesting for cognitive complexity studies is the fact that the neural bases of such complexity can be accessed because of the relative simplicity of the bee nervous system (Menzel, 2001; Giurfa, 2003). PER conditioning has the advantage that it can be combined with a physiological approach, allowing the study of the bee brain while the bee learns or recalls memorized information in vivo. As the bee is immobilized in such a preparation, it is possible to expose its brain through a small window cut in the cuticle of the head. Physiological correlates of the different forms of olfactory conditioning can be found at different levels, ranging from the molecular and pharmacological ones to single identified neurons and neuronal ensembles whose activity can be monitored using modern optophysiological recording techniques.

In most behavioral studies, inference about internal processing can be made only indirectly by observing changes in the behavior in question. In the honeybee, one can additionally study a communicative process between foraging animals, transcending the usual limitations of behavioral studies in invertebrates. This process, which has been described as the honeybee dance (von Frisch, 1967) because of its use of ritualized, communicative behavior indicating distance and direction to a profitable food source, can be "read" by the experimenter, who can record dances in one-frame observation hives with glass walls. Dances therefore constitute true reports on what the outgoing forager perceived, what it learned, and what it considers worth reporting. This unique situation was ingeniously exploited by Karl von Frisch (1967), who discovered through it a vast range of sensory- and experience-dependent capacities.

The work on honeybees has more recently gained from cognitive perspectives (Cheng & Wignall, 2006; Giurfa, 2003; Menzel, Giurfa, Gerber, & Hellstern, 2001). Besides the battery of more traditional assays allowing the study of behavior mentioned above, new paradigms have been conceived both for studies on free-flying bees conditioned mostly with visual stimuli and for studies on olfactory learning with restrained bees. We will focus on three main topics that allow appreciating to which extent cognitive thinking has impregnated new studies on bee learning and memory and how this thinking has changed our vision of the complexity of this insect's behavior. We will concentrate on learning and memory as applied in navigation, communication, and discrimination. For the first context, studies on navigation between the nest and a goal (a profitable food source) have in recent years overtaken the traditional conceptual framework, which posited that navigation along well-defined routes is the main strategy bees use. The structure of spatial memory in bees was reconsidered by adopting a cognitive approach and applying novel forms of experimentation. For the latter case, questions are emerging about the nature of the memories that honeybee dances may activate in dance followers. This questioning contrasts with the traditional view of bees "blindly" following instructions from dance behavior with the notion that their own memories about the environment may be reactivated by dances that would, in turn, allow combining instructions concerning a goal with known routes toward it. Finally, discrimination learning in bees also required a change of framework as the accent is shifted from the study of sensory capacities to the question as to how these capacities are implemented to solve nonelemental discriminations.

LEARNING IN A NAVIGATION CONTEXT

Navigation is an orientation strategy that allows animals to travel between defined locations without having direct sensory access to these locations. In this sense, navigation differs from general orientation and guidance, which include all forms of spatial relationships between the animals' body position and trajectories of movement

relative to sensory conditions. Navigation allows animals to travel over rather long distances relative to their body size and sensory range, according to their knowledge of the structure of their surroundings, which they acquire by sequential experience. Several classifications of navigation have been proposed, reflecting different conceptual frameworks, for example, route and local navigation (O'Keefe & Nadel, 1978), cognitive mapping, piloting and dead reckoning (Gallistel, 1990), egocentric and allocentric navigation (Thinus-Blanc, 1987; Wehner, 1992), random navigation, taxon navigation, praxis navigation, route navigation, local navigation, graph navigation, and map navigation (Gillner & Mallot, 1998). Irrespective of whether the classification focuses on sensory, neural, or mental processes or whether the structure of the external signals was referred to, two basic navigation strategies emerge from these various viewpoints: route strategy (also called graph structure of navigation (Gillner & Mallot, 1998) and local navigation or map strategy (also called cognitive mapping; Gallistel, 1990; Pastergue-Ruiz, Beugnon, & Lachaud, 1995; Tolman, 1948).

Learning during navigation is particularly relevant for cognitive approaches to honeybee behavior because bees navigating between the nest and a food source integrate a large range of sensory inputs to produce rather complex forms of behavior based on a particular form of learning, observatory learning. It is under these conditions that learning transcends elementary forms of associations in particularly clear ways. The evaluating signal for storing experience must come from internal conditions of the nervous system at the time of learning, depends highly 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 that cannot be isolated from each other, and the motor performances involve the most sophisticated sequences of motor programs of which the respective animal is capable. As will be seen, it is still very difficult to prove the cognitive nature of the processes; more elementary interpretations need to be carefully considered, such as tight sensory-motor connections, simple partial matching strategies between experienced and remembered constellations, sequences of picture memories, and other forms of elementary solutions to complex conditions.

Navigation in honeybees has been the subject of intensive and controversial debates because different positions were taken in interpreting the data according to a route strategy and a map strategy. The route strategy concept is based on traditional thinking about navigation in insects, which assumes a tool box of rather simple sensory-motor routines and their stepwise application in rather isolated and independent navigational tasks. These concepts were developed by experiments based on the analysis of route learning (T. S. Collett & Collett, 2002). Bees and ants traveling between their nest and a food source learn the vector components of their movements (direction and distance) by a dead reckoning (path integration) process (Wehner, 1992). Landmarks experienced en route may serve to calibrate measured distances, thus reducing the rotatory and translatory errors that may accumulate during path integration (P. Graham & Collett, 2002; Wehner, Michel, & Antonsen, 1996). Furthermore, landmarks may provide procedural information about which turns to make and what distances to travel next (T. S. Collett, 1996, 1998; T. S. Collett & Collett, 2000; Kohler & Wehner, 2005; Wehner, Boyer, Loertscher, Sommer, & Menzi, 2006) such that apparently complex performances can be built based on these simple rules. Honeybees can, for instance, learn to negotiate complex mazes of adjacent boxes by learning that specific-color disks mean "turn right" or "turn left" (Zhang, Bartsch, & Srinivasan, 1996). Because bees are able to refer to a compass direction even when the sun compass is not available (e.g., in their dance performance; Dyer & Gould, 1981; von Frisch, 1967), landmarks also serve as compass-related directional cues that may act as a backup system under an overcast sky. The redundancy of landmarks is thought to be reduced by reference to contextual information such as the visual panorama (M. Collett, Harland, & Collett, 2002; Kohler & Wehner, 2005). Consequently, "isolated" landmarks may not be necessary for successful navigation, or their information might be suppressed if further-ranging, contextual landmarks were available. Furthermore, a dissociation of behavior may occur that seems to indicate the combined action of separate navigational cues. For example, bees flying in a narrow tunnel search at the correct distance if both local and contextual cues are available. If one of the two cues is shifted or removed, then the contextual cue appears to be of greater importance (M. Collett et al., 2002). Under more natural conditions, a dissociation of distance estimation is found. Chittka and Geiger (1995) set up an experiment in which sequentially experienced landmarks guided free-flying bees over hundreds of meters to a feeding station. The bees' distance estimation is controlled both by the absolute distance as measured by the visual flow field (Esch & Burns, 1996; Srinivasan, Zhang, & Bidwell, 1997) and by the sequence of landmarks. The directional component of flight is also controlled by landmarks (T. S. Collett, 1996), and even novel directions can be traveled if the memories for two different flight directions are retrieved by a particular landmark constellation at the same time (Menzel, Geiger, Müller, Joerges, & Chittka, 1998).

