Working Memory in Bees: Also in Flies?

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Abstract: Decision making requires reference to both actual and remote information in the context of the requirements of the animal. Here, I explore a cognitive approach to decision making in honeybees and ask the question whether flies may share the faculties observed in bees. Examples are drawn primarily from natural behavior in bees, particularly from navigation and communication. I conclude that studies in Drosophila learning and memory in the tradition of Martin Heisenberg may gain from cognitive concepts, meaning that the “internal doing” of the brain should be included in the search for the neural basis of decision making.

Keywords: cognitive neuroscience, insect cognition, learning, memory, navigation, communication

INTRODUCTION

Let us assume, for a moment, Martin Heisenberg will continue performing research for another 20 years. He would build on his discoveries about short-term olfactory memory and those on visually guided operant behavior (Heisenberg, 1989, 2003; Heisenberg & Wolf, 1979, 1984, 1988), and I expect him to embark on new frontiers taking advantage of the exciting and upcoming fantastic molecular genetic tools in Drosophila. Which direction would his research take, which topic would he select and which concepts of behavioral neuroscience would attract his attention? Knowing him as a colleague and friend since the early 1970s, I expect him to critically examine his basic concepts, realizing that if one wants to understand the mechanisms of behavior, one needs to know more than the motor output of the nervous system. Other than conceptualized by him for many years, he might acknowledge that visible behavior, as it appears as motor output of the nervous system, is just the peak of an ice mountain, and what is kept from direct observation might, in fact, be not only much more, but also much more important for understanding why Drosophila does what it does.” He might then turn his attention to the “inner doing” of the brain, those processes that are essential for understanding of behavior but are not expressed in the output of the nervous system. My guess is that he will focus on the search for neural mechanisms of decision making, a topic which has been at the forefront of his thinking for a long time but resisted an in-depth understanding because of—as I see it—a rather narrow conceptual framework in the tradition of insect neuroscience in general.

Since the late 1970s, he, together with Reinhard Wolf, used the flight simulator to study visually guided operant behavior (Heisenberg & Wolf, 1979). Flies learned to control their yaw or thrust to avoid being heated and to guide their behavior by selecting patterns, or their positions, colors, and more (Heisenberg & Wolf, 1984). These studies were driven by attempts to capture the elements of operant activity and operant behavior. Spontaneous activity, an essential component of operant behavior, was understood as a randomly fluctuating component of neural functions (“colored noise”; Wolf & Heisenberg, 1991; Heisenberg et al. 2001), and the selection between “initiating activities” was conceptualized as essentially a stochastic process. These studies certainly capture rudimentary elements of processes potentially underlying decision making as long as the animal cannot know at the outset of the process what to do. However, when animals apply phylogenetically acquired knowledge and when they learn they have to decide between options, and they may follow different strategies, for example, by referring to the salience of the stimulus components in compounds of stimuli (Peng et al., 2007; Tang, 2001; Wang et al., 2008). Without doubt, the early studies, together with those of Brembs, Guo, and others (Brembs & Heisenberg, 2000; Liu et al., 1999), are wonderful examples for the analysis of operant behavior and operant conditioning. The inventiveness in behavioral paradigms, combined with the potentials of...
molecular genetic manipulations of parts of the Drosophila brain, are sensational. However, I would assume Martin Heisenberg will engage in a shift from a learning perspective to a memory perspective. Such a shift in concepts would not be difficult for him, since he has thought about memory dynamics and the role of the mushroom body in short-term memory for a long time.