These ideas about isolated but connected egocentric navigation strategies are strongly influenced by

observations on navigation in some ant species but have also been used to conceptualize data on honeybee navigation. Such toolbox models are considered more attractive because they appear more parsimonious than the assumption of higher-order integration of spatial information based on a multitude of sensory-motor processes and multiple memory systems leading to allocentric, maplike, or relational spatial representations, which allow the insect to travel along novel routes based on some sort of planning. However, toolbox models have limited explanatory power because (a) they are based on very special forms of experimentation with insects (route training), (b) they generalize from rather limited laboratory experiments performed on a reduced spatial scale to open-field conditions and large spatial scales, and (c) they transfer concepts developed for one insect species to another (e.g., running ants, flying bees, and wasps).

These three points need to be elucidated somewhat further. (a) Training bees along a route will establish a particular spatial memory structure, and very different forms of spatial memory may result from exploratory orientation flights that bees perform before beginning their foraging life (Capaldi et al., 2000; von Frisch, 1967). Indeed, it was found that bees without route training were able to return to the nest from sites all around the hive at distances of several hundred meters (Menzel, Brandt, Gumbert, Komischke, & Kunze, 2000), the range over which orientation flights are performed (Capaldi et al., 2000). Comparing such bees with those trained along a route showed that the working memory of the route dominated initial navigation, leading the animals in the wrong direction and suppressing the memory that later leads the animals quickly back to their goal. Because only the initial flight path was monitored in the past and vanishing bearings were taken as measures of navigation, inadequate concepts were derived (Dyer, 1991; Wehner, 1992; Wehner & Menzel, 1990) because the multitude of spatial memories was not considered. Route memory therefore seems to be a real navigation strategy, but it is certainly not the whole of bee navigation. Integrative, more complex strategies are uncovered whenever route memory is unavailable to the flying bees.

(b) Most of the experiments on the role of landmarks on path integration, compass-driven sequential pictorial learning, relationship between "isolated" landmarks, and contextual landmarks were carried out in miniature environments forcing bees to fly into small boxes or mazes through narrow entrances (T. S. Collett & Collett, 2002). All these tests made forced route training necessary, avoided testing the sequential experience of natural landmarks in unhindered flight, and did not expose the bees to the temporal and spatial structures they would experience in free flight. Certainly, such experiments

have the advantage of observing the bee over the full flight close to the goal, but the limitations for generalization to natural conditions are obvious. They reflect only the approaching components and orientation strategies that bees may adopt when close to the goal. Navigation in bees' actual flight ranges (several kilometers) must be guided by compass-related learning of multiple sequences of landmarks that are visible over different ranges of the flight path, some of which are visible only when the bees get close to them. The essence of the navigational problem—whether an animal is able to orient and infer a direction of movement along a novel path aiming toward another location that is not directly accessible—cannot be addressed by such reduced experimental setups. Questions that are not asked in an experiment cannot be answered through it, and generalizations are unjustified that conclude that what has been found is the only capacity the animal has at its disposal. Both errors of argumentation have weakened these studies. On the other hand, working under natural conditions may potentially limit the possibility of untangling the relevant parameters underlying navigation strategies because parameters may not be taken apart as well as in reduced test conditions. Therefore, such naturalistic experiments have a different quality. They are necessarily more descriptive and less analytical; they provide clues for behavioral capacities and may allow only limited mechanistic interpretation.

(c) Most experiments adopting the toolbox model were performed with ants (mostly the wood ant *Formica rufa*, the desert ant *Cataglyphis,* and the Australian desert ant *Melophorus bagoti*). The data were generalized to bees, implying that navigation strategies in running and flying Hymenoptera are similar. Bees fly over distances of kilometers, cruising well above ground with a bird's-eye view, whereas ants run over a few tens of meters and have only close-up views of the terrain. The biology of these groups of insects is so different that different forms of learning and different structures of spatial memory are quite likely. In addition, *Cataglyphis* often navigates in an environment devoid of close natural landmarks, whereas *Formica* and *Melophorus* find their way in an environment rich in landmarks. Thus, even the generalization between these three ant species may be misleading as, for instance, the weight assigned to landmarks may vary from one ant species to the next. Experiments addressing distance estimation in ants and bees clearly show, for instance, that these two insects differ dramatically in their methods for estimating distance. Whereas bees seem to use the optic flow field (the relative displacement of the visual field on the insect retina) experienced en route to the goal (see above), ants do not seem to rely on such an optic flow odometer (Ronacher & Wehner, 1995). Recently, it was

shown that ants can estimate the distance to travel within a tunnel in the dark without any kind of visual information (Thielin-Bescond & Beugnon, 2005), indicating the role of proprioceptive cues for distance estimation in ants.

The toolbox model of insect navigation has been adopted on the basis of intuitive parsimony arguments (Wehner, 1992). Because insects have small brains, and any alternative to the use of a small number of simple sensory-motor routines, for example, a geometric representation of space, appears less complex, this apparently simpler explanation has to be chosen. T. S. Collett and Collett (2002), for example, argued that small brains such as those of the bee need to solve their tasks with less "cognition," meaning with a toolbox of loosely interrelated elementary functions rather than an integrated, allocentric level of spatial representation. However, it should not be overlooked that radical forms of parsimony as applied to behavioral science were (and may still be, at least in part) a historical burden. New approaches were required to correct for eliminating the brain in behaviorisms and making too simple assumptions about the brain's functions in ethology. These cognitive approaches (cognitive psychology, cognitive neuroscience) provide us with novel avenues to brain function. A frequently used argument in navigation studies, which states that reference to cognitive processing (cognitive or mental map) must be avoided as long as simpler explanations are at hand (Bennett, 1996), may warn us about potential traps but should not be accepted as a ban. It should be recognized that we simply do not know whether the integration of the multiple and complex sensory and procedural neural processes into a common spatial memory with geometric organization (a map) may not be a more economical and thus simpler way of representing sequential experiences during navigation (Bekoff, Allen, & Burghardt, 2002; J. Graham & Gerard, 1946; Griffin, 1984).

THE MAP CONCEPT AND ITS EXPERIMENTAL SUPPORT

Local navigation, or map-based strategy, allows goal-directed decisions at any place and toward any intended location in the experienced area, thus resulting in a transfer between routes and inference of novel routes. Such a strategy has until recently not been convincingly documented for insects and is the subject of lively debate (T. S. Collett & Collett, 2002; Giurfa & Capaldi, 1999; Wehner et al., 2006). However, more flexible navigational memories than route memories were found in experiments that avoided route training in bees and proved that bees are able to return to the hive from any place around the hive within a rather

short time (Menzel et al., 2000). It was concluded that bees learn features of the landscape on their orientation flights (Capaldi et al., 2000) and establish a special "landscape memory" that relates landmarks to the bees' headquarters, the hive. It was only recently that the structure of this landscape memory could be critically tested using radar harmonic technology and individual bees equipped with emitting diodes glued onto their thoraxes. In this way, complete paths were recorded for individual bees (Menzel et al., 2005). In this study, three test groups were studied and their flight paths recorded after they were released at many different release sites around the hive. The three test groups were bees that were trained to a feeder, placed at variable locations in close vicinity to the hive, which was moved around the hive at a constant distance (VF bees) and that therefore did not develop a route memory, bees that were trained to a stationary feeder 200 meters to the east of the hive (SF bees) and thus developed a route memory, and bees that were recruited by foragers and that collected food at the stationary feeder (R bees). Although SF bees correspond to those bees tested in most standard studies on bee navigation, bees from the VF group are unique in the sense that they do not have a route memory available such that alternative navigation strategies could be uncovered by studying their behavior. It was found that all bees returned to the hive along fast and straight flights from all regions around the hive. SF and R bees did so after they had performed the vector (distance and direction) components of their trained or instructed route flights; VF bees returned after searching for a while. Most important, SF bees performed either direct flights back to the hive or via the feeder to the hive.

Several operations must be at the animal's disposal: (a) recalling memories of these vectors (segments with defined headings and distances) pointing toward the hive with a large number of landmarks all around the hive that are recognized from different viewpoints, (b) a shift in motivation (fly toward the hive or toward the feeder), (c) reference to the outbound vector components of the route flight from hive to feeder, (d) addition and subtraction of the flight vectors for at least two sets of vector memories—those that would lead directly back to the hive and those that lead from the hive to the feeder. It is difficult to imagine that these operations can be done without reference to vectors that relate locations to each other and thus make up a map. The current question in bee navigation is not so much whether there is a maplike spatial memory but rather, "What structure does this maplike memory have and how is it used?" In any case, the maplike memory in bees is rich and can be used in a flexible way. Any model of bee navigation thus needs to incorporate a strategy based on a maplike

representation of the bees' large-scale home range and a freedom to choose between at least two goals. This further suggests that spatial relations between environmental features appear to be coherently represented in a maplike memory in insects as they are in other animals and humans (Gallistel, 1990; Klatzky, 1998; Shelton & McNamara, 1997).

THE STRUCTURE OF MEMORY
USED DURING COMMUNICATION

In the waggle dance, a dancing bee executes fast and short forward movements straight ahead on the comb surface, returns in a semicircle in the opposite direction, and starts the cycle again in regular alternation (each waggle dance involves several of these cycles; von Frisch, 1967). The straight portion of this course, called a waggle run, consists of a single stride (Tautz, Rohrseitz, & Sandeman, 1996) emphasized by lateral waggling motions of the abdomen. The length of the single waggle runs increases with the distance flown to reach the source, and their angles relative to gravity correlate with the direction of the foraging flights relative to the sun's azimuth in the field and sun-linked patterns of polarized skylight. Thus, by encoding the visually measured distance (Esch & Burns, 1995; Srinivasan, Zhang, Altwein, & Tautz, 2000; Tautz et al., 2004) and the direction toward the goal, the waggle dance allows a forager bee exploiting a profitable food source to share information about the distance and direction toward a desirable goal with colony members (Dyer, 2002; Seeley, 1995; von Frisch, 1967).

Recurrent criticism of von Frisch's hypotheses on the capability of dances to convey information about these environmental features (Wells & Wenner, 1973) has been recently terminated based on navigation experiments using radar (see above) as a tool to track the behavior of bees recruited by dances and released at a novel spot in their environment that they did not know and that has not been previously visited by the dancers (Menzel et al., 2005; Riley, Greggers, Smith, Reynolds, & Menzel, 2005). These bees were caught when leaving the hive after attending a dance and performed as expected: They followed the information they had gathered from the dancing in a straightforward manner, thus demonstrating that von Frisch's (1920) interpretation was correct. This result definitively discards hypotheses on recruited bees following odor plumes left by the recruiters (Johnson & Wenner, 1970; Wells & Wenner, 1973), which have been challenged by other works that investigated navigation on a small scale (Esch, Zhang, Srinivasan, & Tautz, 2001).

Dances thus convey specific information about variations in distance and direction by encoding them in ritualized behaviors that are nonarbitrary, as they are performed in the same manner by the foragers from the same hive. Although Karl von Frisch used the term *dance language*, Premack and Premack (1983) correctly stated that honeybee dances should not be called a language, based on the argument that there is no evidence (yet) that bees evaluate the symbolic nature of their performance. This question can be addressed by asking whether a bee receiving information from the dance responds differently to the information depending on its own experience. Such experiments have yet to be performed. Furthermore, there is some debate as to whether bees employ chain communication, another characteristic of language (see below). The term *language* is also misleading because there is (as far as we know) no semantics or grammar in the ritualized movements of the dance. Rather, the dance language can be characterized as an iconic signal system because, complying with the definition of this kind of system, there is, for each dimension of variation in the relevant environmental feature (the distance or the direction of the food source), a single-transformation rule-mapping variation in that parameter onto variation in the relevant dimension of the signal (Bermudez, 2003). In an iconic signal system, as in honeybee dances, the receiver of the signal has to decode the signal by an inverse mapping.

Because navigating bees benefit from path integration (T. S. Collett & Collett, 2002; Dyer, 1998; Wehner, 2003; Wehner & Menzel, 1990), vector memories derived from recent flight paths might be recalled in the dance context. Indeed, path integration (which constantly informs the animal about its current position with respect to a starting reference point and which requires working memory to continuously record the angular and linear components of the animal's movements) provides ants—and most likely also bees—with global vectors at the end of their outbound paths, which allow them to follow straight return trajectories of the appropriate distance and direction during their inbound path. Although the global vector is emptied each time the animal returns to the nest, desert ants can store a short-lived 180° reversed form of a recently experienced homing path and use it to guide their outbound paths toward previously visited locations (Wehner, 1992). Moreover, when trained bees arriving at a foraging target are held captive for several hours, they subsequently fly farther outward away from the hive along the same hive-target direction (Dyer, Gill, & Sharbowski, 2002). We may therefore assume that forager bees also store a form of global vector that they later recall in the context of the waggle dance. But does the waggle dance encode a global vector, an integrated form of the measures of distance and direction, and/or even code for a location?

Early detour experiments by von Frisch and colleagues (reviewed in von Frisch, 1967) indicated that the bees' visually driven odometer is primarily decoupled from the processing of directional information, indicating that no global flight vector is reported in the context of the waggle dance. When bees are compelled to fly a two-legged detour path to reach the goal, their dances indicate the direction of the straight line toward the goal (computed from the two legs of the detour), even when they followed the detour on the way back to the colony, but they signal the distances actually flown and not the distance of the straight segment connecting the target and the hive's entrance. These early findings were recently confirmed by manipulating the navigational information provided to a dancing bee (De Marco & Menzel, 2005). Thus, one might ask whether the waggle dance encodes spatial information provided only by the actual flight path. The role of landmarks so far has been considered only in the context of resetting (Srinivasan et al., 2000) or calibrating the odometer (Tautz et al., 2004) but not in the communicative process itself. The detour experiments by von Frisch suggest that the directional component reported in the waggle dance may also be derived from stored path integration coordinates of visually defined locations (landmarks). This idea is not without precursors. Early experiments showed that with increasing experience of the terrain, directional information available during the inbound flight may be computed for the purpose of directional indication in the waggle dance (Otto, 1959). If the waggle dance computes directional information that depends not only on the current state of the animal's path integrator but also on information that the animal has associated with landmark views, that is, local vectors associated with landmarks (Etienne, Maurer, Boulens, Levy, & Rowe, 2004), bees would rely not only on an egocentric but also (or possibly only) on a geocentric system of reference because their flight vector is embedded in their spatial memory.