In my view, learning-related perspectives of decision making are forms of single-system perspectives. Such single-system concepts assume that the essence of decision making is captured by learning to map a particular situation (i.e., world state) to actions that maximize reward or minimize punishment by calculating the expected value (Sutton & Barto, 1981). By contrast, multiple-systems perspectives originate from the memory literature, which emphasizes multiple memory systems and their interactions for the organization of behavior (Squire, 2004). The difference between these two perspectives can be nicely illustrated for the navigation literature (Johnson et al., 2007). The stimulus-response (i.e., route-based) concepts favor the single-system perspective and root in the tradition of learning theory (Rescorla & Wagner, 1972). The cognitive map concept equips animals with the ability to plan novel routes and flexibly integrate new information (Tolman, 1948). Animals are thought to store associations between stimuli (not only between CSs and USs), and to plan actions on the basis of expectations emanating from these associations. Planning requires the selection of actions not from a pool of stochastic movements, but rather from multiple directed and value-based motor programs. At the heart of these concepts lies the assumption of neural (i.e., internal) search processes, which predict and evaluate potential future outcomes based on the needs of the animal at the moment of decision making, its relevant memories, and the actual situation as indicated by the external stimuli (Zilli & Hasselmo, 2008; Daw et al., 2005). A parallel line of arguments originates from the behavioral concept of working memory, an active form of memory that integrates retrieved reference memory with recently learned short-term memory together with the current needs of the animal (Schacter et al., 2007; Roediger et al., 2007).

Is there a necessity to invoke working memory functions in the decision making of insects? I shall draw examples from studies in honeybees. There are lessons one can learn from these studies that can possibly be transferred to Drosophila (and other insects): 1) The richness of behavior appears in studies that allow the animal to behave close to normal in its natural environment. Rigid designs of experiments might be necessary to quantify behavior and make it reproducible, but they run into the danger that the animal in its restriction can only do what the experimenter allowed it to do. The conclusion from such experiments is often that, since the animal did what was expected from it, this is the only thing an animal can do; 2) although scientific progress is bound to search for the most parsimonious explanation, it is not obvious what may be more or less demanding for the brain, particularly a small brain as that of an insect. For example, will it be more difficult for a small brain to follow a route-based navigation strategy or a cognitive map-based strategy? Are neural processes derived from behavioristic learning theory computationally less demanding than those derived from cognitive concepts? We must say, at this stage, that we do not know, and the only way to find out is to search for neural mechanisms within a broad conceptual frame; and 3) we need to acknowledge that potential behavioral acts that are not performed by an animal are equally important as the expressed behavior. Only by accepting that an attentive brain is constantly producing potential behaviors, most of which are not expressed, and that it is this capacity that shapes brain function in evolution through which we shall be able to search for the neural basis of the “inner doing” as a prerequisite of decision-making processes.

PROPERTIES OF WORKING MEMORY ILLUSTRATED BY OBSERVATIONS IN THE HONEYBEE

An Active Memory Supports Flexible Comparison between Recently Experienced Stimuli

Delayed Matching to Sample

A standard test of working memory is the paradigm of delayed matching to sample (DMTS) and delayed non-matching to sample (DNMTS). In these paradigms, the animal has to keep, in a short-term store, a recently experienced signal (i.e., the sample) and apply a learned rule afterward when choosing between two or several options. Rule learning presupposes positive transfer of an appropriate response from a known set to a novel set of stimuli. Thus, 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. Since the sample is regularly changed, in the case of DMTS, the animals must learn the sameness rule “Always choose what just has been 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 has just been shown to you (the sample).” Honeybees foraging in a Y-maze learn both rules (Giurfa et al., 2001). Bees were trained in a DMTS or DNMTS problem in which they were first presented with a changing nonrewarded sample (e.g., one of two different color disks) at the entrance of a maze. Then, bees
move on in the maze and are faced with a binary choice situation between the two colors, one of which they had just seen when entering the maze. The bees were rewarded only if they chose the stimulus identical to the sample once within the maze. Bees trained with colors and presented in transfer tests with gratings that they have not experienced before solved the problem and chose the gratings identical to the sample at the entrance of the maze. Similarly, bees trained with the gratings and tested with colors also solved the problem and chose the novel color corresponding to that of the sample grating at the maze entrance. Transfer was not limited to different kinds of stimuli within the visual domain, but could also operate between sensory modalities (e.g., olfaction and vision). These results document that bees learn rules relating stimuli in their environment. The delay between the sample and the choice was found to range up to 5 seconds (Zhang et al., 2005). This value 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 learned to pay attention to one of two different samples presented successively in a flight tunnel (either to the first or to the second) and transferred the learning of this sequence to novel samples.