Thus, navigational strategies applied by foraging bees cannot be fully appreciated if one assumes a hive-centered egocentric form of spatial memory. Instead, it seems that the orientation flights of young or reorienting bees lead to a maplike spatial memory that appears to be derived from repetitive exposure to the same landmarks from different viewpoints. Given this capacity and the fact that bees are recruited by a dancing bee only after they performed their orientation flights, it is tempting to assume that bees attending a dance might recall from their memory of landmarks and homing vectors a corresponding outbound vector that is related to expected landmarks. Under these conditions neither the dance behavior nor the flight path of a recruited bee would be guided solely by two independent measures (direction and distance) but rather by an "expectation" of what could be encountered en route to the goal. A component of this "expectation" would be the route to be followed, as embedded in the maplike memory including sequences of landmarks. Indeed, von Frisch (1968) has already stated that the effectiveness of waggle dances (in terms of successful recruitment) depends on the foraging experience of the dance followers. When two groups of fellow bees have visited two different (and currently exhausted) unscented feeding places, contact with a dancer indicating the accustomed goal is much more effective than contact with a dancer indicating the unfamiliar one. Despite these early findings, however, the role of stored navigational information on the decoding process involved in the waggle dance remains entirely unknown.

An additional dimension of complexity in communication is added when bees in a swarm need to decide between two or more potential nest sites. Bees also communicate about potential nest sites when the swarm has left the old nest and searches for a new nest site. Scout bees inspect potential sites by running in various directions along the walls of the cavity and perform recruitment dances at the surface of the swarm according to the suitability of the cavity as a nest site (its size, humidity, closeness, and possibly other parameters; Seeley, 1977). The kind of learning during these behaviors can be addressed only as observatory learning because no reward is provided to the inspecting animal, the search is focused on potential nest sites only, and the animal has to integrate a large range of sensory inputs that are accessible only by its own exploratory behavior. Seeley and Buhrman (1999) confirmed and extended Lindauer's (1955) origin observations that dancers in a swarm sometimes visit and dance about more than one cavity. Of 113 bees that initially danced about a nonchosen cavity, 34 changed their dances to indicate the chosen cavity. Most of the others stopped dancing, but a few changed to a different nonchosen site. Nine continued dancing about a nonchosen cavity, but about half of the bees that initially danced about the chosen site continued to do so until the swarm flew off. Also, Camazine, Visscher, Finley, and Vetter (1999) and Visscher and Camazine (1999) confirmed that several bees first danced about one cavity, then followed dancers describing a different cavity, and later danced about the latter. Several bees were observed as they visited and danced about two cavities, which provided them with the opportunities to compare dance messages and the cavities themselves. Most intriguingly, some bees changed their dances to match dances they had followed without visiting the indicated cavity, indicating that they exchanged their communicative signals without inspecting the respective cavity themselves. Seeley and

Visscher (2003, 2004) proposed that quorum sensing is the strategy followed by the bees because the scouts do this by noting when one of the potential nest sites under consideration is being visited by a sufficiently large number of scouts.

Griffin and Speck (2004) interpreted this behavior as a rare case of chain communication, and irrespective of whether one would take this flexibility in the communicative process of bees as an indication of some form of animal consciousness, it provides us with a clue about information processing on the level of observatory memories.

Passino and Seeley (2006) recently modeled the social process of nest-site selection in a swarm setting out to choose a new nest site. This form of social decision making, in which the scout bees in a swarm locate several potential nest sites, requires an evaluation of alternative options and a selection between them on the basis of competitive signaling between several or many dancers. The authors developed a model of the social decision process, which is based on the single bees' evaluation and additional social coordinating processes (e.g., shaking signals; Seeley, Weidenmuller, & Kuhnholz, 1998; Visscher & Camazine, 1999) and the acoustic piping signal (Seeley & Tautz, 2001). They found that a balance is kept between the speed and accuracy of decision making by minimizing the time needed to achieve a consensus and maximizing the probability that the best site is chosen. Furthermore, they showed that the probability of choosing the best site is proportional to the relative quality of the discovered sites. Observatory learning on the individual level is the essential substrate of such a social process. Because less than 5% of the bees in a swarm are engaged in scouting and dancing, and many bees (the queen in particular) never reach the outer shell of the swarm where the communication process is going on, the bees in a swarm must differ with respect to their knowledge about the swarm's heading when it takes off. In addition, Katz (1950b) showed that certain bees (most likely the informed ones) fly ahead, and the others follow them using vision rather than olfaction for keeping contact with these "streakers."

COGNITIVE APPROACHES OF DISCRIMINATION SOLVING

Animals, including invertebrates, can sometimes respond to novel stimuli that they have never encountered before or can generate novel responses that are adaptive given the context in which they are produced. This behavior is particularly interesting for studies on cognition because it reveals that spontaneity and creativity may exist even in tiny brains such as those of insects. Generating novel responses or responding to novel stimuli that the animal has never before encountered is usually described as instances of positive transfer of learning (Robertson, 2001), a capacity that cannot be referred to as an elemental form of learning because the responses are aimed toward stimuli that do not predict a specific outcome per se based on the animals' past experience. Moreover, learning to inhibit such a transfer to produce adaptive responses that can be linked to a specific context is also a valuable capacity. It allows, for instance, learning that, given a certain stimulus or condition, a particular response is appropriate whereas given a different stimulus or condition, the same response is no longer appropriate. This form of learning, usually referred to as conditional learning or occasion setting, cannot be viewed as elemental learning because a given stimulus may or may not be predictive of a certain outcome, depending on the particular environment. Relying on its elemental outcome alone, therefore, does not help to solve this kind of problem. In this section, we will focus on these forms of nonelemental learning. We will therefore deal with four main capacities: (a) selective attention, (b) stimulus categorization, (c) rule learning, and (d) contextual learning. We start with selective attention, as it seems to be a necessary requisite for extracting the information that allows solving the other three problems.

Selective Attention

Selective attention consists of the ability to focus perceptual mechanisms on a particular stimulus and to actively process this information while ignoring nonrelevant stimuli (Zentall, 2005). It implies that the representation of the stimulus has been filtered or modified, presumably so that it can be processed or responded to more efficiently. Different approaches have been proposed to the notion of selective attention. Here we will focus on the ecological notion of "search image" (Tinbergen, 1960) and on the more traditional approach of discriminative learning to selective attention (Zentall & Riley, 2000).

Selective attention could be related to the notion of search image because such images are assumed to exist in cruising animals to facilitate detection of relevant stimuli in the environment. Search images, which could be innate or acquired through experience in the field, have been proposed to be a specific means for filtering out sensory information and focusing perception on specific stimulus configurations as a way to more efficiently forage and avoid predation. Innate search images driving the first foraging flights are assumed in insect pollinators such as bees to facilitate the detection of flower sources (Menzel, 1985). Indeed, naïve bees exhibit innate

preferences for biologically relevant floral cues such as colors (Giurfa, Núñez, Chittka, & Menzel, 1995; Gumbert, 2000) or bilateral symmetry (Rodriguez, Gumbert, Hempel de Ibarra, Kunze, & Giurfa, 2004), which make them spontaneously prefer flowerlike stimuli presenting these cues in their first foraging flights.

Traditionally, selective attention has been studied through a discriminative learning approach. Such an approach posits that through selective attention, animals gradually learn to attend to the dimension along which discriminative stimuli differ (Mackintosh, 1975). Free-flying honeybees (Giurfa, 2004) and bumblebees (Giurfa, 2004) trained in color discrimination problems distinguish a given color differently after absolute (training with a single reinforced color) and differential conditioning (training with a reinforced color and nonreinforced alternatives). They become progressively better in discriminating the trained color from colors that are perceptually close after prolonged differential conditioning, whereas they are incapable of such discrimination after the same amount of absolute conditioning. These results can be interpreted along the selective attention hypothesis such that insects gradually learned to attend to the spectral dimension along which discriminative stimuli differed. An alternative interpretation posits that differentially conditioned animals form positive and negative generalization gradients to the rewarded and the unrewarded stimulus, respectively, and thus develop a sharper generalization profile for the learned stimulus. An attentional account may also apply to pattern discrimination experiments in which free-flying honeybees are trained to discriminate black-and-white patterns in which each of four quadrants presented a different grating orientation (Giurfa et al., 1999). In these experiments, honeybees did or did not discriminate the same two patterns depending on the kind of training used, absolute or differential conditioning. Absolute conditioning promoted recognition based on local cues (the lower half of a disk made of different sectors), whereas differential conditioning expanded it to the whole pattern.

Finally, the fact that honeybees can be trained to categorize visual stimuli on the basis of a specific feature (see below) proves that bees can attend selectively to this feature, which is relevant for the categorization task, while ignoring other spatial details of the stimuli that are to be grouped.

Visual Stimulus Categorization

Categorization refers to the classification of perceptual input into defined functional groups (Harnard, 1987). It can be defined as the ability to group distinguishable objects or events on the basis of a common feature or set of features and therefore to respond similarly to them (Delius, Jitsumori, & Siemann, 2000; Huber, 2001; Troje, Huber, Loidolt, Aust, & Fieder, 1999; Zentall, Galizio, & Critchfield, 2002). Thus, categorization deals with the extraction of these defining features from objects of the animal's environment. Although it is currently debated whether or not categories have strict or fuzzy boundaries, there is a general agreement for acknowledging that category boundaries are sharper than those corresponding to the gradual decrease of responding along a perceptual scale underlying generalization and that they are indicative of perceptual discontinuities (Pastore, 1987).

Categorization has been studied and demonstrated in free-flying honeybees trained to visual stimuli. The first study showing generalization capabilities beyond straightforward discrimination in honeybees was, in fact, not concerned about the question of high-level cognitive performances in honeybees. This study focused on the sensory physiology of bees and, more specifically, on the mechanisms of orientation discrimination in honeybees (Homberg & Hildebrand, 1989) such that the term *categorization* was not even mentioned in this work. The authors trained free-flying bees with pairs of achromatic (black and white) disks presenting stripes of varying period and width (10 different stimuli) but with a single orientation that could be varied by rotating the disks. Bees were trained to discriminate two given stripe orientations (e.g., 45° from 135°) by rewarding one of these orientations with sucrose solution. During the training, pairs of stimuli with an extremely different spatial quality were presented in a random succession to the bees. Within each pair, one was oriented at 45° and the other at 135°. Thus, irrespective of their differences in spatial detail, gratings could be classified as displaying either a 45° or a 135° orientation. In this case, gratings oriented at 45° were rewarded with sucrose solution whereas those at 135° were not rewarded. Thus, despite the difference in pattern quality, all the rewarded patterns had the same edge orientation and all the nonrewarded patterns also had a common orientation, perpendicular to the rewarded one. The bees had to extract and learn the orientation that was common to all rewarded patterns to solve the task.

In the tests, bees were presented with novel patterns to which they had not been exposed previously and which were all nonrewarded but exhibited the same stripe orientations as the rewarding and nonrewarding patterns employed during the training. In such transfer tests, bees chose the appropriate orientation despite the novelty of the structural details of the stimuli. The authors concluded that bees detect the orientation of a visual pattern per se, independently of pattern quality. This performance complies with the definition of categorization because bees exhibited appropriate transfer
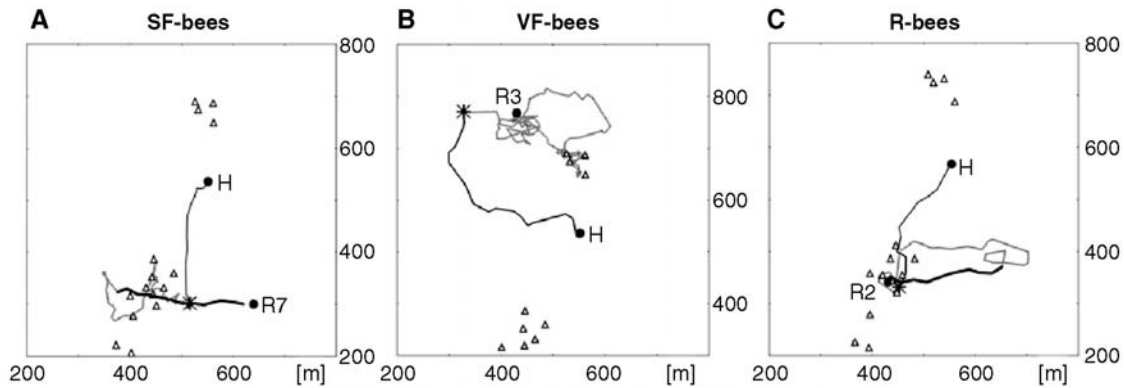
Figure 1: **Three Examples of Flight Paths (A: SF-bees; B: VF-bees; C: R-bees) Showing the Three Flight Phases: Vector Flight (bold line, in SF-and R-bees), Search Flight (dotted line), and Homing Flight (thin line).**
NOTE: The star marks the homing point at each of the three tracks (Menzel et al., 2005).

from known to novel stimuli that were classified according to their orientation. However, although discrimination between classes (orientations) was granted, generalization within classes was not really studied in detail. In other words, when bees transferred their choice to a novel pattern sharing the same orientation as previously rewarded ones, were they really generalizing their choice to novel, distinguishable stimuli? Or were they just choosing the novel stimuli because they could not distinguish them from the previous ones? In the latter case, speaking about categorization would obviously be senseless. The answers to these questions are incomplete because discrimination between all stimuli used was not studied. As a conclusion, one could safely state that bees exhibit generalization of orientation between patterns of very distinct spatial quality, a performance that goes beyond straightforward discrimination. This performance could be viewed as visual categorization; stating this conclusion on a firm ground, however, requires additional control experiments showing that bees treated all stimuli used as distinct independent of generalizing their responses in certain cases and not in others. Although caution is necessary, certain patterns that were treated as equivalent by bees based on their common orientation could obviously be discriminated. Thus, although not all requirements for concluding that categorization occurred were fulfilled, van Hateren, Srinivasan, and Wait's (1990) results strongly suggest that bees could indeed categorize patterns based on their main orientation.

Transfer to novel instances has also been shown in the case of bilaterally symmetric patterns that are vertically displayed (Giurfa, Eichmann, & Menzel, 1996). We asked explicitly whether bees can perceive bilateral symmetry as an independent pattern feature. The term *categorization* was introduced here to account for this

kind of visual performance in honeybees. Bees were trained with triads of patterns in which one pattern was rewarded with sucrose solution and the other two were nonrewarded. For the bees trained for symmetry, the rewarded pattern was symmetric and the nonrewarded patterns were asymmetric. For the bees trained for asymmetry, the rewarded pattern was asymmetric and the two nonrewarded patterns were symmetric. To avoid learning a specific pattern, bees were again confronted with a succession of changing triads during training. During training, the tests were interspersed with the triads, and they consisted of 12 novel stimuli, 6 symmetric and 6 asymmetric, all nonrewarded.