Recently, Neuser et al. (2008) showed that *Drosophila* stores the position of an object and guides its movements according to it, although it is out of view for several seconds. This paradigm illustrates that *Drosophila* decides on its movement behavior according to the content of a working memory. It will be interesting to see whether a transfer between objects occurs, and whether different rules guiding movements after the disappearance of the objects can be established by training.

**Serial Positions and Numerosity**

Learning of stimulus sequences requires memory of the temporal order of occurrences. Under natural conditions, temporal order is usually combined with spatial order. Position in space is also defined by its relation to surrounding cues, giving the position of each item a unique spatial character. Memories developed for sequential spatial positions of items may, therefore, be embedded in a large-scale relational spatial memory (a “mental” or “cognitive” map), in which the sequentially experienced positions are learned as patterns signaling the expected outcome of a choice. For example, honeybees learn to guide their flights into the right or left arm of a continuous T-maze, depending on the serial patterns of two different color signals at four consecutive positions (Menzel, submitted). The rank order of position salience is 1 (closest to the choice point), 2, and 3. No learning is found if the signal appears at position 4 (furthest of the choice point). However, the salience values at the different positions do not simply add up, and sequential patterns of signals are also learned, indicating that serial patterns are configured to, at least partially, form units of guiding stimuli. This requires a flexible working memory that groups sequential signals.

Do bees make their search behavior for a food source dependent on the number of landmarks encountered on the way to the food source? If this were the case, working memory would store some form of number. Indeed, Chittka et al. (1995) set up an experiment in which sequentially experienced landmarks guided free-flying bees over hundreds of meters to a feeding station. The bees searched both at the absolute distance, as measured by odometry, and at the location designated by the sequence of landmarks. Recently, it was found that if the positions of up to four signals in a narrow tunnel were varied during training, bees learned the numbers (up to three) rather than the positions of the signals (Dacke & Srinivasan, 2008). It is also relevant, in this context, that humble bees appear to measure time intervals between signals (Boisvert & Sherry, 2006). The effect of sequentially experienced signals was interpreted to indicate some form of numerosity, but an important prerequisite of numerical ability was not examined, namely, the close to equal salience of the sequential items. Indeed, the precision of local searching differs for different numbers of signals in the study by Dacke and Srinivasan (2008). Thus, it is still unknown whether bees accumulate a number-related content in their working memory.

**An Active Memory Provides Expectations**

**Occasion Setting**

Contextual learning is a term widely used for describing conditional discrimination paradigms, which can be subsumed as cases of the so-called occasion-setting problem (Schmajuk & Holland, 1998). In these kinds of discrimination, a given stimulus, the occasion setter, informs the animal about the outcome of its choice. In one case, bees were trained to fly to either of two feeding stations, one in the morning, the other in the afternoon (Menzel et al., 1998). Indeed, depending on time of day, bees flew in one direction or the other, thus showing that temporal information can act as the occasion setter for a sensory-motor routine. However, when trained bees were captured after arriving at the hive and then released at the “wrong” site (i.e., at the “afternoon site” in the morning, or at the “morning site” in the afternoon), they flew straight back to the hive. Thus, the bees must have retrieved the memory for the correct homeward flight path from long-term memory stores that were established during training and that related local landmarks to the flight path to the hive irrespective of the time of the day.
Working memory

Olfactory cues can also act as occasion setters for the choice of appropriate navigation vectors: Reinhard et al. (2004) showed, by repeating former experiments of von Frisch (1967), that free-flying bees trained to forage at two distinct feeders, placed at different outdoor locations and carrying different scents or colors, recalled the locations (or colors) of these food sites and flew to them when the training scents were blown into the hive. These results indicate that familiar scents can trigger navigational and visual memories out of the context in which these odors were learned in order to define appropriate context-dependent responses. These observations resemble those 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 both directions in successive runs. An elementary description of these results would favor a stimulus-response relationship. A cognitive interpretation claims that animals produce expectations about the respective outcomes and decide on the base of these expectations. As pointed out above, the assumption that the elementary description might be the more parsimonious one is unfounded, but it is certainly correct to claim for more direct evidence in favor of the cognitive interpretation.