Bees trained to discriminate bilaterally symmetric from nonsymmetric patterns learned the task and transferred it appropriately to novel stimuli, thus demonstrating a capacity to detect and generalize appropriately symmetry or asymmetry. Interestingly, bees trained for symmetry chose the novel symmetric stimuli more frequently and came closer to and hovered longer in front of them than bees trained for asymmetry did for the novel asymmetric stimuli. It was thus suggested that bees have a predisposition for learning and generalizing symmetry. Such a predisposition can either be innate and could facilitate better and faster learning about stimuli that are biologically relevant (Rodriguez et al., 2004) or can be based on the transfer of past experience from predominantly symmetric flowers in the field.

Although the training stimuli used in these experiments did not resemble each other, at least to the human eye, the control experiments showing that all symmetrical and asymmetrical patterns were distinguishable from each other are also missing here. Specific analyses performed in this work showed that stimuli varied along several low-level cues that bees usually use while distinguishing patterns (disruption, orientation, subtended
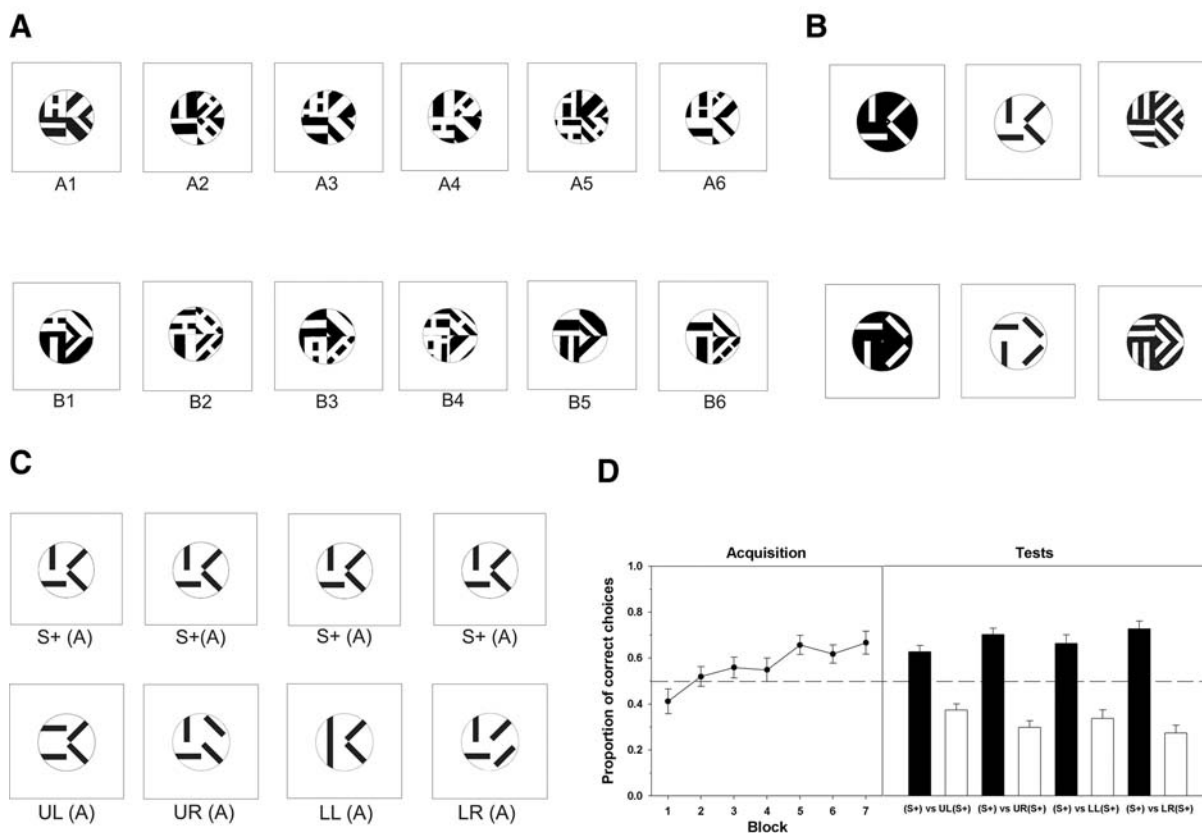
Figure 2:   Categorization Based on Sets of Multiple Features.
NOTE: (a) Training stimuli used in experiments by Stach, Benard, and Giurfa (2004). A patterns (A1 to A6) differed from each other but shared a common layout defined by the spatial arrangement of orientations in the four quadrants. B patterns (B1 to B6) shared a common layout perpendicular to that of A patterns. (b) Test stimuli. Bees appropriately transferred their choice to these novel stimuli if the nonrewarded patterns preserved the basic layout of the trained ones. (c) Test stimuli used to determine whether bees extract the simplified layout of four bars from the rewarded A patterns. The four test pairs shown correspond to the honeybees trained with A patterns. Equivalent tests were performed with the honeybees trained with B patterns (not shown). S+ = simplified layout of the rewarded training patterns; UL = upper-left bar rotated; UR = upper-right bar rotated; LL = lower-left bar rotated; LR = lower-right bar rotated. (d) Left panel, acquisition curve showing the pooled performance of bees rewarded on A and B patterns. The proportion of correct choices along seven blocks of six consecutive visits is shown. Bees learned to discriminate the rewarding patterns (A or B) used for the training (a) and significantly improved their correct choices during training. Right panel, proportion of correct choices in the tests with the novel patterns. Bees always preferred the simplified layout of the training patterns previously rewarded (S+) to any variant in which one bar was rotated, thus showing that they were using the four bars in their appropriate spatial locations and orientations.

angle, area, etc.) but that bees were not responding to these cues but to symmetry or asymmetry. Thus, although the performance of bees in Giurfa et al.'s (1996) experiments is indeed consistent with categorization of figures based on their symmetry, additional controls would be necessary to show that all patterns used in this work were indeed distinct for the bees despite the fact that some were considered equivalent based on their symmetry.

The two examples cited above on orientation and bilateral symmetry categorization have in common that they both assumed that bees focused their attention on a single feature at a time (orientation or bilateral symmetry) to solve the problem. In fact, it has been repeatedly argued that because of limited cognitive capabilities, bees could not do anything but focus on a

single isolated feature at a time (Horridge, 1996, 1997) and could not therefore attain levels of stimulus classification such as configural categorization as exhibited by humans (Maurer, Grand, & Mondloch, 2002). Recently, Stach, Benard, and Giurfa (2004) showed that a further level may exist in honeybee visual categorization. Besides focusing on a single feature, honeybees were shown to assemble different features to build a generic pattern representation, which could be used to respond appropriately to novel stimuli sharing such a basic layout. Honeybees trained with a series of complex patterns sharing a common layout comprising four edge orientations (Figure 2) remembered these orientations simultaneously in their appropriate positions and transferred their response to novel stimuli

that preserved the trained layout (Figure 2b). Honeybees also transferred their response to patterns with fewer correct orientations (Figure 2c), depending on their match with the trained layout. This generic pattern configuration was inculcated by a training in which a randomized succession of changing patterns sharing a common configuration was used (Stach et al., 2004). Thus, the question of whether bees can extract a configuration common to a group of rewarded patterns, made from four different edge orientations arranged in a specific spatial relationship to each other, was answered positively. Bees extracted such configuration and responded to novel patterns that also presented this configuration. These results show that honeybees extract regularities in their visual environment and establish correspondences among correlated features such that they generate a large set of object descriptions from a finite set of elements. This performance could be the basis for configural categorization, although further control experiments would be necessary in this case.

A related conclusion was reported by Zhang, Srinivasan, Zhu, and Wong (2004), who showed that honeybees have the ability to group similar, natural images together. They showed positive transfer to novel stimuli within four groups of stimuli: (a) star-shaped flowers, (b) circular-shaped flowers, (c) plant stems, and (d) landscapes. Although these experiments did not reveal the specific cues used by the bees to assign blossoms to one of these groups, Zhang et al. (2004) excluded the use of color and mean luminance as defining single low-level features. Instead, they suggested that configurational properties of the figures, in which specific features such as circular symmetry, angular periodicity, bilateral symmetry, and the presence of a horizontal, high-contrast edge, the horizon, would be integrated, could help bees classify the different stimuli. Therefore, they suggested that this categorization is based on a combination of low-level features, a suggestion that coincides with that reached by Stach et al. (2004).

It is thus possible to conclude that honeybees perform visual stimulus categorization. Future experiments will have to include additional controls, showing that bees can indeed discriminate between all the stimuli used. Nevertheless, given the nature of many stimuli used in these experiments, it seems obvious that bees do indeed discriminate most of them, thus showing the typical positive transfer characteristic of stimulus categorization.

Rule Learning

Rule learning presupposes positive transfer of an appropriate response from a known set to a novel set of stimuli. In this case, the animal bases its choice not on the perceptual similarity between the novel and the known stimuli, which might not share any common feature, but on a rule that transcends the stimuli used to train it. Examples of such rules are "larger than," or "on top of," which may apply to stimuli that do not share any common feature but that can nevertheless be classified according to the rule. Other examples are the so-called principles of sameness and of difference. These rules are uncovered through delayed matching to sample (DMTS) and the delayed nonmatching to sample (DNMTS) experiments, respectively. In DMTS, animals are presented with a sample and then with a set of stimuli, one of which is identical to the sample and which is reinforced. Because the sample is regularly changed, they must learn the sameness rule, that is, "Always choose what is shown to you (the sample), independent of what else is shown to you." In DNMTS, the animal has to learn the opposite, that is, "Always choose the opposite of what is shown to you (the sample)."

Honeybees foraging in a Y-maze learn both rules (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001). Bees were trained in a DMTS problem in which they were presented with a changing nonrewarded sample (i.e., one of two different color disks or one of two different black-and-white gratings, vertical or horizontal) at the entrance of a maze. Once within the maze, the bees were rewarded only if they chose the stimulus identical to the sample. Bees trained with colors and presented in transfer tests with gratings that they had not previously experienced solved the problem and chose the grating identical to the sample at the entrance of the maze. Similarly, bees trained with the gratings and tested with colors in transfer tests also solved the problem and chose the novel colors corresponding to those of the sample grating at the maze entrance. Transfer was not limited to different kinds of modalities (pattern vs. color) within the visual domain but also could operate between drastically different domains such as olfaction and vision (Giurfa et al., 2001). Furthermore, bees also mastered a DNMTS task, thus showing that they also learned a principle of difference between stimuli (Giurfa et al., 2001). These results document that bees learn rules relating stimuli in their environment. The capacity of honeybees to solve DMTS tasks has recently been verified (Zhang, Bock, Si, Tautz, & Srinivasan, 2005; Zhang et al., 2004). It was found that the working memory for the sample underlying the solving of DMTS is around 5 s (Zhang et al., 2005) and thus coincides with the duration of other visual and olfactory short-term memories characterized in simpler forms of associative learning in honeybees. Moreover, bees trained in a DMTS task can learn to pay attention to one of two different samples presented successively in a flight tunnel (either to the first or to the second) and can transfer the

learning of this sequence weight to novel samples (Zhang et al., 2005).

Despite the honeybees' evident capacity to solve relational problems such as the DMTS or the DNMTS tasks, such capacities are not unlimited. In some cases, biological constraints may impede the solving of a particular problem for which rule extraction is necessary. It is therefore interesting to focus on a different example of rule learning that bees could not master, the transitive inference problem (Benard & Giurfa, 2004). In this problem, animals have to learn a transitive rule, that is, A > B, B > C, then A > C. Preference for A over C in this context can be explained by two strategies: (a) deductive reasoning (Fersen, Wynne, & Delius, 1990), in which the experimental subjects construct and manipulate a unitary and linear representation of the implicit hierarchy A > B > C, or (b) responding as a function of reinforced and nonreinforced experiences (Terrace & McGonigle, 1994), in which case animals choose among stimuli based on their associative strength, that is, on the effective number of reinforced and nonreinforced experiences with the stimuli.

To determine whether bees learn the transitive rule, they were trained using five different visual stimuli: A, B, C, D, and E in a multiple-discrimination task A+ versus B–, B+ versus C–, C+ versus D–, and D+ versus E– (Benard & Giurfa, 2004). Training therefore involved overlapping of adjacent premise pairs (A > B, B > C, C > D, D > E), which underlie a linear hierarchy A > B > C > D > E. After training, bees were tested with B versus D, a nonadjacent pair of stimuli that were never explicitly trained together. In theory, B and D have equivalent associative strengths because they are, in principle, equally associated with reinforcement or absence of it during training. Thus, if bees were guided by the stimulus's associative strength, they should choose randomly between B and D. If, however, bees used a transitive rule, they should prefer B to D.

Honeybees learned the premise pairs as long as these were trained as uninterrupted, consecutive blocks of trials (Benard & Giurfa, 2004). But if shorter and interspersed blocks of trials were used, such that bees had to master all pairs practically simultaneously, performance collapsed and bees did not learn the premise pairs. The bees' choice was significantly influenced by their experience with the last pair of stimuli (D+ vs. E–) such that they preferred D and avoided E. In the tests, no preference for B to D was found. Although this result agrees with an evaluation of stimuli in terms of their associative strength (see above), during training, bees visited more B when it was rewarding than D, such that a preference for B should have been expected if only the associative strength were guiding the bees' choices. It was then concluded that bees do not establish transitive inferences

between stimuli but rather guide their choices by the joint action of a recency effect (preference for the last rewarded stimulus, D) and by an evaluation of the associative strength of the stimuli (in which case preference for B should be evident). As the former supports choice of D whereas the latter supports choice of B, equal choice of B and D in the tests could be explained (Benard & Giurfa, 2004). In any case, memory constraints (in this case, the fact that simultaneous mastering of the different premise pairs was not possible and the fact that the last excitatory memory seems to predominate over previous memories) impeded learning the transitive rule.