Expectation about Reward Strength

Greggers and Menzel (1993) found, for bees foraging in a patch of four feeders that delivered different flow rates of sucrose solution, that bees store the reward properties of these feeders in a transient and active memory. Similar results were found for eight feeders, indicating that the reward properties of eight feeders are stored in feeder-specific memories. The capacity of working memory is, therefore, at least eight items. The time range of these specific working memories could be estimated as lying around 6 minutes. In a different experiment (Gil et al., 2007), bees first learned to associate colors with sucrose reward in an array of artificial flowers closely resembling a natural foraging situation. The question was asked whether and how the sequence of the animals’ experience with different reward magnitudes changed their later foraging behavior in the absence of reinforcement and under an otherwise similar context. In addition to the usual measure of correctness of choice, the bees’ “persistence” during their searches was quantified. It was found that the animals that had experienced increasing volumes of sugar reward during training assigned more time to flower inspection (i.e., showed greater “persistence”) when tested 24 and 48 hours after training. The animals behaved differently neither because they had more strongly associated the related predicting signals nor because they were fed more or faster. Instead, they had changed their “persistence” based on the systematic variations in reward magnitude they had previously experienced during training. Hence, these results indicate that the animals developed different long-term expectations of reward, depending on the serial reward schedule, and that these expectations eventually led to differences in test performance in the absence of reward, and even 48 hours after training.

An Active Memory Selects Behavioral Options

Novel Routes and Goal Selection in Navigation

Local navigation or map-based strategies allow 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 (Giurfa & Capaldi, 1999; Collett & Collett, 2002; De Marco & Menzel, 2008). Navigational memories that are more flexible than route memories are 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 during their orientations flights (von Frisch 1967; Capaldi et al., 2000) and establish a special “landscape memory” that relates landmarks to the bees’ central place, the hive. It was only recently that the structure of this “landscape memory” could be critically tested by using harmonic radar technology to track individual bees (Menzel et al., 2005). In this study, three test groups were examined and their flight paths recorded after they were released at many different release sites around the hive. The three test groups were: 1) bees that were trained to a feeder placed at variable locations in close vicinity to the hive that was moved around the hive at a constant distance and that, therefore, did not develop a route memory (variable feeder bees); 2) bees that were trained to a stationary feeder 200 m to the east of the hive and thus developed a route memory (stationary feeder bees); and 3) bees that were recruited by foragers that collected food at the stationary feeder (i.e., recruited bees). It was found that all bees returned to the hive after a period of search flights along fast and straight flights from all regions around the hive. Stationary feeder bees and recruited bees did so after they had performed the vector (i.e., distance and direction) components of their trained route flights or the indicated vector by the dancing bee; variable feeder bees returned after searching for a while close to the release site. Most importantly, stationary feeder bees performed either direct flights back to the hive or via the feeder to the hive. Thus, stationary feeder bees
made a decision between two potential goals, the hive and the feeder.

Several operations must be at the animal’s disposal to reach one of two goals that are outside of their visual range: 1) constructing a relational map of landmarks by first storing and then later recalling memories of vectors that point from many experienced landmarks toward the hive and that are recognized from different viewpoints; such a “mental” map could consist of either a collection of hive-directed vectors associated to landmarks, or a true relational map that locates the landmarks in a geometric spatial memory store; 2) selection of the goal and shift in motivation (fly toward the hive or toward the feeder); and 3) identification of the goal either as a location in a relational map or by “computing” the hive-directed vector components associated with the landmarks and the vector of the route flight from hive to feeder.

The question now in bee navigation is, What structure does this map-like memory have and how is it used? Any model of bee navigation, thus, has to incorporate a strategy based on a map-like representation of the bees’ large-scale home range and a freedom to choose between at least two goals. A map-like memory requires working memory functions in several respects: 1) the animal needs to localize itself by recruiting remote spatial memory and integrate it with the current views and directions; 2) it needs to select a goal out of several potential goals and decides to aim for one of these goals; and 3) it needs to continuously compare the actual conditions with the expected ones. Analyzing the search flights prior to the fast and straight flights toward the goal leads us to conclude that these three functions of working memory are partially reflected in sequential behavioral routines. Multiple returns to the release site and/or the end of the vector flight indicate that the animal is spotting itself relative to compositions of landmarks. Circling flights are interrupted by stretches of straight flights that resemble potential flight directions to either of the two goals (e.g., hive, feeding place). Active memory processing within expectation theory predicts that animals will pause at decision points (e.g., in a maze) as they mentally explore available possibilities (Johnson et al., 2007). We believe that our analysis of the search flights shows just such behavior.