Conditional Discriminations: Occasion Setting and Contextual Learning

Contextual learning is a term widely used for describing conditional discriminations that can be subsumed in the so-called occasion-setting problem (Schmajuk & Holland, 1998). In this problem, a given stimulus, the occasion setter, informs the animal about the outcome of its choice (for instance, given stimulus C, the occasion setter, the animal has to choose A and not B because the former but not the latter is rewarded). This basic form of conditional learning admits different variants depending on the number of occasion setters and discriminations involved, which have received different names. For instance, another form of occasion setting involving two occasion setters is the so-called transwitching problem. In this problem, an animal is trained differentially with two stimuli, A and B, and with two different occasion setters C1 and C2. When C1 is available, stimulus A is rewarded whereas stimulus B is not (A+ vs. B–), and it is the opposite (A– vs. B+) with C2. Focusing on the elements alone does not allow solving the problem, as each element (A, B) appears equally as often rewarded and nonrewarded. Each occasion setter (C1, C2) is, in the same way, simultaneously rewarded and nonrewarded, depending on its association with A or B. Animals have, therefore, to learn that C1 and C2 define the valid contingency. The transwitching problem is considered a form of contextual learning because the occasion setters C1 and C2 can be viewed as contexts determining the appropriateness of each choice. Bumblebees have been trained in a transwitching problem to choose a 45° grating and to avoid a 135° grating to reach a feeder and to do the opposite to reach their nest (Fauria, Dale, Colborn, & Collett, 2002). They can also learn that an annular or a radial disc must be chosen, depending on the disc's association with a 45° or a 135° grating either at the feeder or the nest entrance: In one context, access to the nest was allowed by the combinations 45° + radial disc and 135° +

annular disc but not by the combinations 45° + annular disc and 135° + radial disc; at the feeder, the opposite was true. In both cases, the potentially competing visuo-motor associations were insulated from each other because they were set in different contexts.

Comparable behavior was found in honeybees wherein distinct odors or times of the day (Menzel et al., 1998) were the occasion setters for a given flight vector. The authors trained individually marked bees to forage at two feeding sites, one at 630 meters from the hive toward 115° north in the morning and another at 790 meters, 40° north in the afternoon. Thus, depending on the time of the day, outgoing bees flew in one direction or the other, thus showing that temporal information can act as an occasion setter for a sensory-motor routine. Furthermore, trained bees were captured when arriving at the hive and then released at the "wrong" site, that is, at the afternoon site in the morning or at the morning site in the afternoon. In both cases, bees flew straight back to the hive. To fly homeward, the bees retrieved the memory for the correct flight path from long-term memory stores that were established during training and that related local landmarks to the flight path to the hive.

Olfactory cues can also act as occasion setters for the choice of appropriate navigation vectors. Reinhard, Srinivasan, Guez, and Zhang (2004) showed that free-flying bees trained to forage at two distinct feeders, placed at different outdoor locations and carrying different scents or colors, recall the locations (or colors) of these food sites and fly to them when the training scents were blown into the hive and the scents and food at the feeders were removed. These results indicate that familiar scents can trigger navigational and visual memories in experienced bees to define appropriate context-dependent responses. These observations resemble those already reported by Lindauer (1957) who successfully stimulated bees to dance at night and found that they indicated the afternoon feeding place before midnight and the morning feeding place after midnight. Most interestingly, around midnight, bees performed either unoriented dances or indicated into both directions in successive runs.

Conclusion

The environment places the same basic demands on animals with small and with large brains. Both are confronted with similar problems as they orient in more or less complex environments, find food for survival, escape from eventual predators, find a partner for reproduction, and so on. The usual conclusion states that insects, with their smaller brains, apply local solutions to these problems, that is, solutions that are specific and isolated, local in a verbal, a mechanistic, and a

behavioral sense. Verbally, a localized solution may mean that it may suit only one specific problem at one particular location in space and time. Mechanistically, local solutions mean that only specific sensory-motor connections in the nervous system may exist, with no cross-talk between them and no common level of memory storage. Behaviorally, local solutions refer to independent behavior routines that are applied without gaining from cross-talk. In other words, the concept of information transfer between sensory-motor routines, translated into an appearance of novel behaviors that allow responding to novel demands of the environment, may be neglected or minimized in the case of insects.

Our review provides considerable evidence against such an understanding, which ignores the enormous richness of insect behavior, its high flexibility, and the cross-talk between different behavioral routines. Although we have focused on honeybee behavior, and within it, on performances detectable when studying free-flying bees, similar cognitive complexity can be found using appropriate experimental protocols, for example in honeybee olfactory learning (Menzel et al., 2001; Giurfa, 2003). Thus, it is appropriate to conceptualize insect behavior from a cognitive perspective, and install memories not only into specific sensory-motor circuits, but into a common reference system as well. As a consequence, many insect species that were studied in this respect were found to extract rules from particular sequences of experience and transfer these rules to other sensory domains. Furthermore, the structure of the memory thus established represents the multiple sensory inputs and related behaviors in an integrated way such that a representation of complex environmental conditions is formed. Such capacities may not be surprising when the underlying neural substrate subserving them is explored in detail. As in larger brains, two basic neural architectural principles of many insect brains are found: specialized neuropiles, which refer to specific sensory domains, and higher-order integration centers, in which information pertaining to these different domains converges and is integrated, thus allowing cross-talk and information transfer. In this sense, both modularity and central integration seem to be basic building principles adopted by different nervous systems to provide flexible solutions to a changing environment. Navigation and communication in social Hymenoptera are particularly telling examples in this respect. Generation of novel responses and transfer, as evinced in the solving of several discrimination problems, may also benefit from cross-talk and integration between neural modules.

Although our review shows that natural behavior in honeybees requires cognitive approaches to appreciate and dissect its full potential, a recurrent argument is that such a cognitive richness derives from a social lifestyle

and that it may not be present in solitary species. This argument has to be taken cautiously, because sociality may be, in a sense, a factor promoting cognitive simplicity rather than richness. Studies on collective decision-making in social insects have shown that collective behavioral patterns arise mostly without any central control, from simple interactions between individuals, which seem to act on the basis of extremely simple behavioral rules. For instance, collective aggregation around refuges results from individual probabilistic rules determining when to stop or resume walking instead of deriving from individual decision-making, evaluation, and comparison of the refuge's characteristics. Similarly, complex architectural structures characterizing ant or termite nests arise without central control, simply based on a restricted set of individual behaviors performed in a rather automatic way, without "knowledge" of the behavioral patterns exhibited by other individuals (Buhl et al., 2004).

The conclusion emerging from these studies on insect collective behavior is that individuals, which may be viewed as extremely sophisticated at the cognitive level when performing some individual tasks, may appear as automatons with limited cognitive capacities when performing collective tasks. This difference could indicate that cognitive richness is lost or at least temporally inhibited in a social context. But this may not be disadvantageous for the individual insects. In an individual and in a social context, the animal will adopt the behavioral strategies leading to adaptive solutions, either boosting or sacrificing what researchers would view as cognitive sophistication. The critical question in this context is therefore, What determines the adoption of one or the other level of cognitive complexity? Which factors are responsible for the fact that an ant or a bee that can learn and memorize several cues while foraging, solve complex discriminations and generate novel behaviors leading to adaptive solutions, and behave like an automaton following a reduced set of repetitive patterns and simple rules when building a comb? So far, we have no answers to these questions, but they can be approached on an experimental level. Studying whether or not individual learning and memory are modified by exposure to social pheromones or by chemosensory cues within a group and whether or not levels of neuromodulators are changed in the presence of a group of cospecifics are just some of the paths that can be followed to provide some answers to these questions.

It is fair to conclude that similar cognitive complexity, based on integrated forms of dealing with the environment, will be found in other invertebrates when looked at more closely. In this sense, research addressing behavioral complexity and its underlying neural substrates is necessary to characterize the real potential of invertebrate learning and memory. Usually such an approach

has been used to characterize behavioral simplicity, rather than complexity. It seems therefore timely to focus on the latter by studying problem solving besides elemental forms of learning.

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