Dance Communication and Goal Selection

As just described, orientation flights of young or reorienting bees lead to a map-like 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 a bee attending a dance might recall from its memory of landmarks and homing vectors a corres-
ponding 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 (e.g., direction and distance), but rather by an “expectation” to arrive at a particular location. A component of this “expectation” would be the route to be followed, as embedded in the map-like memory, including sequences of landmarks. Indeed, already, von Frisch (1968) stated that the effectiveness of waggle dances (in terms of successful recruitment) depends upon the foraging experience of the dance followers.

An intriguing feature of the waggle dance is that it may occur spontaneously (i.e., in the complete absence of foraging) or may be even induced experimentally (e.g., by stimulating the colony with familiar odors and/or sugar solutions). In the cases in which dance behavior was stimulated, dances are performed in accordance with the current position of the sun, even during the night, and without any view of the sky (Lindauer, 1954; see above). Surprisingly, 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). Thus, the marathon dances pose questions related to the memory requirements involved in the task of encoding information in the waggle dance; for instance, 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; how does it recruit from its memory a goal last visited 1.5 months ago? These and other observations lend support to the concept that bees use long-term memories to encode spatial information in the waggle dance, and these remote memories can be retrieved by suitable stimuli learned in the context of the indicated feeding places, put into working memory, and communicated in a flexible, updated way by the dance behavior to other bees.

Analysis of Dance Communication as a Tool to Study Working Memory Functions

The kind of questions to be asked in the future on navigation and communication studies of honeybees differ from those addressed so far. The sensory-motor routines involved are well understood, and they have been analyzed by asking, “What can the animal do?” Now, we need to first ask how the information that animals access in their working memory is stored, processed, and retrieved before we can expand upon our behavioral studies with bees in order to address the structure of internal representations, because the ritualized process of dance communication allows access to processes beyond behavioral acts, processes which may be called operations at the level of the working memory, or operations on
Working memory

representations. These operations are far from simple and transcend elemental forms of association. The richness of these operations is accessible only in animals acting in their natural environment, and the methods are now available for collecting the relevant data. Ultimately, one would like to know how and where the bee’s small brain performs these operations, but the answer to this lies in the future.

WHERE SHOULD WE SEARCH FOR WORKING MEMORY FUNCTIONS IN THE INSECT BRAIN?

The key properties of working memory are: 1) integration of retrieved memory, recent memory, and actual experience in an active form; 2) evaluation of the relevance of these memories with respect to external demands and internal states; 3) generation of expectations of potential outcomes; 4) selection between potential behaviors; and 5) storage of the consequences of the behavior to update remote memory. The requirements for these functions can be summarized by recognizing that an active form of memory is about the value and thus about the expected outcomes of behavior and not about motor routines or stimuli. Values change both with reference to external conditions and internal body states. Thus, both sensory inputs from outside and modulatory inputs reporting about body states need to be continuously integrated.

Working memory functions need not be centralized in a particular neural structure. In the mammalian brain, several structures appear to be involved in different working memory functions, such as orbitofrontal cortex, ventral striatum and dorsomedial cortex in evaluation and action-selection, and the hippocampus in prediction (Johnson et al., 2007). In the insect brain, two neuropils, the mushroom body (MB) and the central complex (CC), will be at the focus of attention not only because Martin Heisenberg and his group have accumulated so much information about the involvement of these structures in sensory and motor processing and memory functions, but also because of their internal neural organization and wiring with other brain regions. The study by Neuser et al. (2008) on delayed spatial orientation tasks points to the ring neurons of the ellipsoid body in the central brain of Drosophila. In this task, the motor components are of particular relevance for solving the short-term memory task, and thus it may not be surprising that neurons of the central complex are involved.

Considering the MB and looking across insect species, it might be fair to compile its functions in the following way, although I realize that this is a dangerous undertaking given the still limited amount of information available, the differences between insect species, and the controversies about some of the data: 1) integrating across sensory modalities at its input, most likely in the fly to a much lesser amount than in the bee; 2) storing sensory memories as an essential component in a distributed memory system; 3) providing information about the value of compound stimulus conditions at its output; 4) updating the evaluation of stimulus conditions by integrating across multiple modulatory inputs; 5) providing inhibitory output onto premotor pathways; and 6) distributing evaluated sensory information to many other regions of the brain. The motor component in behavior may not be processed in the MB or only to a low degree.

It is far from known how these properties of the MB may relate to working memory functions and what the neural underpinnings might be. Short-term memory, as assigned to the gamma lobe Kenyon cells in Drosophila, might reflect a component of working memory, its time-bridging function in the short-term range, and its active form. The role of modulatory inputs to the MB—besides its reinforcing component during associative learning—may relate to the selection of subcircuits as a prerequisite for a selection process, based on the needs and the experience of the animal. The still unknown relations between the short- and the long-term storage components may, in fact, represent processes to shift remote memory components into an active form, and since this is a reciprocal process leading to updated remote and stable memory, one might have seen, so far, only the latter and not the former aspect. The multitude of connections of MB intrinsic and extrinsic neurons might reflect the necessity of this structure to “consult” other regions both within and outside of the MB in decision-making processes. The complexity of neuronal assemblies of the Drosophila MB and their wiring by non-Kenyon intrinsic neurons and extrinsic neurons, as uncovered by Tanaka et al. (2008), could provide the neural structures of working memory functions and possibly other integrating properties in the insect brain. The even more complex calycal laminar structures in hymenoptera reflecting the across sensory modality integration already at the input side of the MB (Mobbs, 1982; Abel et al., 2001; Gronenberg, 1999, 2001; Schröter & Menzel, 2003), and the corresponding areas in the lobes with their multitude of extrinsic neurons (Mobbs, 1982; Rybak & Menzel, 1993; Strausfeld, 2002) may reflect additional complexities, possibly related to navigation and communication in social hymenoptera.

CONCLUSION

The wild speculations presented above are thought to illustrate a potential research strategy in cognitive neuroscience, rather than to highlight specific working hypotheses. Concepts derived from system (i.e., behavioral) analysis and condensed in terms originally thought to capture essentials of formal functions are taken
seriously and literally. These terms provide us with a program to search for neural mechanisms. Memory is such a term, initially a concept, and later a neural mechanism. Many others come to mind (e.g., reinforcement, retrieval, encoding, consolidation, and mental map; see Roediger et al., 2007). So is working memory. We use the term because we believe it provides us with a program to study essential functions of the brain, evaluation, selection, and decision making. Flies and bees may help to get from concepts to mechanisms faster.

I would expect Martin Heisenberg to contribute to this enterprise if nature would allow him to work for the next 20 years. The large collection of GAL4 lines (Tanaka et al., 2008) offers a wonderful tool box for the study of MB functions, and the new avenues opened by functional imaging (Fiala et al., 2003; Schroll et al., 2006; Wang et al., 2003; Ng et al., 2002; Yu et al., 2004) will lead to major discoveries. The limitation in the work with Drosophila, so far, lies in the little information we have about natural behavior and the rather small set of behavioral paradigms that are close to natural behavior. Martin Heisenberg has been extremely imaginative to discover multiple behavioral paradigms in the past, and so we hope he and his coworkers will come up with many more. In the bee, advances are limited by the fact that it has not been possible, so far, to transfer the natural behavior in navigation and communication to the laboratory, and functional studies are still bound to very simple forms of learning behavior. However, multielectrode extracellular recordings can now be performed over several days (Okada et al., 2007), and bees may perform richer behavior when stationary walking on a treadmill. As in the work with Drosophila, new behavioral paradigms and experimental conditions are urgently required that allow to combine physiological studies with close-to-natural test conditions. Solving these methodological hurdles will allow us to trace brain processes that are essential for selection of behaviors before motor programs are executed.

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Working memory


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